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16. ABSTRACT

Due to their increased efficiency and brightness, Light Emitting Diodes (LEDs) are now the first choice in outdoor lighting projects. Unlike High-Pressure Sodium lamps, which produce longer wavelengths and yellow-to-orange light, and Low-Pressure Sodium lamps, which produce near monochromatic yellow light, LEDs are usually full-spectrum white light. Due to the difference in color and intensity and special characteristics like flicker and non-Lambertian emission, LEDs have a different effect on wildlife than past lighting models. There is currently no significant organized body of information about LEDs' effects on wildlife. The study synthesized known or probable effects of LEDs on wildlife to provide agencies with a common set of information to assess environmental impacts and mitigation methods accurately. Specific search terms were used across different databases to gather the body of relevant research using specific screening criteria. Discrete studies were extracted from the final eligible sources. Almost all studied organisms were either chordates or arthropods. The most common chordate studies were on development followed by movement with a significant body of research conducted related to animal husbandry. Most arthropod studies were on movement followed by development with a significant number of studies related to mosquito. Light pollution research can be used to inform the assessment of the effects of LEDs except for specific LED characteristics of flicker and non-Lambertian emittance. Current research supports the mitigation of LED impacts by reducing intensity, controlling spill, reducing duration, and controlling spectrum to avoid peak sensitivities of most groups to shorter wavelengths. Significant variability in photoreceptor sensitivity and flexibility of spectral outputs of LEDs argue for the consideration of specific affected species for efforts to mitigate adverse impacts from LEDs.

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lighting, roadway lighting, light emitting diodes, LEDs, color, spectrum, geographic information systems, wildlife, circadian rhythms, light pollution, photopollution, endangered species, environmental impact analysis

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Effects of LED Lighting on Terrestrial Wildlife

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Principal Investigator

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Chapter 1. Systematic Map of Effects of Light from LEDs at Night on Terrestrial Wildlife

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Executive Summary

Due to their increased efficiency and brightness, Light Emitting Diodes (LEDs) are now the first choice in outdoor lighting projects. Unlike High-Pressure Sodium lamps, which produce longer wavelengths and yellow-to-orange light, and Low-Pressure Sodium lamps, which produce near monochromatic yellow light, LEDs are usually full-spectrum white light. Due to the difference in color and intensity and special characteristics like flicker and non-Lambertian emission, LEDs have a different effect on wildlife than past lighting models.

There is currently no significant organized body of information about LEDs' effects on wildlife. This literature review synthesizes known or probable effects of LEDs on wildlife to provide agencies with a common set of information to assess environmental impacts and mitigation methods accurately.

The review follows the ROSES protocol for development of a literature "map." Rather than a systematic synthesis, a description of research findings and their quality was produced with a summary of findings by topic area. Specific search terms were used across different databases to gather the body of relevant research which was then sorted using the CADIMA program and specific screening criteria. Discrete studies were extracted from the final eligible sources. A study is defined as a unique combination of a population, intervention, comparator, and outcome within a publication.

The greatest number of studies pertained to animal movement, followed by development, reproduction, stress and fear, sleep and daily rhythms, immune response, and finally vision.

Almost all studied organisms were either chordates or arthropods. The most common chordate studies were on development followed by movement with a significant body of research conducted related to animal husbandry, especially poultry. Most arthropod studies were on movement followed by development with a significant number of studies related to the mosquito.

Light pollution research in general can be used to inform the assessment of the effects of LEDs except for specific LED characteristics of flicker and non-Lambertian emittance. Current research supports the mitigation of LED impacts by reducing intensity, controlling spill, reducing duration, and controlling spectrum to avoid peak sensitivities of most groups to shorter wavelengths.

Significant variability in photoreceptor sensitivity and flexibility of spectral outputs of LEDs argue for the consideration of specific affected species for efforts to mitigate adverse impacts from LEDs.

Introduction

Light-emitting diodes (LEDs) are used to produce illumination in nearly all outdoor lighting applications currently being installed. Their configurability, energy efficiency, and associated reduced operating expense has fueled a wholesale transformation of the outdoor lighting market (Hecht 2012). Because LEDs developed for street and area lighting uses are typically full spectrum (white), and their energy efficiency has led to use of even more light, ecologists have expressed concern about their introduction and use, especially in environmentally sensitive areas. A research group specializing on bats and their insect prey questioned if LEDs were "conserving energy at the cost of biodiversity" (Stone et al. 2012). Another group asserted that "LED lighting increases the ecological impact of light pollution" (Pawson and Bader 2014). A horizon scan of threats to conservation in urban ecosystems listed LEDs and white light as an emerging threat (Stanley et al. 2015). Although research on LEDs, their attributes, and their effects on species has expanded following greater LED adoption across the landscape, there are not yet any systematic reviews that synthesize this work to guide land managers, regulators, and environmental planners. Substantial progress could arise from such a synthesis, as a means to target research to areas where evidence is scant, and to guide mitigation approaches where consistent research results in well-designed studies have been found.

Even as research on LEDs is increasing, we do not yet have a broad synthesis of their potential and actual impacts on terrestrial wildlife. Many reviews are, however, now under way or recently published to address the effects of light at night and aspects of the LED conversion. For example, recent reviews have addressed lighting effects on mollusks (Hussein et al. 2020), insects (Owens and Lewis 2018, Desouhant et al. 2019), nocturnal pollination (Macgregor et al. 2015), seabirds (Rodr?guez et al. 2017c), bats (Stone et al. 2015), human physiology (Vetter et al. 2021), and all biological processes (Sanders et al. 2021). Although these efforts encompass the effects of LEDs and effects on terrestrial wildlife, with the exception of the recent meta-analysis by Sanders et al. (2021) and reviews currently underway (Adams et al. 2019, McLay et al. 2019), these reviews have not been quantitative in describing the characteristics of the research. Although reviews address issues that are assumed to distinguish LEDs from other lighting sources, e.g., spectral output, few resources yet compile research on LEDs specifically that might also detect other key differences, such as the potential impacts of flicker (Inger et al. 2014). A synthesis across field and laboratory studies is also necessary, as considerable insight on vertebrate physiology arises from studies of livestock and poultry production.

A synthesis of the known and probable effects of LEDs on terrestrial wildlife is therefore needed. LEDs are associated with greater environmental impacts in environmental review because they tend to be broad-spectrum sources. Because the lighting standards followed by engineers for roadway lighting have been achieved using orange-hued high pressure sodium lights for nearly 60 years, a switch to a full spectrum light with the same photometric performance standards will appear to be far brighter to humans and many wildlife species. Combined with this phenomenon, there is a tendency to use more of any product when it is less expensive, which is known as the "rebound effect" (Greening et al. 2000, Kyba et al. 2014). Given these trends, and the growth of transportation systems and the desire for sites in high wildlife value areas to be illuminated with LEDs for traffic safety, a thorough understanding of the state of research on LEDs is indeed important.

A review related to LEDs and wildlife is important to the practice of environmental assessment and management in several ways. LEDs are currently treated as a monolithic category in many discussions about impacts. However, although the LEDs first introduced for outdoor lighting were quite similar, this similarity has decreased over the past decade. Early LEDs that were cost-effective consisted of a blue diode that was coated with a phosphor that reradiated light across the longer wavelengths. These products had a high correlated color temperature (CCT) and "cold" appearance. Subsequently, technologies have advanced so that full spectrum LEDs can be much lower color temperatures, through combinations of phosphors and filters, and appear yellow and "warm" white through the cold white originally associated with the technology. Although spectrum, and now the flexibility of spectrum, has been a distinguishing characteristic of LEDs, it is not known whether their other attributes, especially flicker, have different effects on wildlife than do legacy lighting sources.

This topic is tied to regulatory policy and practice through the environmental review process for new construction and repairs, and compliance with protected species legislation. New lighting of any kind, and conversion of legacy technology to LEDs, both have the potential to impact sensitive natural resources and individual species protected by law. For transportation agencies, the regulatory landscape includes compliance with state and federal regulations, and consultation with the cognizant wildlife agencies that hold natural resources in trust. A literature review can provide a common set of facts and understanding about the state of research for agencies in this position to ensure accurate assessment of environmental impacts and formulation of feasible and effective mitigation measures.

To develop this review, we consulted practitioners working at California Department of Transportation, California Department of Fish and Wildlife, and U.S. Fish and Wildlife Service who are tasked with evaluating impacts from LED conversions and installations and mitigating those impacts. We took conversations about impact assessment into account in developing the protocol so that all relevant information would be located.

The protocol defines the production of a systematic map of the literature and the critical assessment of the quality of each study. It provides a quantified description of the current state of knowledge about the effects of LEDs on wildlife at night, facilitating a qualitative description of the major findings.

Objective of the Review

The objective of this evidence map and synthesis is to find, organize, and characterize all relevant studies on the effects of light from LEDs on terrestrial wildlife at night. We classify studies by topic (e.g., behavior, growth, movement) and identify areas of strength and weakness in the literature that can guide further research and reviews. The results will be used to develop taxonomically specific tools for impact assessment and mitigation, and provide a shared knowledge base for practitioners tasked with collaboratively evaluating and mitigating impacts of LEDs on terrestrial wildlife.

Question

Main Question

What is the evidence of the effects of light from LEDs at night on terrestrial wildlife?

Secondary questions

Additional questions to be addressed by the review that contribute to building up the evidence surrounding the primary question:

Does light from LED sources differ from other non-solid state lighting sources in its effects on terrestrial wildlife?

What information is available to address questions pertaining to street and area lighting?

How extensive and what quality is the evidence regarding different responses of wildlife to LEDs, such as orientation, space use, growth rate, reproduction, and circadian rhythms?

Components of the Main Question

The following constituent components of the question will be used to screen studies for inclusion in this review. Only those studies that include the defined population, impact, comparator, and outcome will be included.

Population

Terrestrial wildlife species: arthropods, reptiles, amphibians, birds, mammals

Impact

Exposure to nighttime light produced by light emitting diodes (LEDs)

Comparator

Same study site before or after intervention; similar study site lit or unlit with different light source (defined as different spectral power distribution)

Outcome

Changes in behavior, occupancy, density, or distribution

Methods

We followed the advice of the ROSES protocol for systematic evidence synthesis (Haddaway et al. 2018) to construct a systematic map of the evidence and to assess study quality. Because of the wide array of outcomes, no attempt at systematic synthesis is proposed, but rather a qualitative description of research findings and their quality was produced, along with a summary of findings by topic area.

We used the free tool CADIMA (Kohl et al. 2018) to register the review and manage the data associated with it.

Searching for Articles

Search Strategy

We conducted extensive scoping efforts to arrive upon a search strategy that yielded relevant results. We consulted currently registered reviews (Adams et al. 2019, McLay et al. 2019) to develop search terms. The search was not limited by geography or climate zone but was limited by date to work published in 2000 or later. LEDs were not commercially viable lighting sources with widespread use before 2000 and so no relevant research was expected to be excluded in this manner. Reviews were not included, nor were theoretical or conceptual studies.

Search Terms

Search terms were used in combinations representing a population, intervention, and outcome. We did not use a comparator term but filtered for the comparator later in the process. Broadly, the search terms were as follows.

Population	Bird* OR Birds OR Aves OR avian*, Mammal* OR mammals OR mammalia, arthropod*, “Insect” OR “Insecta” OR “Insects”, reptil*, worm* OR “terrestrial annelids”, Invertebrate*, Gastropod*, amphibian*, “and slug” OR “land slugs” OR “slug” OR “slugs” OR “terrestrial slug” OR “terrestrial slugs”
Intervention	"LED Light" OR "LED Lights" OR "LED Lighting" OR "light emitting diodes"
Outcome	behav* OR occup* OR densit* OR distribut* OR migrat* OR feed* OR communicat* OR eclos* OR emerg* OR commut* OR diapaus* OR dispers* OR consum* OR cue* OR nest* OR ecolog* OR mov* OR stress* OR signal* OR prey* OR bask* OR learn* OR phototax* OR hatch* OR "sea-finding*" OR fly* OR coloniz* OR walk* OR run* OR fight* OR orientat* OR aggreg* OR attract* OR roost* OR chorus* OR vocali* OR kill*

These search terms reflect the use of a wildcard appropriate to each database to include alternate forms of each word. Each of the three search terms (population, intervention, outcome) were combined within the search using the Boolean AND operator. Terms were linked within categories with the OR operator. We added the NOT operator to exclude topics pertaining to other aspects of light pollution research not the focus of the review (NOT (traffic* OR vehicle* OR engineer* OR astronom* OR tumor* OR tumour* OR cancer*)). Alternate spellings and hyphenations were included in the search strings.

Serial Searches

Depending on the database, the complete search required a different number of steps. For example, within ALAN db, a primary search on the *intervention* and *outcome* would then be filtered by excluding matches with the exclusion terms and filtering again by matches with the *population* terms.

Language

All searches were conducted in English and results were limited to sources published in English.

Publication Databases

We searched the following online databases:

1. Web of Knowledge
2. Wiley Online
3. CAB Abstracts
4. COPAC (British Union Catalogue)
5. Index to Theses
6. Agricola
7. JSTOR

Specialist Sources

We queried a specialist database maintained by the International Dark-Sky Association:

1. ALAN (Artificial Light at Night) db

Article Screening and Study Eligibility Criteria

Results of all searches were uploaded to the CADIMA website and duplicates excluded. Their management through successive screening steps was then managed within the CADIMA tool as follows.

Screening Process

Articles were first assessed on the basis of the title and abstract and judged to either fall within or outside the scope of the review using the eligibility criteria. To check consistency among members of the review team, a subset of 10% of articles were each reviewed by two team members. Cohen's kappa coefficient was calculated to assess the degree of inconsistency. When inconsistencies arose, each case of disagreement was discussed, and the inclusion criteria were clarified within the project team.

Those studies marked for inclusion based on title and abstract were passed through to an assessment of the full text. The same eligibility criteria were applied to the full text, with 10% of articles assessed by two members of the review team.

Eligibility Criteria

Population Does the study pertain to terrestrial wildlife, which include insects and other arthropods, reptiles, amphibians, birds, mammals, land slugs & snails, and worms (terrestrial annelids)?

Intervention Does the study evaluate exposure to light from LEDs in darkness (in the field or in the laboratory)?

Comparator Does the study compare exposure to light from LEDs to either a control, other lighting type, or other LED?

Outcome Does the study measure changes in physiology, survival, behavior, occupancy, density, or distribution in response to different light sources?

Studies were not excluded based on experimental design.

Study Extraction

Once all research items that met eligibility criteria were identified, each document was reviewed again to extract individual studies. Studies were defined as a unique combination of a population, intervention, comparator, and outcome within a publication. Many publications contain results of several different outcomes with the same population, intervention, and comparator. We separated each of these out so that summary information about the breadth of knowledge would reflect the actual range of research. Each study was assigned a unique identification number within CADIMA.

Study Validity Assessment

The quality of each study was assessed using pre-defined criteria pertaining to study type, design, length, controls, and replicates. Within each category, points were assigned to develop an overall measurement of study quality, following Pullin and Knight (2003). For type, studies were described as sampling (single location, single time; 0), monitoring (single location, time series; 1), correlative (comparing conditions in different places or times; 2), and manipulative (experimenter changes conditions over space or time; 3). Length of study was coded as less than 1 year (0) or more than 1 year (1). Controls were described as none (0), comparison between treatments but no control (1), comparison with control (2), or before/after control/impact design, measuring treatment and control systems before and after treatment (3). Treatments were described as random (1) or non-random (0). Replicates were characterized as none (0), spatial *or* temporal (1), or spatial *and* temporal (2).

Appraisal of studies was done by one reviewer, with weekly discussion among all reviewers of questions during the review period (approximately 3 months).

Data Coding Strategy

To summarize the topics and major findings of the studies, a database was constructed to record the following information: article identification number, study identification number, publication year, publication title, study name, type of study (laboratory or field), location continent, location country, location state, location city, phylum of study species, class of study species, order of study species, treatment description, summary of outcome, phenomenon investigated (movement, circadian rhythm, phenology, predator/prey, development, gene expression, pollination), and scale of phenomenon investigated (organismal physiology, individual, population, community).

Results

We identified 3,066 records through database searching, which were narrowed down to 174 articles through screening of abstracts and full text (Figure 1). In those articles, 342 discrete studies were identified.

Laboratory investigations were conducted predominantly in Asia, followed by North America and Europe, while field investigations were conducted most in Europe, followed by North America, and Oceania (Figure 2). Most studies originating in Asia pertained to agricultural and physiological implications of light exposure at night rather than ecological implications.

The number of studies overall increased substantially over time, which was especially evident in field studies of movement in response to LEDs at night, while laboratory studies on development (mostly poultry) peaked around 2015 (Figure 3). Topic areas of development and local movement contains most of the studies, with topics such as gene expression, predator/prey relations, reproduction, sleep, and stress comprising the remainder.

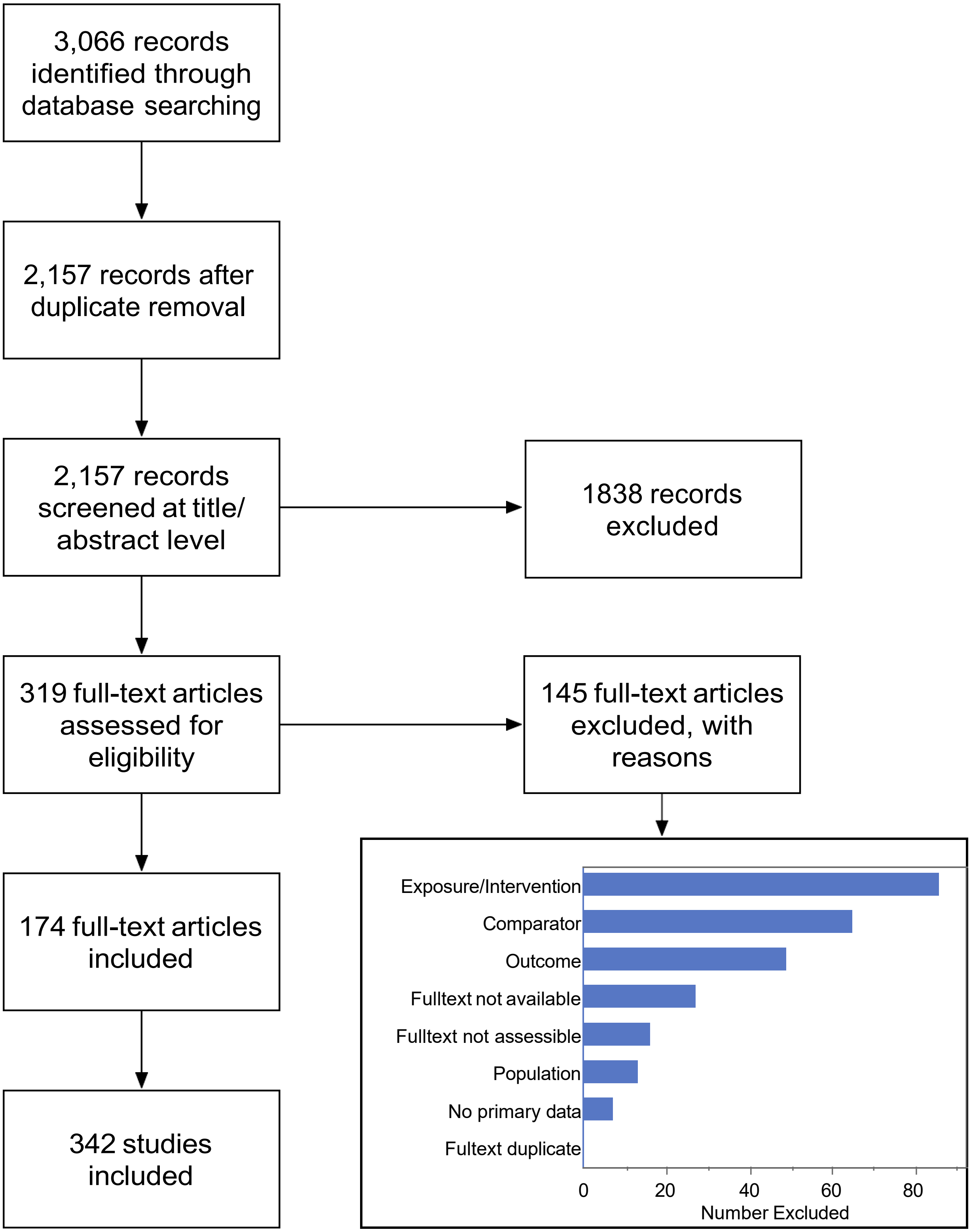

Figure 1. Flowchart of study evaluation and extraction.

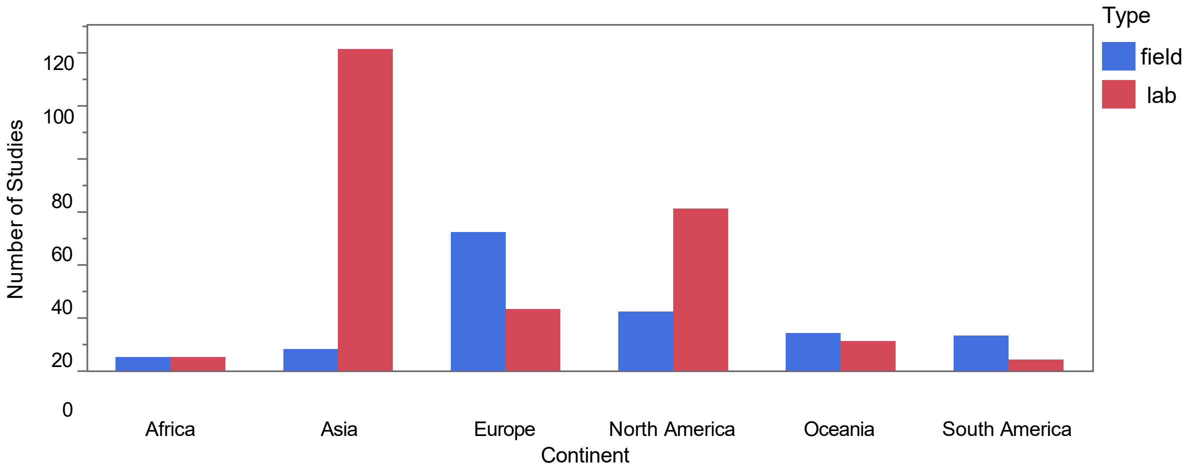

Figure 2. Number of studies by geographic location for research conducted in the field and laboratory settings on the effects of LEDs on terrestrial wildlife.

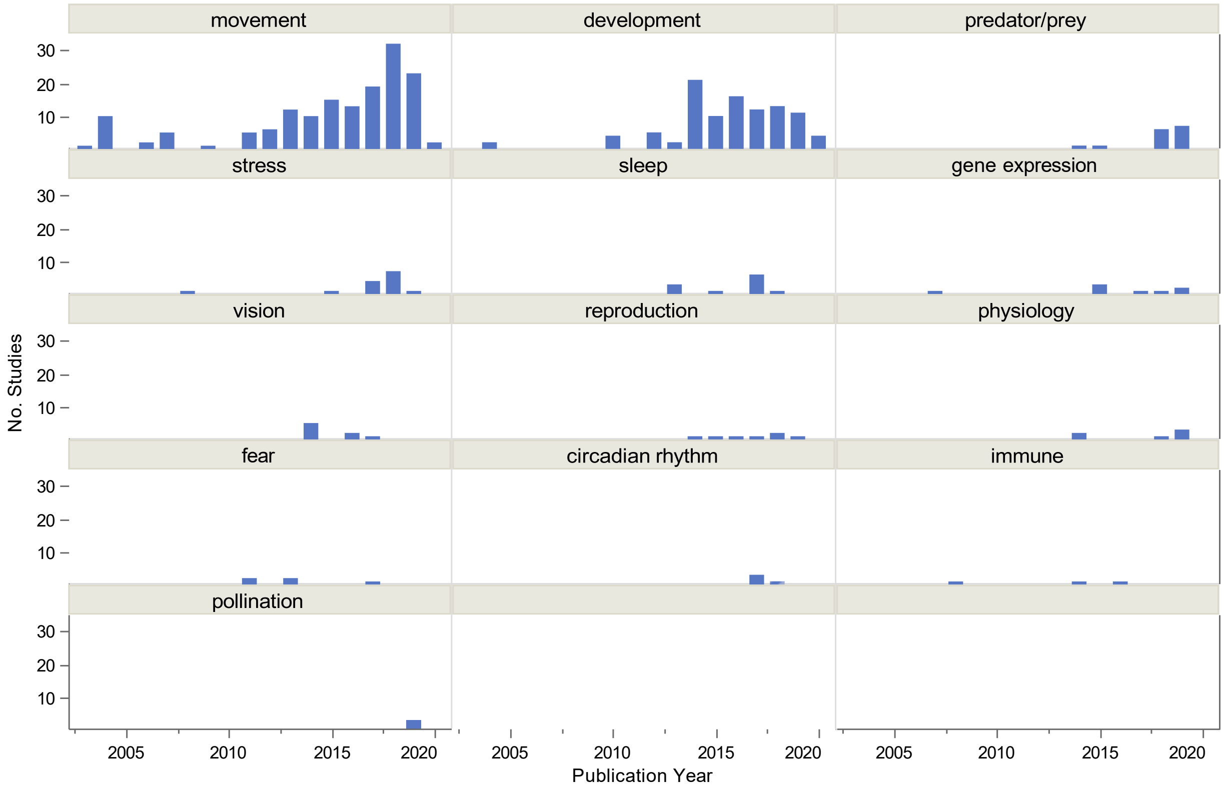

Figure 3. Number of research studies over time on LEDs and terrestrial wildlife, by topic area, 2000–2020.

The bulk of research on LEDs and wildlife focuses on Arthropods and Chordates. A few studies are on other invertebrate groups (Annelida, Mollusca, Nematoda) (Figure 4). Field studies on Arthropods and LEDs date back to our earliest records in 2002 and have increased over time, especially since 2012. Laboratory research on Arthropods has also increased with time. Field research on Chordates and LEDs started later, being published around 2014, while laboratory research (mostly on poultry) peaked in around 2015 and may have leveled off or is declining.

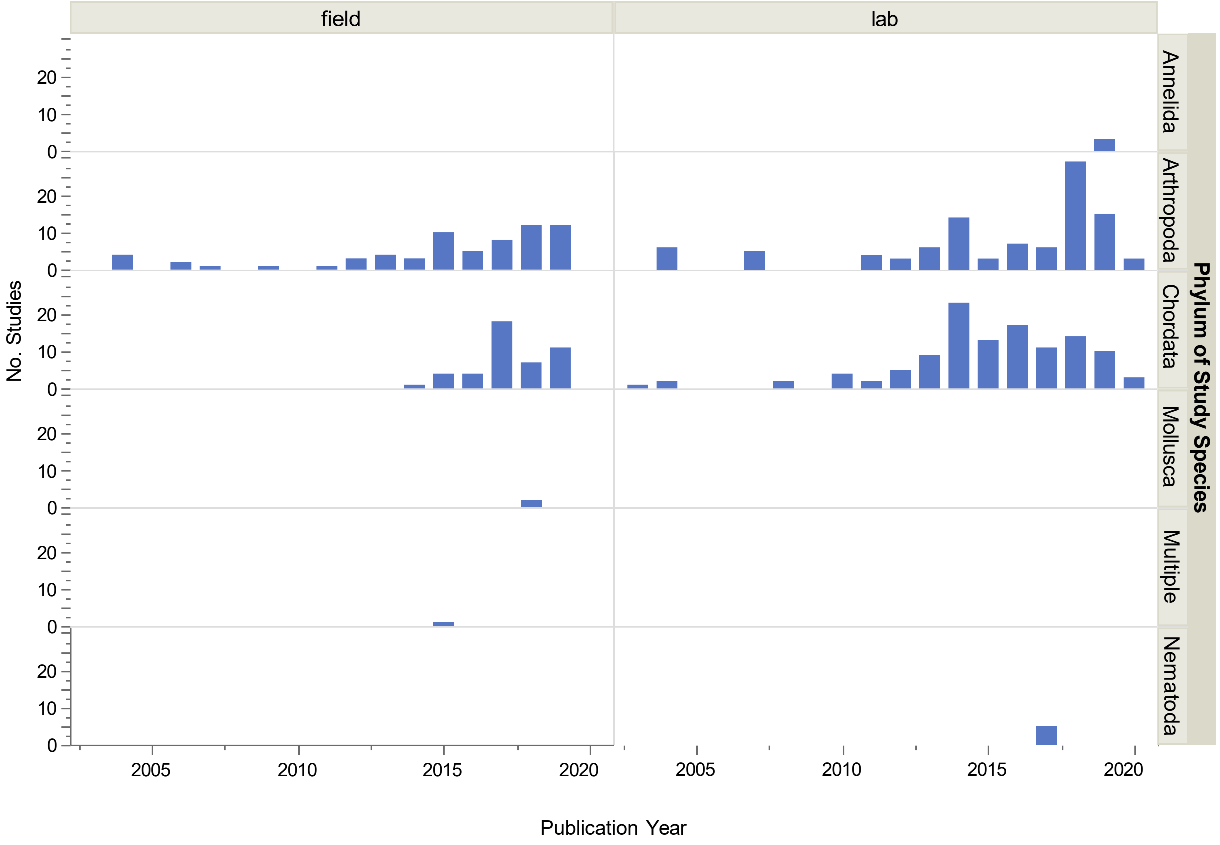

Figure 4. Number of research studies over time on LEDs and terrestrial species, by phylum and field or laboratory setting.

Taxonomic focus within the major groups showed much higher attention to conventional laboratory species or test organisms (Figure 5). Within the Arthropods, the most research has been done on Diptera, followed by Lepidoptera, Hemiptera, multi-Order studies, and Coleoptera, reflecting a combination of laboratory and field studies. Studies on Arachnida included both spiders and scorpions. Within the Chordates, the most research has been on Aves, followed by Mammalia and Amphibia. The Aves research is, however, inflated by extensive studies of LED effects on poultry production (Galliformes, Anseriformes) exclusively in laboratory conditions, with studies of the Passeriformes predominating the field studies. Within Mammalia, the most studies have been completed on Chiroptera, followed by Rodentia (mostly in the laboratory), and Primates. Of these, only bats have been studied in the field. Only a handful of studies have been done on Amphibia and Reptilia, all in the lab. Other research with lights at night (but not using LEDs) exists as well, but the field studies specifically using LEDs are focused most on insects (largely attraction), songbirds (a considerable amount of ecophysiology research), and bats (foraging and movement across the landscape) (Figure 6).

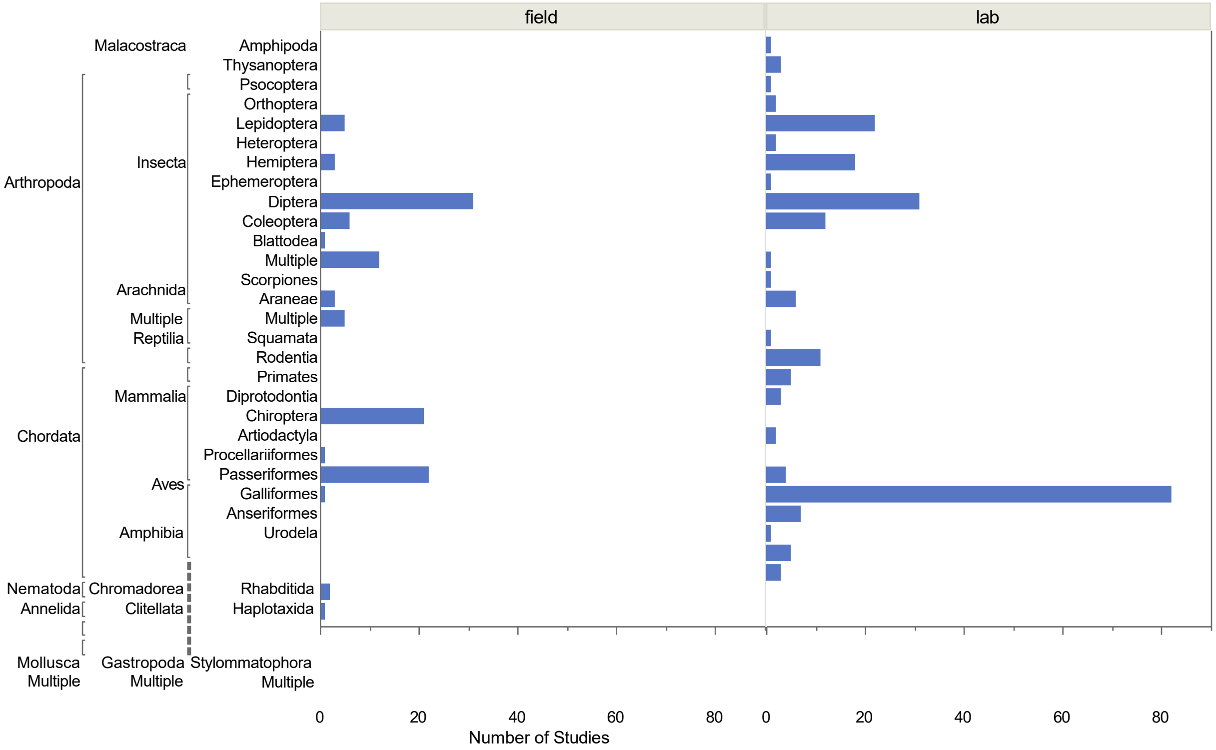

Figure 5. Studies of the effects of LEDs on wildlife at night by order and field or lab setting, 2000–2020.

Quality of studies varies based on our scoring scheme but is on average high (median 7 of 10). Field studies tended toward slightly higher scores (mean 7.5) compared with laboratory studies (6.5) because of studies being of longer duration in the field, including multiyear studies necessary to detect ecological responses (van Grunsven et al. 2018). Studies on pollination, predator/prey relationships, and reproduction had the highest quality scores among the identified topic areas. The quality scores for arthropods were higher (mean 7.25) compared with chordates (mean 6.5), presumably because of the greater ease of running experimental replicates and having higher sample sizes with arthropods because of their abundance.

The topic areas located in the literature map were further reviewed and the findings summarized. They are reviewed here in order of the quantity of research in each area.

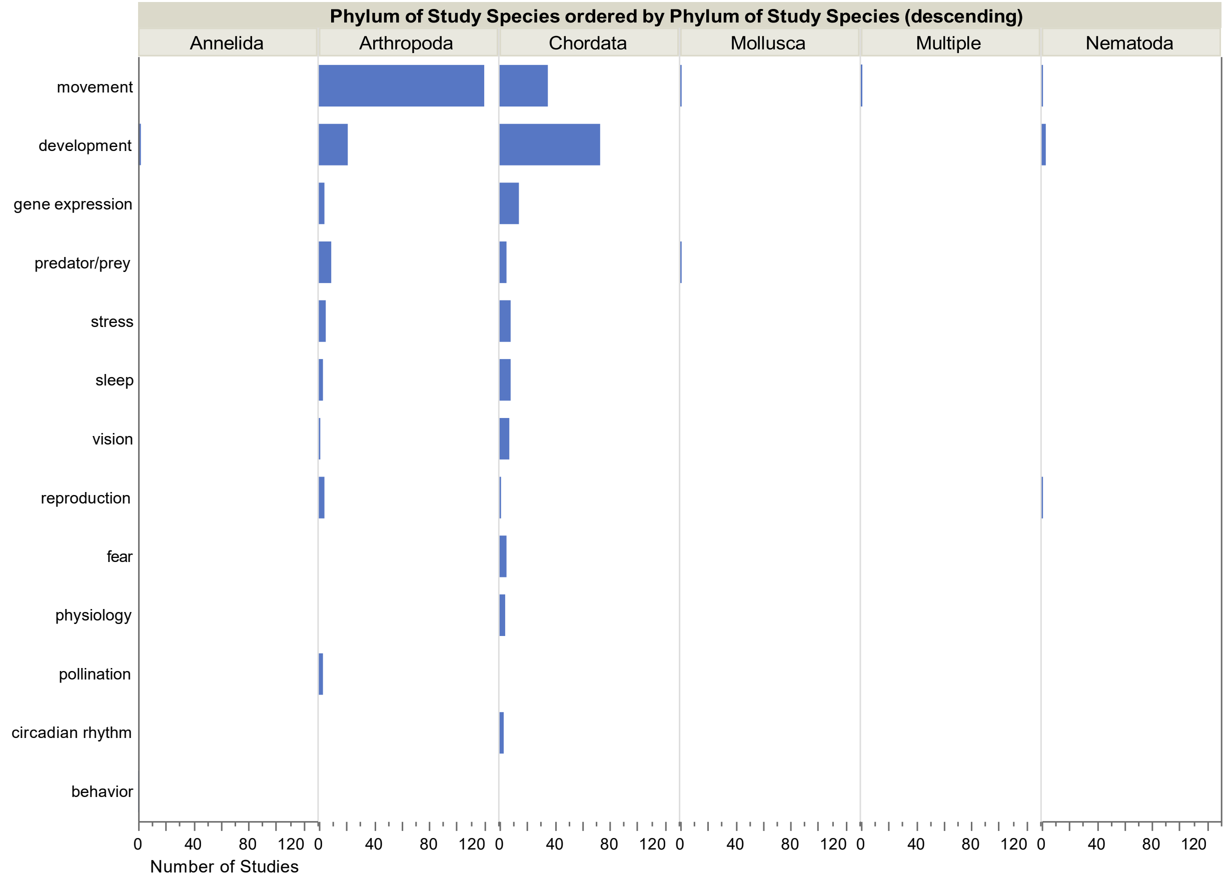

Figure 6. Studies of the effects of LEDs on wildlife at night by topic area and phylum.

Movement

One of the earliest documented influences of anthropogenic light at night was its ability to attract or repel wildlife (positive and negative phototaxis) (Longcore and Rich 2004). Attraction and repulsion underly the most conspicuous of adverse impacts of artificial light at night, including mortality of birds at buildings and other tall structures such as communication towers and light houses (Longcore et al. 2012, Loss et al. 2012), attraction of hatchling sea turtles and repulsion of nesting females (Witherington and Martin 1996), and the mortality of insects attracted to lights (Eisenbeis 2006, Frank 2006).

Movement of organisms in response is important, even if it does not result in mortality. Artificial light can affect nutrient flux and composition of communities. For example, a study that added full spectrum white LEDs over a stream, causing 10–12 lux at 1 m at the stream surface, resulted in an increased average body size of terrestrial insects entering the stream by 309% while the body size of emergent insects decreased by 76% (Meyer et al. 2013). Very bright (250–310 lux) white LEDs (4000–4500 K) next to rivers changed the insect community composition trapped (Russo et al. 2019b).

Studies of influences of LEDs at night on movement are reviewed below by order of quantity of research, starting with insects.

Insects

By far the most research on the effects of LEDs on the movement of wildlife has been conducted on insects, across many taxa. This arises from the conspicuous nature of insect attraction and the subsequent fouling of luminaires and the importance of insect attraction (or repulsion) to the assessment and management of insects as crop pests and disease vectors.

Discussion of insect attraction is aided by two overlapping considerations: intensity and spectrum of light. There are general patterns that emerge across all insect groups, but only as the sum of different responses in different taxonomic groups. As an overarching feature, the attraction of insects at night is correlated with light intensity within the range of wavelengths perceived by insects (extending into the ultraviolet), although this correlation may level off at higher intensities (Bishop et al. 2004, Costa-Neta et al. 2018). Many studies confirm the intensity effect over orders of magnitude of light (Mangan and Chapa 2013, Snyder et al. 2016).

The perception of light intensity depends on the ability of the organism to perceive light in the wavelengths emitted and so it is almost impossible to separate the question of intensity from spectrum. An effort has been made to describe the average sensitivity across the spectrum for all insects (Donners et al. 2018). This sensitivity pattern includes a peak at shorter wavelengths as the result of both blue and ultraviolet photoreceptors, followed by a lower but broader peak at the green but extending to the beginning of red. Because it was developed to reflect the "average" insect, it does not account for species or groups with sensitivity outside the normal, such as for fireflies and other bioluminescent insects, which may have peak sensitivity elsewhere. This very point was shown in a study using conventional 3000K LEDs and filtered LEDs (blue removed) in the Peruvian Amazon –– the generic curve from Donners et al. (2018) predicted attraction for most insect groups, but not for bioluminescent beetles (Deichmann et al. 2021). Experimental work with prosthetic mushrooms and a green LED light source suggests that bioluminescent fungi emitting light around 530 nm are targeting the green sensitivity peak that is present in flies, beetles, true bugs, sawflies, ants, wasps, and bees (Oliveira et al. 2015).

Studies looking at attraction of insects to LEDs are consistent, with some exceptions, with the overall assessment that shorter wavelengths (ultraviolet and blue) are more attractive. For example, white light (all wavelengths but not UV) attracted more insects than yellow or orange at airports in Africa (Hauptfleisch and Dalton 2015). However, order diversity did not follow the same pattern, underlining the variation between groups. Similarly, arthropods across many groups were less attracted to ~2700 K lamps than to ~3500 K lamps and custom LEDs modified to reduce light in known attraction spectrum of insects successfully reduced attraction at same intensity (Longcore et al. 2015). Fluorescent lamps attract three times the number of insects as similar color temperature (2700K) LEDs (Poiani et al. 2015). Another comparison with fluorescent lamps (which have substantial emissions in the shorter wavelengths) showed lower attraction of nontarget insects and natural predators for 350 nm and 420 nm LEDs, while being most attractive to two pest species with peak sensitivities at 350 and 420 nm (Bian et al. 2018), again demonstrating diversity among taxa, but predictability within groups. Eisenbeis and Eick (2011) found that LEDs attracted fewer insects along a river than metal halide and high-pressure sodium, and that higher CCT LEDs attracted more than lower CCT LEDs.

Limited research has been done on the effects of flicker on insect attraction (Inger et al. 2014). One study, however, used an experimental setup and demonstrated that insect attraction was reduced for most groups by 120 or 240 Hz flicker of LEDs (Barroso et al. 2017).

A few studies of overall insect attraction in response to LEDs show unexpected results. Pawson and Bader (2014) found no significant difference in attraction of insects to a range of LEDs with CCT 2700–6500, in a study design where all lights were visible at once. Similarly, Wakefield et al. (2016) did not find any difference in insect attraction between 2700 K and 5000 K LEDs, although they did find that the two LEDs attracted fewer insects than fluorescent and tungsten lights (as expected). One explanation for findings such as these is the possibility that they are being undertaken in systems that are already depauperate. For example, at a suburban site with two sites converted from mercury vapor to LED, three sites with mercury vapor remaining, three new LED sites and control, insect biomass trapped was unaffected by the change in light type (Haddock et al. 2019). The results from the Amazon in a light-na?ve environment suggest that the physiologically-based predictions of attraction are accurate when an insect fauna has not been depleted (Deichmann et al. 2021). Differences among insect groups, however, should be incorporated in studies as such knowledge increases (Kamei et al. 2021).

Diptera

Mosquito attraction is not simple; different species have different preferences (Burkett et al. 1998), but patterns are generally consistent with shorter wavelengths being more attractive (Browne and Bennett 1981). However, some trials showed that full spectrum white (incandescent) attracted more mosquitos overall than (in order) blue, green, orange, yellow, red, no light, and infrared (Burkett et al. 1998).

Studies of Diptera include many that are focused on pest species, such as mosquitos, sand flies, midges, and gnats. Diptera also feature prominently in studies of whole-community attraction. The patterns of attraction include many comparisons between narrow-spectrum (colored) LEDs and full spectrum sources. Leaving aside the details of location and species composition, they can be summarized as follows.

Full-spectrum (white) is reported as being most attractive when compared with colors for studies of number of mosquitos (Burkett et al. 1998, Tchouassi et al. 2012, Ponlawat et al. 2017), sand flies (Rodr?guez-Rojas et al. 2016), and Diptera overall compared with yellow LEDs

(Deichmann et al. 2021). In comparisons, LED white is more attractive than incandescent white (Rodr?guez-Rojas and Rebollar-Téllez 2017). Ultraviolet alone is reported as being most attractive for the number of species of mosquitos (Gonz?lez et al. 2016), number of mosquitos (Obenauer et al. 2013, Peck et al. 2018, Mwanga et al. 2019), number of midges (Bishop et al. 2006, Snyder et al. 2016), number of sand flies (Gaglio et al. 2018), and number of fungus gnats (Stukenberg et al. 2018). One study indicates that UV is not attractive to mosquitoes (Degener et al. 2019) or is less attractive than white (Ponlawat et al. 2017). Blue has been measured as most attractive for number of mosquitos (Rodr?guez-Rojas and Rebollar-Téllez 2017, Costa-Neta et al. 2018, Silva et al. 2019b), midges (Sloyer et al. 2019), and sand flies in early evening (Silva et al. 2016). Green has been found most attractive for number of mosquitoes (Silva et al. 2015, Gonz?lez et al. 2016, Costa-Neta et al. 2017), sand flies (Silva et al. 2016, Silva et al. 2019a), fruit flies (Liu et al. 2018a), all flies pooled (Schmid et al. 2017), and midges (Bishop et al. 2004). Red has been found most attractive for one species of sand fly (Mann et al. 2009) and sand flies (Hoel et al. 2007), but least attractive to midges (Bishop et al. 2004). One study found little distinction between different colors for attraction of sand flies (Fern?ndez et al. 2015).

This array of peak sensitivities is consistent with the range of photoreceptors in the biting flies that are typically the focus of these studies. They are on average less attracted to UV than are moths, and so green light is suggested as an alternative to UV for Diptera-specific trapping (Wilson et al. 2021). The LED studies confirm that overall yellow and red light are least likely to attract Diptera when compared with shorter wavelengths.

Lepidoptera

Investigation of impacts on the Lepidoptera is focused mainly on moths, as they contain most of the nocturnal species. Pre-LED research has established the attractiveness of ultraviolet and blue wavelengths to moths (Cleve 1964b), which has been extensively verified (Cowan and Gries 2009, van Langevelde et al. 2011, Barghini and de Medeiros 2012, Somers-Yeates et al. 2013, Bates et al. 2014). In whole community studies, the blue through ultraviolet content of lights (including LEDs) drives the number of individuals attracted. There are variations in attraction between families (Somers-Yeates et al. 2013) and only some moth species are not attracted by short-wavelength light (Mikkola 1972). In studies with LEDs, the results for moths follow this general pattern, including for coastal sage scrub in California (Longcore et al. 2015), riparian systems in Europe (Eisenbeis and Eick 2011), and tropical forest in South America (Deichmann et al. 2021) and Asia (Bishop et al. 2006).

Studies of individual species yield more detailed insights. The diamondback moth *Plutella xylostella* was attracted most to green in a choice experiment (98.3% of the time), followed by UV (90.0%) (Cho and Lee 2012). A pyralid moth species was attracted to all lights (UV, green, and white) compared with darkness, but was most attracted to UV (Sambaraju 2007). In a comparison with white light, green light was most attractive to a noctuid moth species (Kim et al. 2018a).

Hemiptera

Most information about attraction of the true bugs arises from studies of disease vectors and agricultural pests. In general insect surveys with LEDs, higher CCT LEDs attract more species and greater numbers of bugs (Deichmann et al. 2021).

The vector of Chagas, *Triatoma dimidiata* (Kissing bug), exhibits positive phototaxis and both males and females were most attracted to blue wavelengths (430 nm) and less to longer wavelengths (Pacheco-Tucuch et al. 2012). Separately, white LED was found to be more attractive than yellow (Pacheco-Tucuch et al. 2012). In choice tests between light colors, the kissing bug *Triatoma rubida* exhibited high attraction to 470 nm (blue)and 390 nm (UV), but all lights, including red and yellow were more attractive than dark control (Indacochea et al. 2017).

The other true bugs subject to investigation are whiteflies, because of their relevance to horticulture. Several studies show attraction of various whitefly genera to green LEDs over other colors (Chu et al. 2004, Jahan et al. 2014, Castresana and Puhl 2015, Zhang et al. 2020). Some studies show even higher attraction with UV light plus green (Stukenberg et al. 2015) and others show no additional attractiveness (Zhang et al. 2020). Two other true bug species (crop pests) were more attracted to green and blue light than to yellow and red LEDs (Yang et al. 2014), while one predatory bug species was most attracted to violet (males) and ultraviolet and violet (females), but no attraction to orange or red (Uehara et al. 2019).

Aphids had lower abundance under amber lights compared with other colors in a mesocosm (Bennie et al. 2018).

Coleoptera

Studies of responses of beetles to light involve pest species and general insect surveys, with bioluminescent species as a special case.

As also seen in Lepidoptera, some beetle species are positively phototactic and do not decrease activity under higher illumination, others decrease activity and mobility and are not attracted (Eccard et al. 2018). Ladybird beetles, for example move more under increased nighttime light intensity (Tan et al. 2014), and scarab beetles are captured more at pheromone traps that have illumination with an LED than without (Zaragoza-Ortega et al. 2017). For non-bioluminescent beetles, higher CCT LEDs (3000 K) are more attractive than yellow and amber filtered LEDs (Deichmann et al. 2021).

Different responses of beetles to light have been investigated to deter crop pests. Chinese rose beetle (*Adoretus sinicus*) feeds at night and 2 lux of an unreported color LED was sufficient to keep them from feeding while not impacting the associated crop's detection of daylength

(McQuate and Jameson 2011). Other species prefer light, however, and have spectral preferences. At equal photon intensity, Colorado potato beetles (Coleoptera) preferred white, UV, blue, green, yellow, and then orange over darkness in choice tests (Ot?lora-Luna and Dickens 2011). They preferred yellow and green over other colors and had sex differences in attraction, such as females preferring UV over blue and red, while males showed no preference (Ot?lora-Luna and Dickens 2011). In comparison, green light enhanced attractiveness of chemical lure 4.5 times for the sweet potato weevil (McQuate 2014), while ptinid beetles are attracted most to UV light (Miyatake et al. 2016, Hironaka et al. 2017).

Bioluminescent beetles have visual sensitivity in the area of the spectrum used for visual communication, which ranges in the green to yellow (Lloyd 2006). Behaviors of bioluminescent beetles are influenced by very small increases in illumination, as low as 0.014 lux, with intensity significantly increasing effects(Firebaugh and Haynes 2018, Van den Broeck et al. 2021). Longer wavelengths do nothing to mitigate the effects on them, and in fact yellow and amber lights may attract some species, as seen in the Peruvian Amazon study (Deichmann et al. 2021).

Psocoptera

Bark lice (Psocoptera) are an ancient lineage that scavenges on fungi, algae, lichens, and organic debris. The little information available shows variation in movement relative to light, with some species showing negative phototaxis (Spieksma and Smits 1974) and some positive (Diaz-Montano et al. 2016). In a study with LEDs, one species was not phototactic at all, and in another species the females were positively phototactic to UV and green LEDs (Diaz-Montano et al. 2018).

Hymenoptera

Few studies address movement of Hymenoptera relative to LEDs specifically, but attraction is documented using other light sources, with a preference for blue and green wavelengths in wasp species (Kim et al. 2019b). A field study using LEDs showed a 3000 K white light attracting far more individuals and species than yellow, and the yellow far more than amber (Deichmann et al. 2021).

Thysanoptera

A few studies have looked at thrips (Thysanoptera) relative to LEDs. *Thrips palmi* was most attracted to 470 nm (blue), followed by 355 (UV) and 405 (violet), then longer wavelengths (Murata et al. 2018). *Frankliniella occidentalis* is attracted to 590 nm (yellow) (Yang et al. 2015) and *Megalurothrips usitatus* to 461 nm (violet) (Tang et al. 2015). Other studies using different light sources show broad spectral range for attraction (Kim et al. 2019b).

Ephemeroptera

Mayflies have an aquatic larval phase but fly as adults. They are highly phototactic and responsive to polarized light as well (Kriska et al. 1998, M?ln?s et al. 2011, Szaz et al. 2015).

More species and greater numbers were attracted by 3000 K vs lower CCT LEDs in tropical forest (Deichmann et al. 2021). Their intense phototaxis can be exploited to keep females confined over a water body so that they will not be attracted away and have their eggs wasted. Bright high CCT LEDs hung down below a bridge deck during a mayfly flight was sufficient to overpower the attractiveness of other lights and keep adult mayflies within the river habitat (Egri et al. 2017). Such an approach, however, should only be considered for the very short flight period of relevant species in very particular situations where the disruption from additional illumination could be offset by protection of the mayfly flight.

Blattodea

Cockroaches can exhibit both positive and negative phototaxis. They do not perceive red light (Appel and Rust 1986, Snoddy 2012), and so exhibit less attraction to sources with more longer wavelengths (e.g., lower CCT), but will move toward them relative to lights perceived as brighter if negatively phototactic (Burhan and Gencer 2020). In tropical rainforest, more cockroach species were captured at light traps with 3000 K LED compared with lower CCTs, but very few individuals were captured overall (Deichmann et al. 2021).

Other Invertebrates

Other invertebrate groups show a mixed set of responses to light from LEDs. African nightcrawlers (*Eudrilus eugeniae*) convert organic matter to vermicompost better in the dark, compared with when illuminated by white, blue, green, or red LEDs (Mishra et al. 2019). Surface and subterranean amphipods studied under white LEDs and red, blue, yellow and green light from filters at 27–66 lux were photonegative with little difference by intensity at these levels (Kennedy 2019). The number of slugs increased at a lighted field (from 2000 K HPS, then 4000K LED) over the course of several years (van Grunsven et al. 2018).

Research on spiders reveals behavioral changes that respond to the behaviors of insect prey. For example, spiders constructed webs under 20 lux of cool white LED light instead of in darker areas, presumably to help them catch more insects attracted to the lights (Willmott et al. 2019). In another study, more spiders were found under all lights (cool white LED at 1.2 and 0.3 lux, part-night cool white, and amber LED at 1.3 lux) than under controls in both day and night measurement (Davies et al. 2017). In other instances, however, web-weaving tetragnathid spiders decreased in abundance when going from 0.1–0.5 lux conditions to 0.6–2.0 lux conditions created by strings of LED lights (Meyer et al. 2013). Family richness declined by 16% as well (Meyer et al. 2013).

Scorpions react in their movement behaviors in response to light. Activity is greatest when UV irradiance is similar to that during sunset and during the night their behavior is more steady and deliberate under the dimmest light natural light conditions and become faster and more sporadic under higher light intensity (Gaffin and Barker 2014).

Bats

Movement of bats in response to lights is relevant in at least three contexts: light at or around the roost, light affecting movement across the landscape, and light affecting potential foraging opportunities. Considerable research on bats and lights has been done (Rydell 2006, Stone et al. 2015), and summarized for practitioners (Voigt et al. 2018a). More recent research includes explicit consideration of LEDs and their differences from previous outdoor lighting technologies.

Illumination of bat roosts can adversely impact the willingness of bats to leave the roost (Downs et al. 2003, Boldogh et al. 2007). This desynchronizes foraging time with peak activity periods for prey items (Azam et al. 2016). It is therefore recommended that no lights shine on roost entrances, and changing color is of far less influence than intensity on this effect (Downs et al. 2003).

Subsequent to emergence from roosts, lights may create barriers for photophobic species in their movement across the landscape to foraging locations (Stone et al. 2009, Stone et al. 2015). The bright, full-spectrum nature of most LED installations has raised considerable concern for impacts on bats (Stone et al. 2012). Consideration of bat movement across the landscape is therefore relevant for LEDs, with the tendency to use full-spectrum LEDs along roadways, for monument and building lighting, and other outdoor area lighting.

Lighting then affects bats while foraging in a manner that reflects both the behavior of their insect prey (see previous section) and their own strategies for avoiding predation. More maneuverable species tend to forage more at lights, while less maneuverable ones will avoid lights because of their own increased predation risk (Rydell 2006). For example, big brown bats, gray bats, evening bats, and tri-colored bats avoided 5,600 lumen 4000 K street lights, while red bats foraged at them (Cravens and Boyles 2019). Total bat activity declined at rivers under bright white LEDs (>200 lux), but unevenly with decrease in *Myotis daubentonii* and increases of *Pipistrellus kuhlii* (Russo et al. 2019b). In response to bright white light (>200 lux), forest bat species that hunt in open spaces or edges did not decrease use of drinking site that was illuminated, but forest interior specialists did have a negative response (Russo et al. 2019a). In comparison, all desert species avoided the floodlights (Russo et al. 2019a). These results are typical, showing increases or decreases in bat activity in response to differences in lighting that vary according to each species behavioral ecology.

The effect of color temperature on bat activity appears to be linked to both insect behavior and bat visual system. On a migratory corridor ~3 lux of warm white LED did not attract additional bats, while 1.8 lux of red LED did (Voigt et al. 2018b). Both nocturnal insects and bats have reduced sensitivity at the longer wavelengths of light (red). Similarly, red-flashing lights did not affect rate of bat fatalities at wind turbines (Bennett and Hale 2014). In an experiment under white, red, and green lights, bats were more active at the green lights (Spoelstra et al. 2015), which may represent a balance of bats attracted to insects and not as many photophobic species repelled as under white light. One study found no significant difference in number of bat buzzes, or number of species at cool LEDs (4000–5700 K) compared with low pressure sodium at previously illuminated site (Rowse et al. 2016). This result may be attributable as much to the insect fauna becoming depauperate over time at illuminated sites, consistent with other studies of effects of CCT on insect attraction at long-illuminated sites (Wakefield et al. 2016).

Replacement of mercury vapor lights with LEDs reduced activity of some species that exploit insects at lights (*Pipistrellus pipistrellus*), while increasing activity of light adverse *Myotis* spp. (Lewanzik and Voigt 2017), which makes sense because ultraviolet vision is widespread in bats (Müller et al. 2009, Gorresen et al. 2015) and mercury vapor lights have significant ultraviolet output. But even with UV, responses differ. In another experiment, a UV LED light source increased activity of some species (*P. pipistrellus*) and decreased others (*P. pygmaeus*) (Straka 2019).

Few studies document thresholds below which bats are not affected by lighting. Bat vision is extremely acute, with visual acuity retained at 10^{-3} lux, the illumination of a clear, moonless night (Bell and Fenton 1986). Benefits from darkness may be found at higher illumination levels, however, with unlit serving as a refuge for clutter-adapted bats and edge-space foraging species, with thresholds for the dark refuge at 0.29–0.66 lux (Haddock et al. 2019). Given that natural illumination conditions range downward 2–3 orders of magnitude from this threshold, and moonlight (<0.3 lux) suppresses bat activity (Prugh and Golden 2014), this result can be interpreted as being "better" for bats than brighter conditions, but not ideal.

Non-volant Mammals

Notwithstanding the many studies done using terrestrial mammals, and the wide array of circadian biology studies undertaken on mice and rats, only one study met our inclusion criteria. In areas illuminated with white, green, or red LEDs at 8.2 lux on the ground, the number of wood mice observed on the ground was strongly decreased under all lights (Spoelstra et al. 2015). As chronobiologists use and report details of studies with LEDs, LED-specific insights will increase. However, existing studies are sufficient to draw some conclusions about full-spectrum LEDs. In a meta-analysis of responses mammal species to lunar cycles, moonlight was found to decrease activity on average by 13.6% across all species, which was consistent with decreased activity by 18.7% with a predator present (Prugh and Golden 2014). These effects were most closely tied to phylogenetic relatedness, visual acuity, and habitat cover. Species that forage by smell had decreased activity under moonlight, while visual foragers increased activity. Moonlight increased primate activity, but decreased rodent, lagomorph, carnivore, and bat activity. As expected, moonlight had more influence in open habitats. Such findings will apply to deployment of LEDs, especially full-spectrum lamps, with species-specific adjustments for spectral configurations that reduce intersection with the visual acuity of different species and groups (Longcore et al. 2018).

Birds

Light affects bird movement and space use in many ways, and the literature on this was recently reviewed (Adams et al. 2021). The major areas of research identified are the aggregation and mortality of birds at lighted structures, which involves the attraction or disorientation of birds by lights, effectiveness of lights as deterrents for birds, and the effect of continuous lighting on habitat use and selection (Adams et al. 2021). Much of the research does not note whether LEDs produce light in question (e.g., studies of migratory attraction), even though such lights may be present. LEDs usually arise and are specifically mentioned in the context of producing particular spectral characteristics in experimental work. It is reasonable to expect that existing research on birds and light applies to LEDs inasmuch as the color of light is taken into account.

Attraction of birds to light, especially in nocturnal migrants, is well-known and long studied. Recent advances using radar detection of bird movement has confirmed that light emanating from cities and other lit areas acts to alter migratory courses and habitat use by nocturnal migrants (McLaren et al. 2018). Such attraction is seen down to the scale of a single installation (the Tribute in Light in New York) (Van Doren et al. 2017) or a single building (Van Doren et al. 2021). Research at the landscape scale does not distinguish LED contribution (e.g., La Sorte et al. 2017, Cabrera-Cruz et al. 2018, Horton et al. 2019), but rather if LEDs contribute to upward glare or skyglow, they can be presumed to increase such effects.

The most important research into the mechanism of disorientation under lights of different colors included use of blue and green LEDs, finding that migratory direction was maintained using the local geomagnetic field under these colors (Wiltschko et al. 2003). This research contrasts with previous research showing that migratory direction is not maintained under red light (Wiltschko et al. 1993, Wiltschko and Wiltschko 1995, Wiltschko et al. 2010). Field-based studies of nocturnal migrant attraction based on light color have yielded varied results (Evans et al. 2007b, Poot et al. 2008, Zhao et al. 2020, Syposz et al. 2021), and the patterns are likely different by taxonomic group and even by species. For nocturnal migratory songbirds, flashing lights are preferable to steady-burning lights (Longcore et al. 2008, Gehring et al. 2009), which is facilitated by LEDs that turn off and on easily. In research on seabird attraction, there is some indication that longer-wavelengths are preferable. For example, shearwaters grounded the most under metal halide lights, followed by white LED and then high pressure sodium, which concentrates spectral output in the red and yellow (Rodr?guez et al. 2017a). Another shearwater study found less attraction with red compared with blue and green lights (Syposz et al. 2021).

Not all results in this research area are reliable, because of comparison of broad-spectrum lights with a dominant wavelength to narrow-band output lights, and failure to account for the fact that equal power delivered to a light will produce a different number of photons at different wavelengths because of the physics of light.

Influence of continuous lighting on bird habitat and space use includes studies using LEDs. Great tits avoided areas illuminated by any light colors as roost sites (de Jong et al. 2016). Green and White LEDs at 1.2 lux appear to reduce daily energy expenditure in great tits, with more food availability (i.e., caterpillars) in these conditions compared with red and dark control (Welbers et al. 2017). Local illumination did not affect probability of pied flycatcher using nest box or on laying date, brood failure, or fledgling mass (de Jong et al. 2015a). However, full-spectrum light of 8 lux at ground level increased nighttime activity of another songbird species, when compared with green or red (Ouyang et al. 2017). The poultry science literature offers insights as well, but fewer studies clearly investigate night lighting. The results are difficult to extrapolate to wildlife. For example, hens under red light were more active (feather pecking, ground pecking, ground scratching, and tail wagging) and spent more time perching under blue light (Sultana et al. 2013a). Chicks under 30 lux LED ("white") were more active than under dim (<1 lux) controls (Li et al. 2020).

Amphibians

Light levels are associated with salamander and frog space use and behaviors (Buchanan 1993, Buchanan 2006, Wise and Buchanan 2006, Perry et al. 2008). One study on juvenile salamander *Ambystoma maculatum*, a primarily nocturnal species, found crepuscular activity an hour before dark and emergence from cover with greater activity under 0.1 and 1 lux LEDs compared with a 0.0001 lux control (Pascone 2014). Other studies, using incandescent light, documented greater abundance of salamander (*Plethodon cinereus*) individuals under 0.0001 lux compared with 0.01 lux (Wise 2007), suggesting that responses may differ by species, habitat, light source, or other factors.

Development

The topic area with the second highest concentration of research within the review scope was growth and development. Because this constellation of research studies arises from the economic incentive to understand lighting and development within animal husbandry and a similar interest in inhibiting development of pest insect species, only a few studies on non-pest, non-domesticated species were located. Many studies of LED-produced light on poultry did not have a substantial dark phase (Liu et al. 2015, Yadav and Chaturvedi 2015, Nunes et al. 2016, Yang et al. 2016a, Yang et al. 2016b, Cusack et al. 2017, Liu et al. 2018b, Yang et al. 2018, Takeshima et al. 2019), so that birds were exposed to the same light for all 24 hours in an indoor setting. Although this configuration met our screening criteria, we expect few similar situations to be found for free-roaming wildlife.

Invertebrates

With few exceptions, unnatural levels of light at night appear to be deleterious to the development of invertebrate species. These effects are seen across developmental stages and taxonomic groups.

Light at night from LEDs can be lethal, as shown for flour beetles (*Tribolium confusum*) exposed to bright blue LEDs, fruit fly (*Drosophila melanogaster*) pupae exposed to LEDs at 378–508 nm, fruit fly eggs exposed to blue (467 nm) light for 48 hours, fruit fly larvae and adults, and mosquito eggs after 72 hours of 417 nm light (Hori et al. 2014). Another fly species (*Bactrocera dorsalis*) died prematurely when exposed to green LEDs at 200 lux for 150 days, while 19.8% of those exposed to red light survived, and 27.2% of those experiencing darkness at night (Liu et al. 2018a). Forty-two days comparing white, blue, green, and red 0.5-Watt LED light with controls found that darkness results in the highest earthworm survival rates (Mishra et al. 2019).

Light can affect egg hatch rates. Nematode egg hatching is inhibited by LED light (white, blue, and UV), most for UV and least for white (Abdel-Rahman et al. 2017). Adults developing from eggs exposed to blue, UV, and white lights moved differently from controls, suggesting an effect of egg exposure (Abdel-Rahman et al. 2017).

Larval development can be advanced by exposure to light at night from LEDs, but this is not likely to be a benefit to an organism that needs to be tied to local phenology. For example, light at night generally shortens the developmental period of a ladybird (*Hippodamia variegata*), with longer daylength and higher intensity shortening immature phase (Tan et al. 2014). Blue and green light made it shortest, while red and yellow the longest and closest to natural period (Tan et al. 2014). Armyworms (*Mythimna separata*; Noctuidae) exposed to monochromatic green LEDs at night (200–250 lux) showed more rapid development of larvae (Kim et al. 2020). In these larvae, juvenile hormone, which postpones metamorphosis until proper size has been reached, decreased with 10 h green LED light at 200–250 lux at night (Kim et al. 2019a). In contrast, UV light slowed the growth of aphids and red and blue LEDs advanced development rates (Acharya et al. 2016).

Light exposure can also affect pupae. Twenty-four hour exposure to green LED light increased eclosion rate of pupae of the fly *Bactrocera dorsalis* (Liu et al. 2018a). Armyworms exposed to monochromatic green LEDs at night had more rapid eclosion of pupae (Kim et al. 2020), although results for juvenile hormone in pupae were conflicting (Kim et al. 2019a).

Effects of light at night exposure carry forward to adult characteristics, including weight and reproduction (next section). For example, flies (*Bactrocera dorsalis*) exposed to light at night were heavier at 12.3 mg (green) at 11.8 mg (red), compared with controls (11.2 mg) (Liu et al. 2018a).

The only study located in the literature search showing no effects of light at night on the development or emergence of an invertebrate was for the tiny crop pest *Thrips palmi* (Murata et al. 2018).

Birds

The majority of studies obtained through the search addressed poultry, and used light exposure levels (5–30 lux) that would only be found directly under or in the vicinity of outdoor lighting installations (Liu et al. 2010, Min et al. 2012, Hassan et al. 2014b, Zhang et al. 2014a, Zhang et al. 2014b, Hassan et al. 2016, Olanrewaju et al. 2016, Thomson and Corscadden 2018, Li et al. 2020). Only in studies of free-living wild birds do we find lower exposures more typical of natural habitats near roadway lighting (e.g., 3 lux) (Sun et al. 2017). Studies of the effects of light on growth include those using monochromatic treatments (blue, green, yellow, and red), white of varying color temperatures, and custom poultry-specific spectral configurations (Huth and Archer 2015).

Exposure to blue LED illumination promoted growth, weight gain, feed intake, and feed conversion of chickens in later stages compared with white and other colors (Liu et al. 2010, Cao et al. 2012, Mohamed et al. 2017). Other studies show higher weight for broilers with green, but that switching from green to blue increased body weight (Rozenboim et al. 2004). However, blue light at night delayed time to laying first egg (Min et al. 2012). Blue light increases weight gain in ducks as well, compared with full-spectrum white light (Hassan et al. 2016, Hassan et al. 2017).

Monochromatic green LEDs also increased weight gain, feed intake, and feed conversion in broilers, compared with white light, especially in the earlier stages of development (Rozenboim et al. 2004, Liu et al. 2010, Cao et al. 2012, Mohamed et al. 2017). In some studies the effect was equal to blue light, but in other studies, green light resulted in higher body weight in broilers than blue light (Rozenboim et al. 2004). Application of green light directly on eggs had no effect in one study but increased growth hormones, testosterone, insulin-like growth factor, and others markers in another (Zhang et al. 2014b). Chicks that had been incubated under green LEDs had significantly greater body weight and pectoral muscle percentage than those that were not (Zhang et al. 2014a). Green light also increased weight gain in ducks when compared with white light (Hassan et al. 2016, Hassan et al. 2017). These finding suggest that like blue light, green light at sufficient intensity (>5 lux) can alter developmental patterns in birds.

Constant yellow LED during incubation was associated with the highest chick weight and shortest incubation time compared with complete darkness or a daily pattern of yellow light and darkness (El-Sabrout 2017). Shortened development time and higher chick weight also found when comparing with natural light-dark regime (El-Sabrout and Khalil 2017).

Chickens exposed to red light at night exhibit some developmental differences. Hens reared under red LED light produced more and ate more food than under blue LED, white LED, or incandescent (Min et al. 2012). The red light birds also laid eggs with thicker shells, and laid eggs sooner (Min et al. 2012). It is not clear how much these responses varied from natural conditions, because there was no dark control. The other experiments with red LEDs showed red light having the least effect on growth and development than green and blue (Liu et al. 2010, Hassan et al. 2014a). Although a small effect on growth and development is not the desired outcome in the poultry production context, reducing such impacts is the goal of wildlife conservation.

Full spectrum white light delivered all night also affects growth and development of poultry, influencing egg production, egg shell strength, food conversion ratio, egg weight, cholesterol, saturated and unsaturated fatty acids, meat characteristics, carcass weight, ovary weight, and nutritional content (Kim et al. 2013, Hassan et al. 2014b, a, Hassan et al. 2016) (Min et al. 2012, Kim et al. 2014). Such studies have little relevance for wildlife beyond indicating that bright lights for extended periods alter bird physiology.

Studies of effect of CCT of white light on avian development might provide some insights for wildlife effects, but results have been limited. No difference was found in weight or food consumption when comparing a 2850K compact fluorescent light and 3000–3200K LEDs at 10–13 lux for hens (Thomson and Corscadden 2018). No difference was found between incandescent (2010 K), compact fluorescent (2700 K), white LED (3500 K), and poultry light (5000 K) at 5 and 10 lux in terms of growth performance of broiler chickens (Olanrewaju et al. 2016). Other comparisons of different LEDs and incandescent find little difference (Sharideh and Zaghari 2017). In just one study, however, cool LEDs (5000 K) resulted in higher body weight than 2700 K LED (Olanrewaju et al. 2015), which is consistent with its higher blue content and the results obtained from monochromatic blue LEDs. Although the study had no natural control, it does suggest that higher CCT may accelerate development compared with lower CCT sources, especially when interpreted in the context of studies on monochromatic blue, green, yellow, and red light.

For studies on development of wild birds and LED, nestlings of two tit species exposed to 3 lux inside the nest box did not gain weight over 3-day period while a control group did gain weight (Sun et al. 2017). In comparison, when the light was outside the box, there was no effect on laying date, brood failure, or fledgling mass for great tits in a comparison of white, green, red, and dark controls (de Jong et al. 2015a). The results from the poultry industry and in-box lighting suggest that light at night can influence wild bird developmental patterns, but indicate that impacts might be limited in situations where nests are directly illuminated. It is of course possible for nests to be directly illuminated within a zone around lights, but it seems that it would be limited to illumination levels typical of direct glare and not of skyglow.

Mammals

In comparison, we only have a few studies explicitly addressing LED lighting impacts on mammalian development. The extensive chronobiological literature using mammalian study organisms should apply, but the light sources are not often identified as being LEDs. From our search, we found a report of suggestive evidence that red light at night exposure (from LEDs) is associated with myopia (Kang et al. 2016), and that cows produce less milk under yellow and blue light from LEDs compared with white, and that milk fat and protein in milk was lowest under cows kept under blue light (Son et al. 2020). Most insights into the effects of LEDs on mammals therefore can rely on studies of light in general, with the assumption that LED effects will differ according to the intensity, duration, flicker frequency, and color composition of each lamp.

Reproduction

Exposure to light at night can affect reproduction in wildlife through disruption of perception of season through alteration of apparent daylength, direct effects on physiology of mature forms, spillover effects from exposure of immature forms, and interference with intersex visual communications.

Alteration of perceived daylength and associated impacts on reproductive state and timing is best studied in birds. Although not using LEDs, the research on the effects of ambient and artificial lighting on bird reproduction goes back to the 1920s (Rawson 1923, Rowan 1938). This research theme has been picked up with the use of LEDs. Light of 0.3 lux can move reproductive seasonality of songbirds by a month and cause irregular molt progression (Dominoni et al. 2013a, Dominoni et al. 2013b). A songbird (Tree Sparrow; *Passer montanus*) exposed to 6 lux in the laboratory secreted luteinizing hormone earlier than controls, and urban birds exposed to 3–5 lux exhibited this pattern in the field; both of these responses were statistically associated with night lighting (Zhang et al. 2014c). For Great Tits (*Parus major*) exposed to warm white LED at 0.5, 1.5, and 5 lux, gonadal growth increased with illumination, and was even present at 0.5 lux (Dominoni et al. 2018). Female great tits exposed to white and green light laid their eggs significantly earlier in the season than dark controls (Dominoni et al. 2020). These effects on bird reproduction, and their mechanistic pathways are mirrored in studies of poultry. For example, in broilers, exposure to 15 lux of green light inhibits expression of the reproductive hormone GnRH-I by increasing melatonin secretion, when compared with white, red, and blue LEDs (Zhang et al. 2017).

Effects of light on reproduction of insects has been documented from mechanisms that appear physiological or behavioral. Pheromone from a noctuid moth (*Mamestra brassicae*) was strongly reduced under warm white, green, or red light at 17 lux (Van Geffen et al. 2015a). Geometrid moth mating was inhibited most by 10 lux of green light and least by red LED, with white intermediate, and a strong reduction in female moths present under green light (van Geffen et al. 2015b). In the fly *Bactrocera dorsalis*, adults oviposited earlier when exposed to 200 lux of green light from LEDs at night, while red did not advance maturation (Liu et al. 2018a). For fireflies, the visual communication between the sexes can be impacted and even eliminated by light at night; female fireflies exposed to 57 lux of LED floodlights did not flash at all and males did not flash near females in lit plots (Firebaugh and Haynes 2018).

Knock-on effects from earlier light at night exposure have been documented in nematodes and armyworms. Nematodes reared from eggs exposed to black light and blue light produced fewer progeny as adults, while rearing in darkness resulted in the most prolific reproduction (Abdel-Rahman et al. 2017). Armyworms (*Mythimna separata*; Noctuidae) exposed to monochromatic green LEDs at night (200–250 lux) showed decreased fecundity and oviposition in adults (Kim et al. 2020).

As with developmental studies, only one showed no effect of light at night and for the same group. Exposure to different colored LEDs did not affect number of eggs laid by a thrip (Thysanura) species (Murata et al. 2018).

Gene Expression

Researchers document gene expression in response to light exposures as a means by which to document the molecular basis of observed physiological and behavioral changes and to quantify those responses. Research corresponds to other observed responses to light at night. For example, the increase in chicken body mass under green light is correlated with an upregulation of gene expression for muscle development (Zhang et al. 2014a). In birds, the mRNA transcript levels of genes linked to germ cell development are increased under 0.5 lux warm white LED (Dominoni et al. 2018). In cotton bollworm, circadian clock genes decreased in expression in response to UV (365 nm), blue (450 nm), and green (505 nm) LEDs at the start of scotophase (Yan et al. 2019). Gene expression can similarly be used to document a lack of impact from light; simulated moonlight (0.03 lux) did not affect circadian rhythm of gene expression in fly eyes (Bachleitner et al. 2007).

Predator/Prey Relationships and Pollination

Visual detection often governs predator-prey relationships, including herbivory, and influences other interactions such as pollination. Consequently, a significant proportion of light pollution research addresses these relationships, some of which has focused on LEDs in particular, usually arising from the differences in spectral composition compared with other outdoor lighting sources.

Effects of LEDs on these interspecific interactions may arise from several different pathways. First, lights can extend activity periods, thereby increasing the period for predatory and foraging activity. For example, ladybird beetles consumed more prey with illumination of 150 lux from LEDs (Tan et al. 2014).

Second, behavioral changes associated with light attraction or repulsion may affect interspecific interactions. For example, in a grassland mesocosm experiment the abundance of an herbivorous insect was decreased significantly in presence of white light from LEDs and predators, but not when predators were not present (Bennie et al. 2018). In another example, spiders take advantage of insect phototaxis to choose placement for webs. Spider webs constructed under 20 lux of cool white LED captured prey at significantly higher rates than at control sites, and 94% of the spiders selected the illuminated side of the arena to construct their webs (Willmott et al. 2019). This preference persisted regardless of success, suggesting it is an ingrained trait, and one that has been observed extensively in the field for different lamp types.

The relationships between bats and their insect prey represent the most well-studied system for LED effects on predation. Interactions can be affected directly. In an experiment comparing LED street lights with dark controls, the anti-predator behavior of moths was reduced under the lights (Wakefield et al. 2015). Interactions also vary by bat foraging specialty and insect niche. For example, LED illumination at 4250K increased feeding activity of light-opportunistic bat species but reduced activity of light-adverse bat species and the effect decreased with dimming (Rowse et al. 2018). Portable outdoor LEDs at 4000–4500 K in a forest environment did not affect foraging of most species but increased activity of two light-opportunistic species (Russo et al. 2019a). In a desert environment, one bat species foraged significantly less under 4000–4500 K LEDs (Russo et al. 2019a). Sites lit with 5000K LEDs affected diet and consumption rates for bats; lit sites had higher moth consumption and decreased beetle consumption for two bat species, but a beetle-specialist showed increased consumption of beetles around lights (Cravens et al. 2018). Consistent with behavior of insect prey, foraging of bats was not elevated under red lights (1.8 lux) compared controls unlit controls (Voigt et al. 2018b).

Third, lighting may interfere with signals between species that use bioluminescence. Females of some firefly species mimic the flashes of other species to attract and eat males of those other species. An LED floodlight creating 174 lux at the ground decreased number of flashes by the male firefly prey species and by the female predator species (Firebaugh and Haynes 2018), disrupting both this predator-prey system, and presumably the intraspecific mating that the female fireflies exploit to attract other species as food.

Finally, the interspecific interaction of pollination depends on behavior of pollinators under and near lights. In experiments, presence of lights has a negative effect on pollination with seed mass lower closer to LED lights (Macgregor et al. 2019). Such effects may have spillover effects on whole pollinator communities, including diurnal species (Knop et al. 2017).

Stress and Fear

Another response of organisms to light at night is the physiological response of increased stress (usually measured through presence of stress hormones or other physical manifestations) and behavioral responses that are associated with fear. LEDs have been used in such studies, often to provide different colors of light as treatments, both in the laboratory and in the field.

In the laboratory most studies show increased stress from exposure to light from LEDs at night, although there is nothing in these studies to indicate that LEDs are any different than other light of similar spectral composition and intensity. These results include:

- Increased oxidative damage in the nematode Caenorhabditis elegans under white, blue, or UV light compared with controls (Abdel-Rahman et al. 2017).
- Earthworms (*Eudrilus eugeniae*) exhibiting stress in terms of weight loss under white LEDs, with red LED the second most stressful (Mishra et al. 2019).
- The stress hormone cortisol elevated in the milk of cows exposed to 150 lux of blue light at night (Son et al. 2020).
- Enhanced fear response in mice with blue light compared with controls, but very little effect if the light was very dim (0.01 μW/cm2) (Warthen et al. 2011).

Experiments with poultry are somewhat difficult to interpret because several studies use a 23:1 photoperiod and the light treatment is given for the full 23 hours. The results in such studies suggest that the provision of full spectrum light during the photophase that is more like daylight is more important than the nighttime exposure. For example, chicks on a 23:1 photoperiod had a decrease in stress response in chicks with increasing color temperature (Olanrewaju et al. 2015). In other poultry studies, it seems that blue light alleviates stress in broilers and ducklings, but this is in a 23L:1D situation so it is unclear if the benefit would be equal with 12L:12D (Xie et al. 2008, Sultana et al. 2013b, Soliman and Hassan 2019). Finally, some studies show little effect of LED light (white, red, green, blue) on stress on hens (Sultana et al. 2013a).

A few studies investigate the effects of light at night under field conditions on stress and related behavioral markers. Most notably, wallabies in an enclosure with white and amber LEDs had no difference in lipid peroxidation, an indicator of physiological stress (Dimovski and Robert 2018). Under both treatments, with a range of exposures based on distance to the light, antioxidant capacity declined over a 10 week period (Dimovski and Robert 2018).

Other studies, in birds, found a range of responses to different LED treatments. Nighttime exposure to 3 lux white LED did not affect exploration behavior in great tits (Sun et al. 2017). Telomere length (the caps on the end of chromosomes) did not relate to light exposure with white, green, or red street lamps at 8.2±0.3 lux at ground level beneath nest boxes (Ouyang et al. 2017). Shorter telomeres are associated with higher mortality. Birds exposed to white, green or red light at 8.2 lux (at ground level) had no difference in haptoglobin, a signal of inflammatory disease (Ouyang et al. 2017). Birds in areas illuminated with white light had a greater probability of malaria infection (Ouyang et al. 2017). Birds most active at night had higher levels of oxalic acid, which is a marker for sleep debt (Ouyang et al. 2017).

Results from insects confirm light at night pathways to physiological stress. Oriental armyworm (*Mythimna separata*) exhibited time-dependent increase in stress from illumination by green (520 nm) LED at 200–250 lux (Kim et al. 2018b) and UV light was associated with expression of some neuropeptides in cotton bollworm (Wang et al. 2018).

Sleep and Daily Rhythms

The literature on sleep and daily rhythms in animals is vast and anchored in the field of chronobiology. Lights have been used during the dark phase of organisms in laboratory situations for decades, and in more recent years such light has been supplied by LEDs, both as broad-spectrum white light and narrow-spectrum sources, used to test the influence of different colors on circadian rhythms (Sheppard 2013, Allen et al. 2016). Aulsebrook et al. (2018) provide a review of the effects of artificial light (from all sources) at night on sleep. They summarize the known impacts, including earlier morning activity in songbirds, longer daily activity in songbirds, and suppression of melatonin production in some urban birds, mammals, and fish (at 0.3–1 lux). The technology and field techniques to measure sleep in wildlife are only now becoming available and used (Robert et al. 2015, Aulsebrook et al. 2018, Aulsebrook et al. 2020a, Aulsebrook et al. 2020b). From laboratory studies, artificial light at night (again, from any source) can be seen to affect sleep via three pathways (Aulsebrook et al. 2018): 1) entraining circadian rhythms through suppression of melatonin, 2) interrupting sleep without affecting circadian rhythms as measured by melatonin, and 3) extending activity periods of diurnal species into nighttime. Research into these topics is ongoing and no evidence has yet emerged that LEDs have any differential effect on sleep outside of the characteristics of the light that they produce in terms of intensity, spectrum, and, although infrequently studied, flicker. Our literature search yielded 16 studies of the effects of LEDs on sleep in wildlife, with most studies on birds, followed by mammals and insects.

Cavity-nesting birds have been the subject of research on sleep because of the relative ease of manipulating nest boxes, with most studies on great tits and blue tits. A white LED at the nest box entry kept some great tits from reentering the box during an experimental night and those that were exposed woke earlier, left the nest box earlier, and got around 5% less sleep (Raap et al. 2015). Sun et al. (2017) report that white LEDs of 1.6 lux at the nest box entrance reduced sleep in great tits, which woke earlier and left the nest earlier. But subsequent research found no effect of 0.3 lux at entry to nest box on sleep (Raap et al. 2018).

A 3 lux LED illuminating the interior of a nest box reduced total amount of sleep by half in great tit females (Sun et al. 2017). Chicks begged for food longer and more often at night when illuminated (Sun et al. 2017). The 3 lux treatment delayed sleep for great tits, while 1.6 lux delayed sleep onset in females but not overall (Sun et al. 2017). The time of birds entering the nest box also varied by season, being unaffected in December but delayed in February (Sun et al. 2017). Both blue tits and great tits experienced increased evening latency (got to sleep slower) under 3 lux light, and great tits fell asleep later, woke up earlier, and lost 50 minutes of sleep

(Sun et al. 2017). Blue tits and great tits are both affected by light at night, showing increased evening latency (time between nest-box entry and sleep onset), altered sleep bout length, and decreased frequency of sleep bouts (Sun et al. 2017).

A few studies have addressed light spectrum and sleep on birds. In the lab, exposure to 5 lux of red, green, or white LED light at night for 10 hours increased activity during the night and decreased activity during the day (de Jong et al. 2017). At lower intensities (e.g., 0.15, 0.5, 1.5 lux), the green light was less disturbing than white light (de Jong et al. 2017). In the field, no influence was found from white, green, or red LED streetlights with illumination of 5–10 lux under lamps on timing of dawn chorus in birds (Da Silva et al. 2017). Aulsebrook et al. (2020b) investigated the response of Black Swans (*Cygnus atratus*) to filtered amber LEDs (2100 K) and unfiltered LEDs (3700 K) in an enclosure. Both treatments significantly reduced the amount of sleep but did not affect melatonin. The treatment was naturalistic with ground-level intensities ranging 0.1–10 lux from six lamp poles placed within the enclosure. Aulsebrook et al. (2020a) assessed the response of feral pigeons and Australian magpies (*Cracticus tibicen tyrannica*) to white (18 lux of 4190 K) and amber (18 lux of 2140K) LEDs, and found that both lamp types caused reduced sleep duration, less REM sleep, less intense sleep, and more fragmented sleep. No attempt was made to adjust intensities so that the melanopic strength of the two treatments was the same. Effects were lessened under amber lights for the magpies, but not for pigeons.

The most relevant study in mammals showed a significantly smaller effect on melatonin production in wallabies from amber LEDs compared to white (probably 5000 K) LEDs in an enclosure experiment (Dimovski and Robert 2018). This result was consistent with research on free-roaming wallabies that showed desynchronization of reproductive cycles and reduction in melatonin levels on a brightly lit military installation compared with unilluminated bushland (Robert et al. 2015). Remaining studies on rodents confirm the importance of blue light on melatonin suppression in the laboratory (Mas?s-Vargas et al. 2019). A review of this field is provided by Grubisic et al. (2019), who compile studies showing melatonin suppression across wildlife species, including at extraordinarily low illumination (<0.01 lux).

Research in insects similarly shows the ability of dim light (0.03 lux) to synchronize circadian rhythms (Bachleitner et al. 2007).

Immune Response

The poultry science literature includes studies that assess immune response to LED lights. These studies are somewhat difficult to translate to non-captive situations because the daytime exposure in the studies is inevitably artificial light indoors. Two studies returned by our search strategy associated greater T-lymphocyte proliferation with green LEDs when compared with other color lights (Xie et al. 2008, Chen et al. 2016) and a study of broiler chicks showed lower antibody levels under white light than under monochromatic red, yellow, green, and blue (Hassan et al. 2014a).

Vision

Exposure to high color temperature (6500 K) LEDs at 750 lux was linked with possibility of damage to vision in a rat model. Compared with similar illumination and color temperature of compact fluorescent light, the LED-exposed rats manifested significantly greater retinal cell death (Shang et al. 2014). More recent work after our study period confirms this result in mice and at lower illumination (250 lux) at 7378 K, but with no effect on cell death for 2954 K at illuminations under 3000 lux (Xie et al. 2020). Subsequent studies with cell cultures confirm that retinal cell viability decreases as color temperature increases, with 1900 K lights not differing significantly from controls at ~600 lux, while 3000 K and above saw increased cell death by 25–50% (Jin et al. 2021).

Conclusion

The literature search and resulting map of studies, and their summaries reinforce several points about light pollution research in general, many of which are contained in a recent horizon scan of important research questions for the field. In particular, the state of knowledge of the effects of LEDs on terrestrial wildlife highlights the following research needs (Hölker et al. 2021a):

- To harmonize measurement of light exposure in ways that are relevant to the associated responses and comparable across disciplines (e.g., physics, visual ecology, circadian biology, lighting engineering and design).
- To summarize and further investigate differences in photoreceptors across organisms, and to incorporate these differences into research and environmental assessment.
- To estimate illumination thresholds at which species responses occur, integrated with the spectral power distribution of stimuli.
- To document long-term effects of light exposure on biodiversity.
- To research the effects of light pollution on landscape-level connectivity, for which virtually no research focused on LEDs exists.

Thankfully, it appears that the effects of LEDs on terrestrial wildlife in current studies are arising from the intensity and spectrum of the light itself, and not the fact that it is produced by an LED source. This means that with the possible exception of LED characteristics about which there is little research (e.g., flicker, non-Lambertian emittance), light pollution research in general can be used to inform assessment of the effects of LEDs. The literature argues for nuance in approaches to reduce impacts from artificial light at night because responses do vary considerably among taxonomic groups (Longcore et al. 2018, Owens and Lewis 2021). Absent specific target species for mitigation, however, research on LEDs supports an approach of mitigation of adverse impacts by: 1) reducing intensity, 2) controlling spill, 3) reducing duration, and 4) controlling spectrum to avoid peak sensitivities of most groups to shorter wavelengths. As the results of the review show, taxonomic variability in photoreceptor sensitivity argue for careful consideration of affected species when devising spectral mitigation.

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Chapter 2. Relative Importance of Intensity and Spectrum of Artificial Light at Night in Disrupting Behavior of a Nocturnal Rodent

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Executive Summary

The influence of light spectral properties on circadian rhythms is of substantial interest to laboratory-based investigation of the circadian system and to field-based understanding of the effects of artificial light at night. Outdoor night lighting characteristics are rapidly changing because of increasing deployment of light emitting diode (LED) lamps. LEDs are also increasingly used in animal husbandry for experimental studies of circadian biology, but the implications of this shift are not widely discussed. Because the visual systems of model organisms and of wildlife differ in spectral sensitivity from human vision, spectrum can greatly influence responses to light when the dose is measured in terms defined by human vision (i.e., lux). Furthermore, investigations of circadian responses to light at night often only consider light >5 lux, when species in their habitats routinely experience natural conditions that are orders of magnitude dimmer, and which may affect behavior and physiological circadian responses. The tradeoffs between intensity and spectrum regarding circadian rhythms are largely unknown, even for well-studied organisms.

We used a custom LED illumination system tunable to different spectral outputs and adjustable to naturalistic illumination levels (e.g., 0.01 lux) to document the response of wild type house mice (*Mus musculus*) to 1-hr nocturnal exposure to all combinations of four intensity levels (0.01 lux, 0.5 lux, 5 lux, and 50 lux) and three correlated color temperatures (CCT; 1750 K, 1950 K, and 3000 K).

The higher intensities of light suppressed activity substantially, and consistently more for the higher CCT light (at 50 lux, 91% for 3000K; 53% for 1750 K). At the lower intensities, mean activity was increased, with the greatest increases for the lowest CCT (12.3% increase at 1750 K; 3% increase at 3000 K). A multiple linear regression confirmed the influence of both CCT ($p<0.001$) and intensity ($p<0.001$) on change in activity ($r^2=0.66$, $F_{9,171}=3.33$; $p<0.001$) with the scaled effect size of intensity 3.6 times greater than CCT.

These results are consistent with the ecology of a species naturally active at night under starlight but decreasing activity with illumination in response to predation risk and confirm that laboratory studies should include naturalistic lighting levels as controls in circadian studies. The significant differences by spectral composition both illustrate a need to account for spectrum in circadian studies of behavior and physiology and confirm that spectral controls can mitigate some, but certainly not all, of the effects of light pollution on species in the wild.

Introduction

The fields of chronobiology, with its focus on physiological responses to daily cycles, and conservation biology, in its attention to the question of nighttime light pollution, are beginning to coalesce (Dominoni 2015, Dominoni and Nelson 2018, Grubisic et al. 2019, Aulsebrook et al. 2020b, Hölker et al. 2021b). Researchers have investigated patterns of sleep, hormone production, and activity patterns in model organisms for decades in the laboratory and increasingly now with wild organisms (Robert et al. 2015, Rattenborg et al. 2017, Aulsebrook et al. 2018, Aulsebrook et al. 2020b). The influences of artificial light at night have long been documented for foraging (Goertz et al. 1980, Sick and Teixeira 1981, Kotler 1984, Frey 1993, Rohweder and Baverstock 1996), activity patterns (Barber-Meyer 2007, Wise 2007), and reproduction (Rawson 1923, Rowan 1938) across a range of taxonomic groups. Research is now linking laboratory and field-based studies to describe the mechanisms and thresholds associated with these influences (de Jong et al. 2015b, Dominoni et al. 2019, Schirmer et al. 2019, Simons et al. 2022).

Assessment and mitigation of the effects of nighttime light exposure has focused on spectrum, because of the characteristic pattern of the melatonin suppression curve (Brainard et al. 2001). Manipulating spectral composition of light is a means to influence melatonin production and associated physiological responses, both in humans (Rea et al. 2010, Brainard et al. 2015, Souman et al. 2018, Nagare et al. 2019) and in wildlife (Dimovski and Robert 2018). Avenues of influence on nocturnal behaviors need not be limited to melatonin suppression, with the differing visual systems of taxonomic groups allowing for behavioral responses that are profoundly influenced by the spectral composition of light. For example, many insects see in the ultraviolet spectrum, and insects generally exhibit positive phototaxis to light in this portion of the spectrum (Cleve 1964a, Donners et al. 2018), even while humans do not perceive it at all. These behavioral responses have already been the subject of proposals to mitigate effects of light pollution (van Grunsven et al. 2014, Longcore et al. 2015, Rodr?guez et al. 2017b, Longcore et al. 2018). While researchers agree that both light intensity and spectrum are important to wildlife (Gaston et al. 2012, Davies et al. 2013, Longcore and Rich 2017), their relative importance deserves more investigation, such as has been done to some degree in laboratory studies with model organisms. Furthermore, the influence of naturalistic levels of light at night, which fall in the range of conditions experienced in nature without light pollution, deserve far more investigation, both for laboratory studies focusing on mechanisms (Walbeek et al. 2021) and to understand natural responses to these conditions in wild organisms as a baseline to understand light pollution, even if that pollution may “only” increase illumination from that similar to a quarter moon (0.01 lux) to that of a full moon (~0.1–0.3) (Brown 1952, Kyba et al. 2017). Typical laboratory chronobiological studies with model organisms consider 5 lux to be “dim” light (Walbeek et al. 2021), and this is also the typically cited minimum illumination that causes melatonin suppression in humans.

Some barriers inhibit studies that fully explore the effects of light at night at naturalistic intensities and at different spectral compositions in the laboratory and field. In the field, it is difficult to deliver a constant and known dose of light to species, given existing light pollution at study sites and technological limitations of both lights that might be deployed and the equipment to measure both intensity and spectrum at naturalistic (<0.3 lux) conditions. Rather, studies often use distance from brighter lights of known spectral composition to create gradients that then decrease to the ambient conditions (Wang and Shier 2017). Laboratory studies often keep model organisms (mice and rats) in near-total darkness as the nighttime control, even though this condition is highly unnatural and outside the range of natural conditions in which these species evolved (Aulsebrook et al. 2022). To move forward understanding of the interaction between intensity and spectrum and its influence on both behavioral and physiological responses of animals, logistical constraints to provision of light of specified spectral characteristics across gradients that include naturalistic levels must be overcome.

Custom laboratory lighting systems using light-emitting diodes (LEDs) now allow for delivery of specific spectral outputs to the same organisms over time and at different intensities. Such systems can deliver different color temperature light by using combinations of individual colors of LEDs making up an array. Through the use of dimming and neutral density filters these spectral compositions can be delivered across a range of ecologically relevant intensities. Field studies of wildlife habitats using new measurement tools, such as calibrated cameras collecting hemispherical images (Pendoley et al. 2012, Jechow et al. 2017, Simons et al. 2020) can define naturalistic conditions for species and habitats of interest.

In this study, we evaluated combinations of intensity and spectral composition of light in controlled conditions for their impact on a behavioral response in house mice (*Mus musculus*). The lowest light levels used are comparable to measurements taken in open desert habitat that is home to many nocturnal rodent species. *M. musculus* is nocturnal and despite long use in laboratory settings, retains its strongly suppressed behavior under light at night (Busch and Burroni 2015). Not all rodents have a similar response, but prominent sensitive species in California in the Heteromyidae family show this strong moonlight/light-at-night aversion (Prugh and Golden 2014). We therefore used house mouse in a laboratory setting to investigate the interactions of intensity and spectrum on nighttime activity and circadian entrainment. This species serves as a proxy for rare and endangered rodent species found in the open habitats of southern California.

Spectral response curves for melatonin suppression and visual responses are known for mice. Based on preliminary calculations with these response curves and the spectral power distributions of the proposed light sources based on Longcore et al. (2018), we hypothesized that 1) lower color temperature lights would deviate less from control conditions because they overlap less with the mouse visual and melanopic responses, and that 2) illumination similar to the darker half of the lunar cycle would result in greater activity compared with much darker conditions regularly created in laboratory conditions (see also Walbeek et al. 2021).

Methods

The study involved nocturnal exposure of house mice to a pulse of light of varying intensity and correlated color temperature, and evaluation of the change in mouse activity between these different light treatments.

Light Treatments

We exposed mice to four levels of light (0.01, 0.5, 5, and 50 lux), each at three different CCTs (1750, 1950, 3000 K). To calibrate the dimmest light exposure, field data were taken in the Coachella Valley, California along State Route 62 as an example of open desert habitat > 3 km from the nearest urban development. Data were collected using a Sky Quality Camera (Euromix Ltd., Llubljana, Slovenia) on nights with a new moon and after astronomical twilight. Cloud cover, which reflects light and increases light pollution, was variable. Both cosine-adjusted illuminance and hemispherical illuminance were extracted from the imagery. We plotted the relationship between hemispherical illuminance and cos-adjusted illuminance because hemispherical illuminance is important to exposure (light from all directions) while light meters used to measure light in laboratory conditions measure cos-adjusted illuminance. The average scalar illuminance at 15 locations from 10–400 m from a highway was 0.020 lux. This corresponded to a cos-adjusted illuminance of 0.007 lux. These compare with the illumination produced by a quarter (crescent) moon at its brightest of 0.008 lux (Krisciunas and Schaefer 1991). The lower limit of our light meter is 0.01 lux, so we set this as the lowest exposure for the experiment so that we could measure it accurately. At the upper end, we chose both 5 lux, which is known to affect rodent circadian rhythms and could be experienced by rodents near roadway lighting and 50 lux, well above known impact thresholds to see the maximum influence of spectral differences. Between these extremes we selected 0.5 lux (below the lower limit of most lighting design software calculations).

Custom lighting systems using LEDs were obtained from Ecosense Lighting (now Korrus Lighting; Los Angeles, California). The systems could be adjusted to spectral output to achieve different color temperatures. Because any particular correlated color temperature can be achieved in different ways, we compared possible outputs against known lamp types in terms of their predicted melanopic effect, using methods described in Longcore et al. (2018). We selected three configurations to represent a range of melanopic effects when compared with daylight (D65) and that fall within the range of commercially available outdoor lighting. Ordered from highest melanopic effect to lowest compared with D65, they were Ecosense 3000 K (54%), Ecosense 1950 K (30%), and Ecosense 1750 K (13%). For comparison, the melanopic effect as a percent of D65 for typical lamps is as follows: 4200 K LED streetlight (56%), 3000 K LED streetlight (45%), high pressure sodium streetlight (18%), phosphor-coated amber LED streetlight (10%).

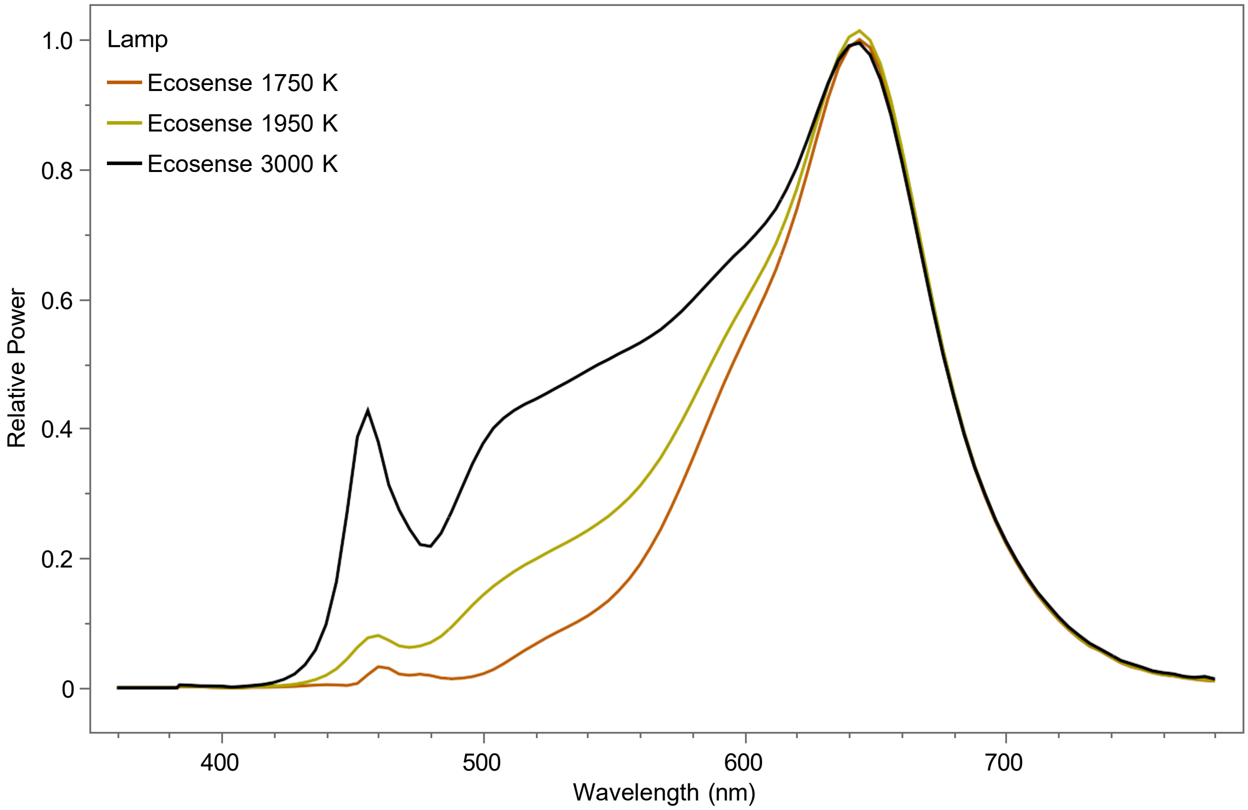

Figure 7. Relative power distribution of lights used in experiment of 1750, 1950, and 3000 K CCT (Ecosense Lighting, Los Angeles, California).

Study Organism and Protocols

Sixteen laboratory mice (C57 Bl6/J strain; 8 male, 8 female) were obtained at 3 months of age and placed into the environmental control chambers. All animal care and treatment protocols were reviewed and permitted by UCLA's Animal Care Committee. Each mouse was individually housed to obtain locomotor activity rhythms from each animal. Each cage was outfitted with a passive infrared detector to measure all activity. The environmental chambers control sound, maintain temperature, humidity and allow the light to be varied in intensity and spectral properties using the custom LED illumination system. Mice were entrained in a light/dark cycle consisting of 12 hrs of light (350 lux; 3000 K) and 12 hrs of dark. We then exposed each mouse to 12 light spectrum and intensity combinations, with one treatment per night. The treatment consists of 1 hour of exposure to the light during the subjective night. Mice were tested once per week with recovery in 12:12 conditions between tests, so that mice were exposed to all treatments over the course of 12 weeks.

Home cage activity was monitored using a top-mounted passive infra-red (PIR) motion detector reporting to a VitalView data recording system (Mini Mitter, Bend, OR). Detected movements were recorded in 3 min bins, and analysis was carried out using the El Temps chronobiology program (A. Diez-Noguera, Barcelona, Spain; http://www.el-temps.com/principal.html). Cage activity during the light exposure was compared to activity at the same phase (ZT 14-15) in the prior day. The % change in activity was then calculated.

Analysis

We analyzed the data with intensity and color temperature as continuous and categorical variables. Because CCT can be achieved in many different ways, the effects of different CCT lights on mouse behaviors are not necessarily related in a linear fashion, so we treated CCT as a categorical rather than continuous variable. We compared suppression of mouse activity using CCT and illuminance both as categorical variables and testing for significant differences for each while holding the other constant (Tukey-Kramer HSD for multiple comparisons). To account for potential interactions between CCT and illuminance, we built a generalized linear model (Nelder and Wedderburn 1972) with a normal distribution and log link function using suppression as the dependent variable and CCT, illuminance, and CCT*illuminance as the independent variables. Effect sizes (the relative contributions of each variable) were compared by centering each factor at the mean and scaling by half of its range. All statistical tests were performed using JMP Pro 16 (SAS Inc., Cary, NC).

Results

Light intensity and color temperature affected activity patterns of mice (Figure 8). Light at 0.5 lux and brighter, except for the 0.5 lux/1750 K treatment, reduced activity of mice (Table 1). All 0.01 lux treatments, and the 0.5 lux/1750 K treatment, increased activity during the treatment. Within color temperatures, the effect of illuminance on mouse activity was only significantly greater for 50 lux at 1750 K, and at 0.01 lux, CCT was not statistically significant, although 1750 CCT increased activity more than 3000 CCT.

Mouse activity was associated with light conditions in a generalized linear model ($p<0.001$) with significant contributions of illuminance ($p<0.0001$), spectrum ($p<0.0001$), and the interaction term ($p<0.002$). The influence of illuminance on mouse activity across the 0.01–50 lux range was several times greater than the effect of CCT across the 1950–3000 K range with the influence of CCT decreasing at the lowest light strength.

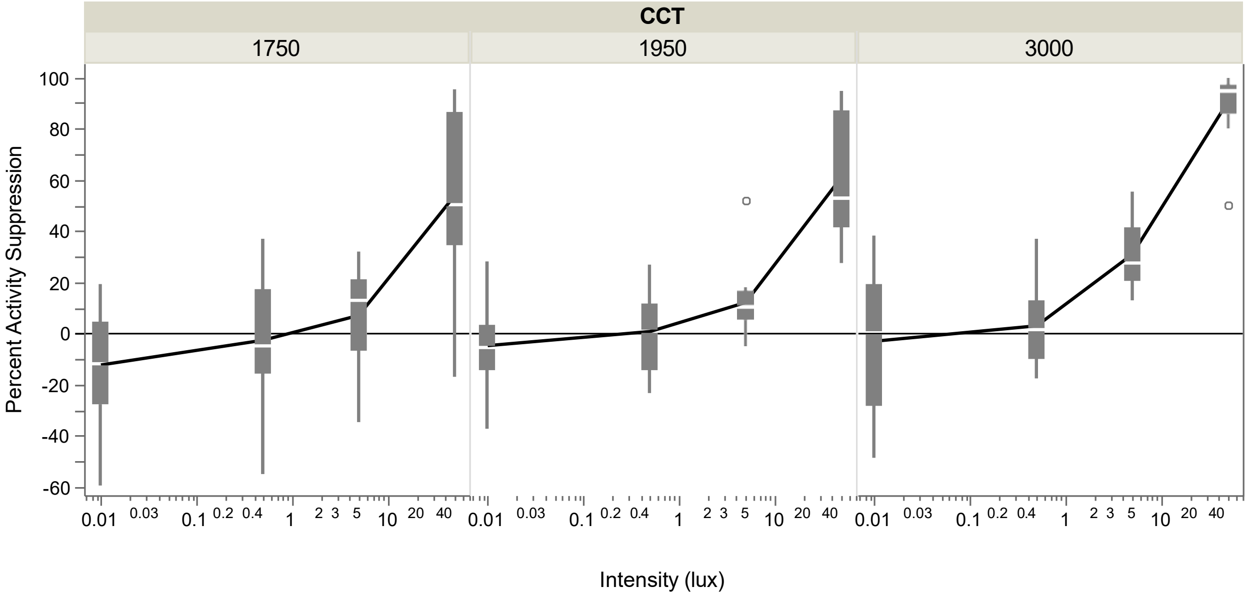

Figure 8. Suppression of mouse activity (percent change) by combinations of illuminance and correlated color temperature. The black lines connect means, while box plots indicate median, 25th, and 75th percentiles, and 1.5 times the interquartile range or maximum and minimum values if there are no outliers.

Table 1. Mean percent suppression mouse activity under light of different illuminance and spectrum. Letters indicate significant differences in both columns and rows when treating both intensity and CCT as categorical variables.

		Illuminance (lux)			
		0.01	0.5	5	50
	1750	-12.3^{A}	-2.6^{A}	7.0^{A}	53.7^{B}
CCT (K)	1950	-4.7^{A}	0.8^{A}	12.2^{A}	61.0^{B}
	3000	-3.0^{A}	3.0^{B}	30.9^{C}	90.4^{C}

Discussion

We found, consistent with predictions and previous literature, that lower correlated color temperature reduced the effect of light on an organism sensitive to shorter wavelengths of light than humans when the treatment is measured in lux. The difference can be attributed to the reduced sensitivity of the rodent visual system to light in the red region of the spectrum when compared with humans. Rats and mice have sensitive low-light vision with a preponderance of rods with peak absorption at 498 nm (Bridges 1959, Govardovskii et al. 2000) and are dichromatic, with an ultraviolet and a green cone (Jacobs et al. 2004). Although recent research shows that red light can be absorbed through the rod-dominated retina for rats to form images (Nikbakht and Diamond 2021), they are much less sensitive to long wavelength light, and therefore also to low CCT light than to shorter wavelengths. Lower CCT light also overlaps less with the melanopsin absorption spectrum, which we calculated a priori for the treatments in this study. It appears that this mechanism is operating, and the effects of color temperature on mouse activity increase at intensities well documented to cause melatonin suppression (e.g., >5 lux).

Increased activity under 0.01 lux light, which is somewhat below that produced by a half moon in normal conditions, is a phenomenon newly summarized in the circadian biology literature (Walbeek et al. 2021) and familiar to ecologists (Prugh and Golden 2014, Aulsebrook et al. 2022). Many small mammal prey species reduce their activity during full moon conditions and forage more and more boldly under half-moon and darker conditions. By the same token, near-complete darkness, or infrared-dominated conditions as found in laboratory conditions with activity monitoring devices, would be darker than natural conditions and result in reduced visual acuity. Addition of light could then aid foraging behavior at relative mouse-perceived intensities and then suppress activity as the illuminance increased to levels instinctively associated with greater predation risk (e.g., 0.5 lux) and even more so as the mechanistic pathway of melatonin suppression and circadian entrainment is triggered. Moonlight entrains circadian rhythms in hamsters and mice (Evans et al. 2007a, Butler et al. 2012), so this effect should be expected and increase with intensity.

The results offer important new information for the approach of mitigating the adverse effects of light at night on wildlife. Adjusting the spectrum of light to be most visible for humans while being less stimulating for other species (known as "spectral tuning") is seen as a means to balance human needs with potential adverse impacts (Poot et al. 2008, van Grunsven et al. 2014, Longcore et al. 2015, Longcore et al. 2018). Spectral tuning has, however, been approached with some skepticism because it may not work across all taxa, especially those bioluminescent organisms that exploit the longer wavelengths generally used to mitigate overall effects of light at night (Owens and Lewis 2018, Owens and Lewis 2021). This work illustrates that the effect of light intensity is much greater than spectrum, and at low enough intensities, the spectrum of the light becomes less relevant to an example behavior in a study organism. However, spectrum becomes increasingly important as intensity increases, as shown by the significant interaction term between CCT and intensity. These results suggest that when light intensity cannot be reduced (e.g., to meet design standards on a roadway), then achieving those standards with lights that overlap more with human vision than with sensitive organisms surrounding the location would be a valid mitigation approach.

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Chapter 3. A Database of Species Visual Responses to the Spectral Distribution of Light

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Executive Summary

The presence and proportions of photopigments, which are responsible for the visual and physiological purposes of light, vary between taxonomic groups. This leads to differing wavelength sensitivities ranging from UV (<400 nm) to IR (>780 nm), and complicates the balancing of roadway lighting spectra to maximize human visual acuity while mitigating light pollution effects on wildlife.

This research develops a database and synthesizes spectral response information for terrestrial wildlife for various sources to create generalized spectral response curves by taxonomic phylum, class, and order. The spectral sensitivities of species commonly requiring inter-agency consultations for CalTrans projects are then inferred from the generalized spectral response curves based on their taxonomic similarity. Existing data on species visual sensitivity was collected from previous research using three methods: behavioral responses, electroretinograms (ERGs), and reflectance within the eye.

Resulting summaries of sensitivity allow for some general observations. Overall, longer wavelengths provide the highest possibility for supporting human visual acuity 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. The possibility of mitigation by using longer wavelength light for human tasks at night is based on the assumption that a higher spectral sensitivity value directly translates to a behavioral response, which is confirmed for certain organisms, but not yet for others. The diversity of visual response systems across terrestrial wildlife species is too large to provide a “perfect” lighting spectral composition, and as such, spectral tuning should be considered as an incremental benefit that may provide additional benefits when other mitigation measures have been exhausted.

Introduction

Roadway lighting constitutes a substantial proportion of the artificial light at night in the environment and is an especially large contributor at rural locations where safety concerns lead to introduction of lights in otherwise dark environments. Illumination from roadway lights has documented adverse impacts on wildlife and their habitats, such as nest location choice in 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 and Salmon 2005), attraction and repulsion of bat species (Stone et al. 2009, Voigt et al. 2018), migration of fish (Riley et al. 2013), and even altering plant phenology (Massetti 2018). Mitigation of the effects of roadway 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 roadways is often set by policy, regulator, or risk management considerations. Most jurisdictions follow guidelines adopted by professional organizations such as the Illuminating Engineering Society (IES) or, internationally, 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 specify illumination levels to be met in specific situations, as measured in lux or lumens. In those locations where roadway lighting has been determined to be necessary, relatively little latitude is available in terms of the intensity of lighting, which leads to avenues for project-specific environmental analysis and mitigation. The first is to calculate and map impacts to wildlife habitat in terms of changed light levels (illumination) and visibility (glare) accurately. Second is to pursue design choices that reduce impacts off the roadway by controlling light distribution and potentially by selecting a light spectrum that maximizes human visibility while minimizing adverse effects to other species. This report develops resources to guide the choice of color spectrum for lights and to estimate the potential impact of lights on wildlife species with different visual systems.

It is not novel to observe that 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 light spectrum on different group 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 hatchings are more influenced by shorter wavelengths (Witherington and Bjorndal 1991, Witherington and Martin 1996), leading to regulations for turtle-friendly lights with strict limits on shorter wavelength emissions in coastal areas in Florida. 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. Even so, yellow lights (low pressure sodium, high pressure sodium) were known for being less attractive to insects, while mercury vapor, with its emissions in the ultraviolet, was extremely attractive to insects (Eisenbeis and Hassel 2000, Eisenbeis 2006, 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, interest in spectral tuning became more refined (van Grunsven et al. 2014, Longcore et al. 2015, Longcore et al. 2018).

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 animals and birds, matching spectral outputs of lamps with sensitivities of turkey, duck, chicken, cat, rat, mouse, and human vision (Saunders et al. 2008). This general approach was taken by van Grunsven et al. (2014) to investigate insects, for which they located two insect attraction curves (Cleve 1964, Menzel and Greggers 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. Then, 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 a both Cleve and Menzel and Greggers 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 in the paper. It was further tested in a field study of insects in the Peruvian Amazon Basin, where the 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 (Seymoure 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 and Lewis 2021). 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.

The purpose of the research described in this report is to locate, digitize, and synthesize spectral response curves for terrestrial wildlife to complement those few already commonly used. 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 on the visual sensitivity of species most closely related to sensitive species for which environmental review is required while analyzing construction 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 a parallel compilation of peak sensitivities of photopigments. Finally, the species most commonly the subject of consultations for CalTrans projects are discussed with reference to the spectral response curves that most likely apply to them, as inferred from taxonomic similarity.

Background

Photopigments

Opsin 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 thousands of documented opsins, which fall into eight classes, including melanopsin, which is involved in determining circadian rhythms and pupillary reflex (Terakita and Nagata 2014). The opsins within taxonomic groups tend to be quite well conserved, leading to the ability to generalize about visual systems among related organisms (Saunders et al. 2008, Shichida and 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) 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. 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, Stavenga et al. 1993, Govardovskii et al. 2000). 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 vision 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. For example, a generalized insect spectral response curve was fit using field data along with the peak sensitivities of the most common insect photoreceptors (Donners et al. 2018). Without such data to fit a model combining individual opsin sensitivities and structural filters, the peak wavelengths of the photopigments alone can reveal the general spectral sensitivity of different organisms, for example whether they have ultraviolet vision, and it is for this purpose they are discussed 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, or the strength of the response to a constant quantal flux by wavelength) 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.

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 (Remy and Emmerton 1989, Maier 1992). 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 a number of 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.

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 which have been dissected from the animal and continue to produce electrical signals for a limited period. 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 small voltage produced first declines, followed by an increase. 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 electrical impulses emanating from the eye, which do not necessarily correlate with specific behavioral responses in the real world. For example, ERGs show that nesting sea turtles perceive 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 and 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 and Stavenga 1979, Bernard et al. 1984). 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 and Franceschini 1969). The optical approach has been applied to Diptera, Hymenoptera, Orthoptera, and other invertebrate orders.

There are two additional ways to determine visual sensitivity: microspectrophotemetric measurements (MSP) and intracellular 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.

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 an available review of the spectral sensitivity of wildlife (Davies et al. 2013). Papers referenced in this compendium 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.

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 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 (Ruchty et al. 2010, Longcore et al. 2015). Data were then imported into JMP Statistical Discovery Software 16 (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 paper or a 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 value measured. Curves were then added to a database with species names, taxonomy, curve type (behavioral, ERG, optical), and adaptation state (dark or light). 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 and added to the dataset.

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.

Finally, a database of environmental assessment consultations with U.S. Fish and Wildlife Service or California Department of Fish and Game was obtained from Caltrans staff. Data were compiled and a list of species subject to the most consultations was developed.

Results

Visual Pigments

We located measurements of peak sensitivity for 932 photopigments for 320 distinct entities with terrestrial habitats. 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). 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), 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 sensitivity to the longest wavelengths (Figure 9). 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 included species with known use of color vision at night, including bats (foraging), moths (pollination, nectaring), and fireflies (mating) (Figure 10). Overall, the photopigments of species with daytime activity have an average sensitivity of 478 nm compared with 473 nm for species with no daytime activity, but this difference is not statistically significant.

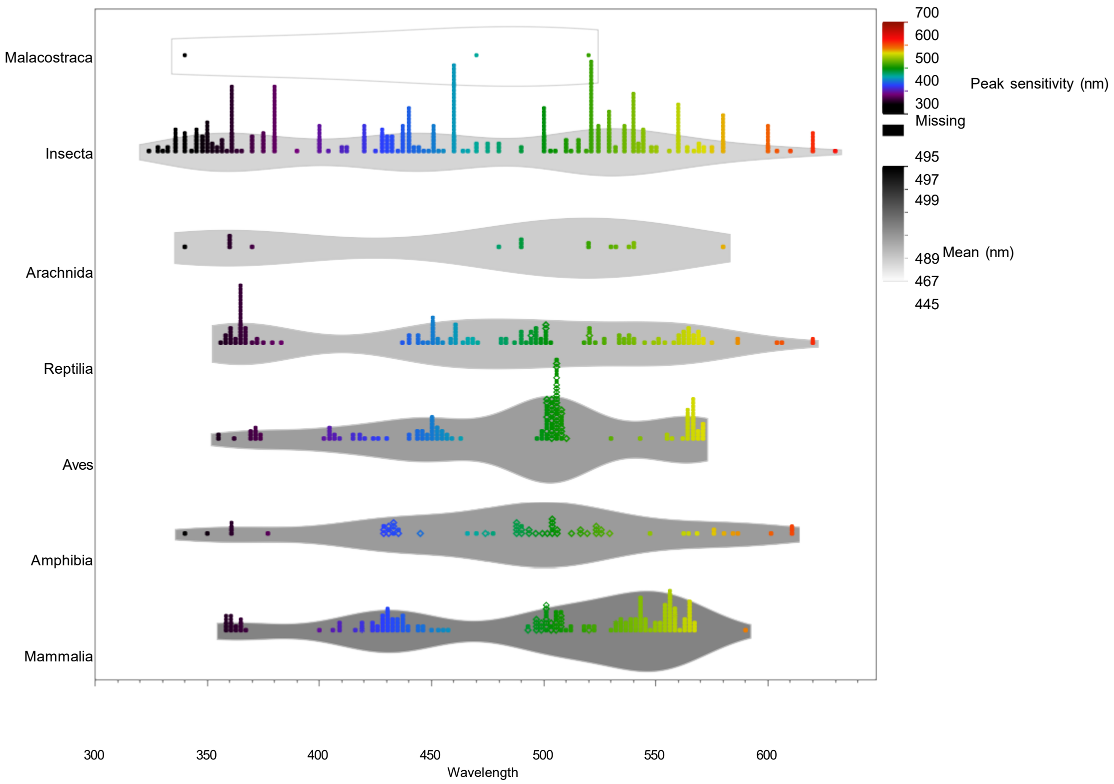

Figure 9. Peak sensitivity of visual photopigments by class of terrestrial wildlife.

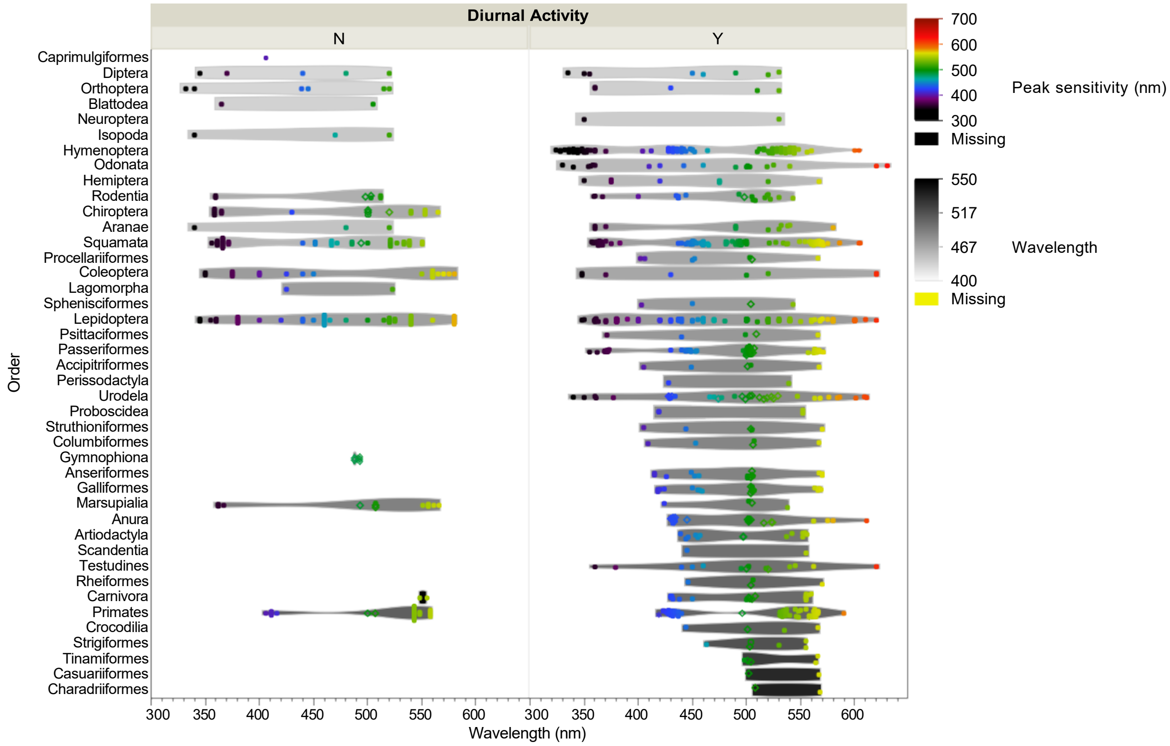

Figure 10. Peak sensitivity of visual photopigments of terrestrial wildlife and presence of diurnal activity. Orders are sorted from top to bottom by the average wavelength of peak

sensitivity of all pigments recorded for the group. Gray background reflects density of opsins by wavelength and is colored by average peak sensitivity in each group.

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 groups included in the dataset lacked ultraviolet sensitivity.

Spectral Response Curves

Spectral response data from 174 cases derived from either behavioral assays, ERGs, or reflectance were compiled, digitized, and fit with curves. 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). In some instances, both photopic and scotopic curves were available, and both were used, 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%) (Figure 11). 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%; 134/158), 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 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% (Figure 12). 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.

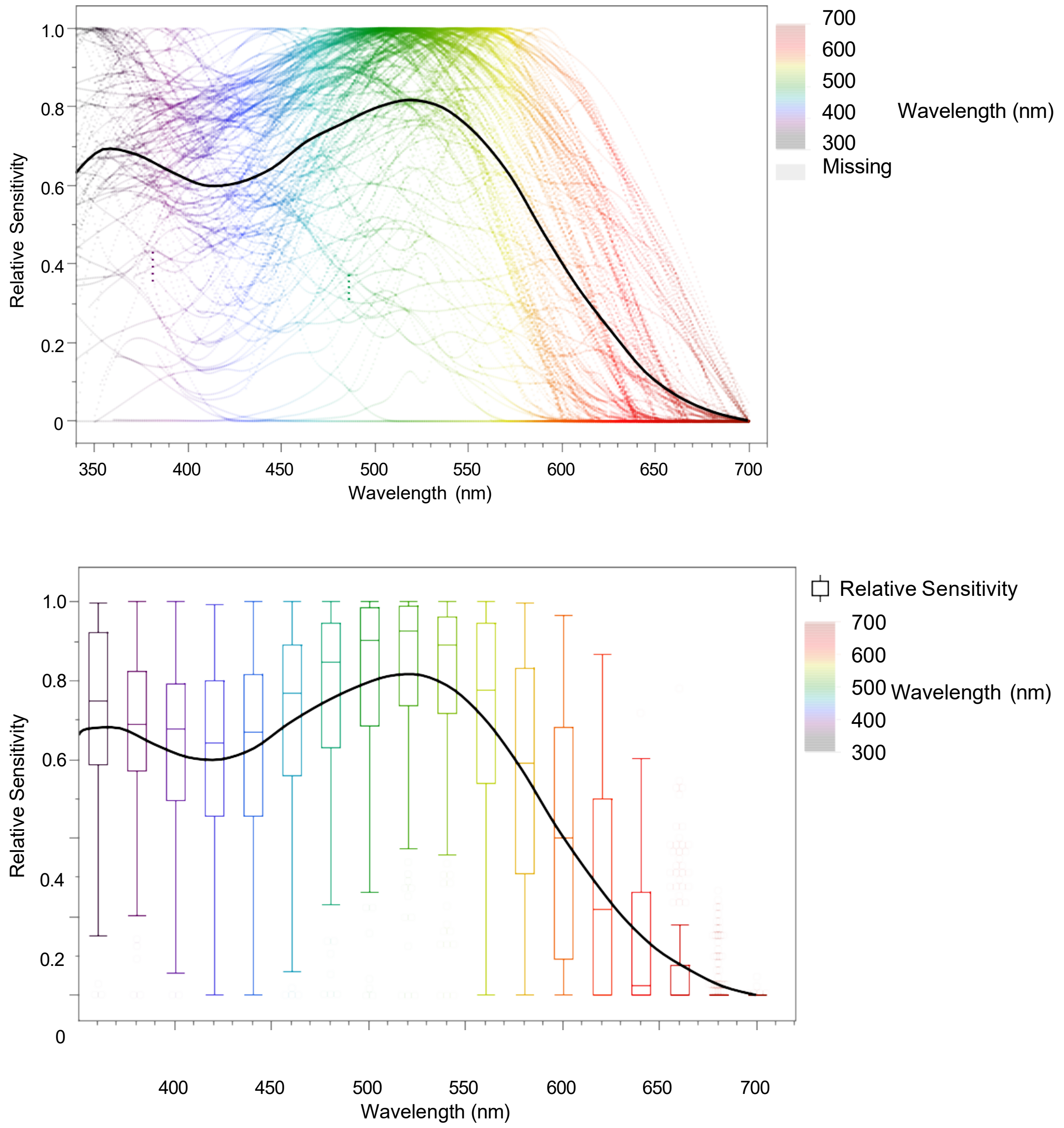

Figure 11. Top) Spectral sensitivity curves (n=158) complied from 81 families, fit with a cubic spline. Bottom) Box plots showing distribution of Spectral sensitivities at 20 nm increments.

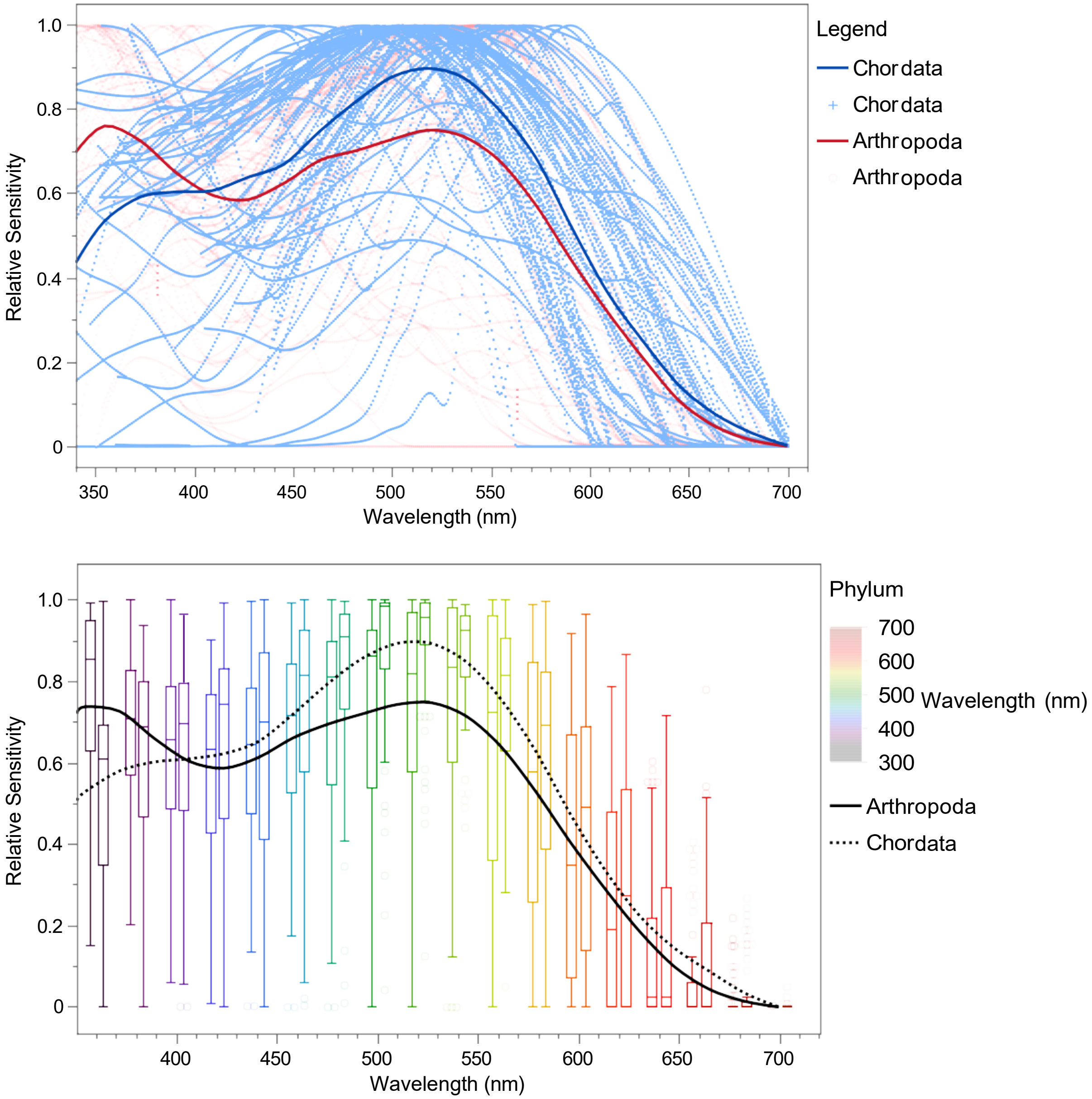

Figure 12. Top) Comparison of spectral sensitivity of chordate (n=71) and arthropod (n=87) species curves. Bottom) Box plot comparisons of spectral sensitivity at 20 nm increments. Both graphs are fit with cubic splines.

Visualization of the response curves at the class level makes apparent both the number of curves available to make inferences, and the degree of variation within these large taxonomic groups (Figure 13A). At this level, the two human visual response curves (photopic and scotopic) are graphed separately for comparison. 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 (Figure 13B). Box plots of sensitivities at 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.

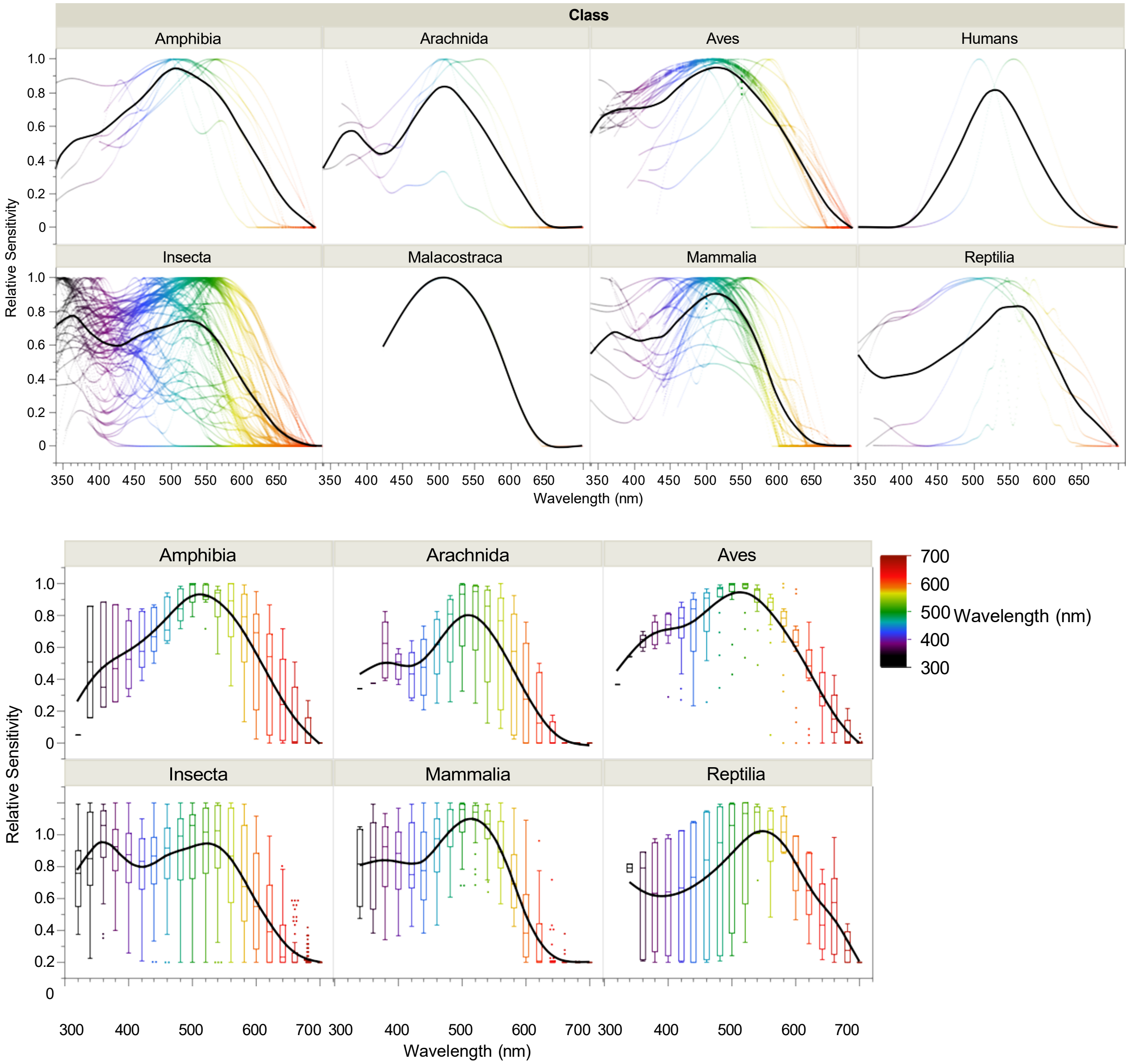

Figure 13. Top) Spectral sensitivity curves by class, fit with cubic splines. Bottom) Box plot comparisons of spectral sensitivity at 20 nm increments for selected classes, with cubic spline.

Moving to summaries by class, there are many classes for which only one or two curves are available, while many were found for others (Figure 14; Coleoptera, Diptera, Lepidoptera, Rodentia). Those insect classes consistently sensitive to violet and ultraviolet light are evident, including Battodea, 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 has a narrow peak around 490 nm. The limited curves for lizards and snakes (n=3) show significant variation, but little sensitivity in the blue or violet.

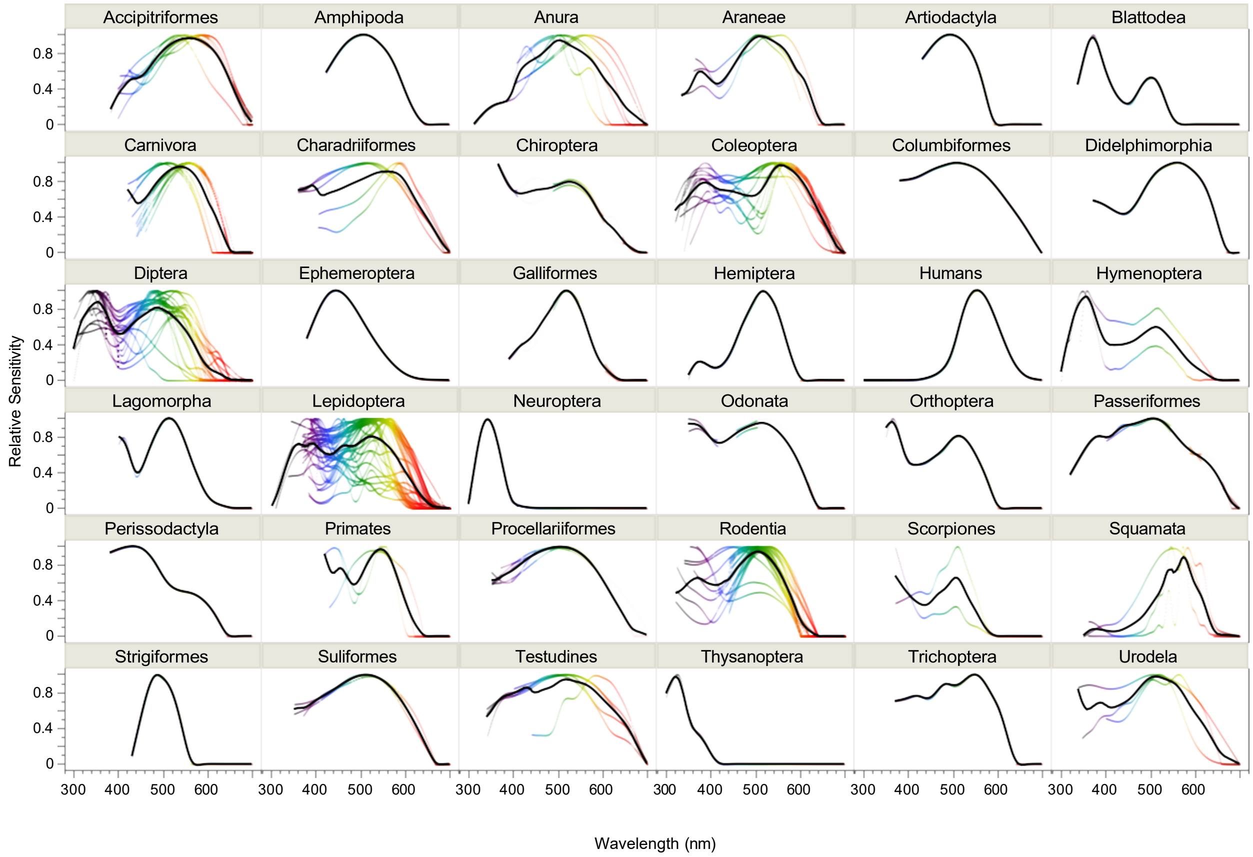

Figure 14. Spectral sensitivity curves by order, with cubic splines.

Finally, to illustrate the differences between human vision and that of different classes of wildlife, we plotted human scotopic and photopic vision with the aggregate curves by class (Figure 15). Human photopic vision is more sensitive to longer wavelengths of light than the mean values for other classes. Human scotopic vision has a peak like 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 (>3 lux), or in the realm of mesopic vision with both systems contributing between ~0.003 lux and 3 lux.

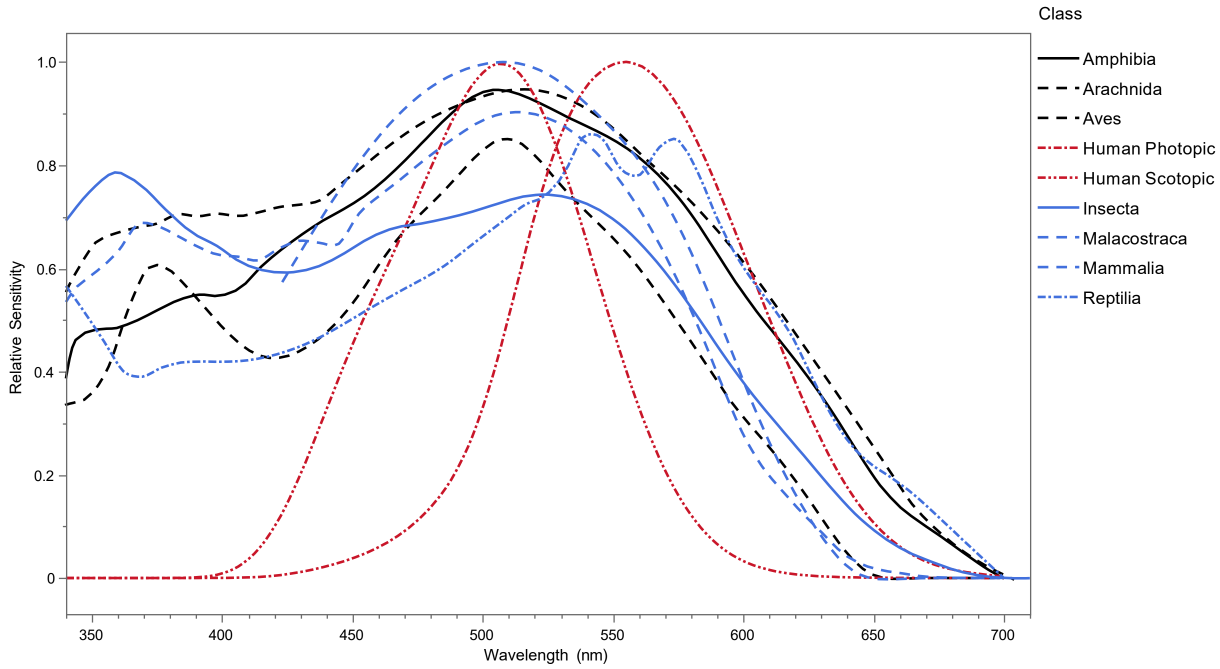

Figure 15. Spectral sensitivity of human photopic and scotopic vision, with aggregate sensitivity for other classes of terrestrial species.

Focal Species

CalTrans provided a list of species for which consultations were undertaken in the environmental review process for transportation infrastructure (Table 2). Based on this list, the light pollution risks to each species or groups of species are reviewed, along with the known visual sensitivity of the species or closely related taxa.

Two species were added to the list to review at the request of the scientific panel for the project, two kangaroo rat species, for which there is concern about lighting impacts and potential future need for consultation.

California Tiger Salamander

California tiger salamander (*Ambystoma californiense*) is largely nocturnal and, like other salamander species, is susceptible to a range of impacts from exposure to light at night (Wise and Buchanan 2006, Wise 2007, Perry et al. 2008). These include alterations to foraging time arising from photophobia, potential effects on development, misorientation under different light conditions, and a range of physiological responses. Phototaxis is also documented (Liebgold and Carleton 2020). Salamanders and newts also have extraocular photoreceptors, which contribute to their magnetic orientation, which can be disrupted by the wavelength and intensity of light present (Phillips et al. 2001).

Table 2. Species of interest to Caltrans relative to environmental assessments, ranked by number of recent consultations with U.S. Fish and Wildlife Service and California Department of Fish and Game.

Name	**Binomial**	**Number of Caltrans-Agency Consultations**
California tiger salamander	*Ambystoma californiense*	30
desert tortoise	*Gopherus agassizii*	14
Mohave ground squirrel	*Xerospermophilus mohavensis*	10
Alameda striped racer (whipsnake)	*Masticophis lateralis*	8
giant garter snake	*Thamnophis gigas*	7
Swainson's hawk	*Buteo swainsoni*	4
foothill yellow-legged frog	*Rana boylii*	2
San Joaquin (=Nelson's) antelope squirrel	*Ammospermophilus nelsoni*	2
San Joaquin kit fox	*Vulpes macrotis*	2
southern rubber boa	*Charina umbratica*	2
Stephen's kangaroo rat	*Dipodomys stephensi*	0
San Bernardino kangaroo rat	*Dipodomys merriami parvus*	0

Information about the photoreceptors for *A. tigrinum*, the eastern tiger salamander, is available (Figure 16). Though spectral sensitivity shifts somewhat from hatching to aquatic to terrestrial stages , the species has sensitivity across the spectrum from the ultraviolet (361 nm peak sensitivity) to long wavelengths (586 nm peak sensitivity) (Perry and McNaughton 1991, Isayama et al. 2014). Two rods, with sensitivity in the blue (428 nm) and green (516 nm) are found, which should dominate sensitivity at low light levels.

Although response curves for each of the cones is available, the only composite curve for *Ambystoma tigrinum* was for its rods (Figure 17). Then two photopic response curves are available for other salamander species.

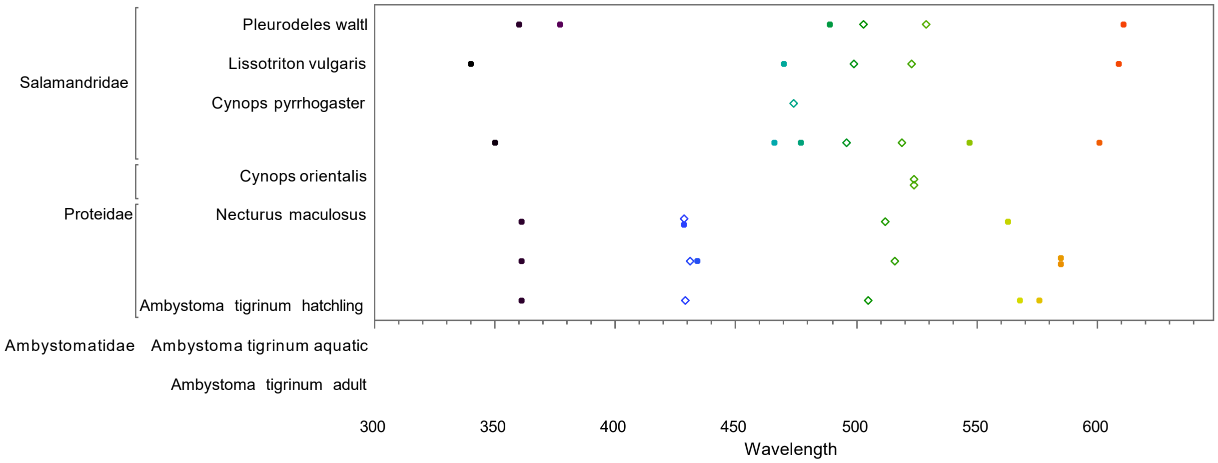

Figure 16. Photopigments for salamander species by family. Cones are closed circles and rods are indicated by open diamonds. Results are not exhaustive.

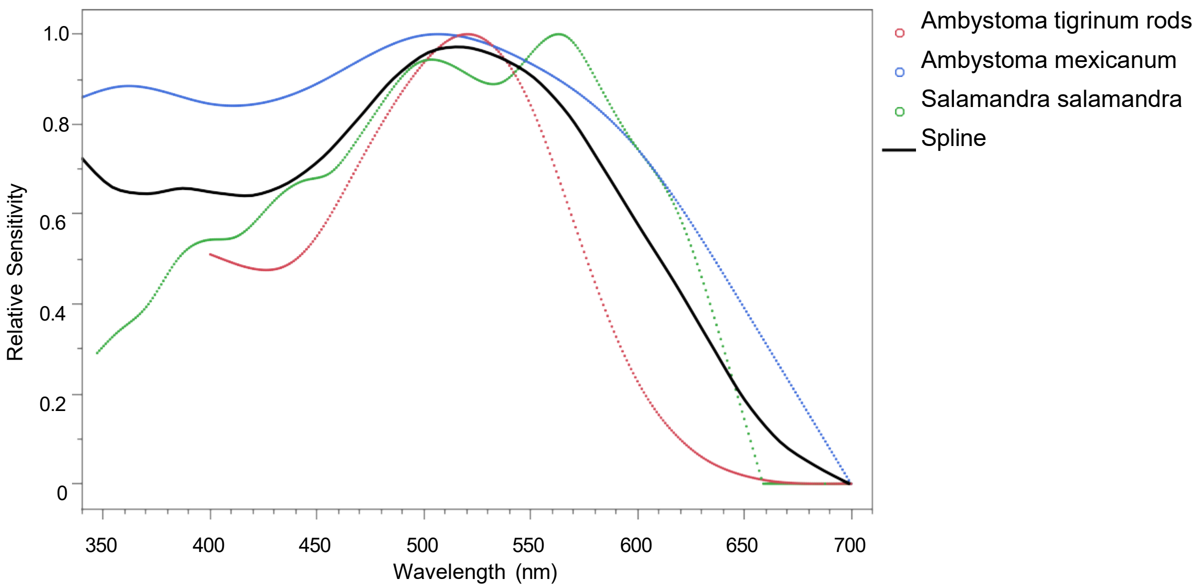

Figure 17. Spectral response curves for salamander species: rods-only scotopic response for *Ambystoma tigrinum* and photopic responses for *Ambystoma mexicanum* and *Salmandra salamandra*.

Taken together, the photopigment peak sensitivities and spectral response curves indicate conservation of the visual system within the salamanders generally, and suggest that during dark conditions, all species will be more sensitive to shorter wavelengths than longer wavelengths, but during brighter conditions spectral sensitivity will be broad. Mitigation approaches should consider that longer wavelengths of light are visible and may induce behavior change. In an experiment with dim glow-sticks, the most tiger salamanders were attracted to the color orange over green, yellow, pink, and blue, even though the green and yellow would have appeared brighter to the species (Liebgold and Carleton 2020).

Desert Tortoise

Direct information on the visual system of desert tortoise was not found. Visual systems of all turtles are presumed to be largely similar, however, and consist of a rod in the 500–520 nm range, and red, green, blue, and ultraviolet cones (Figure 18) (Katti et al. 2019). The long-wave cones of the sea turtles are, however, sensitive to shorter wavelengths than those of the other groups. This is a visual system with sensitivity across the whole spectrum of human vision and beyond. Sensitivity to yellow and red are characteristic of diurnal species and almost certainly is present in desert tortoise.

Desert tortoises are almost exclusively diurnal, except perhaps for emergence from burrows at night during rare rainstorms (Luckenbach 1982). An extensive camera trap study found only 23 instances of nocturnal activity of 993 trapping events (2.3%) (Agha et al. 2015). Given these diurnal habits, the documented photopigments of other turtle species (Figure 18), and the spectral response curves of other turtle species (Figure 19), it can be assumed that G. agassizii has broad-spectrum vision that extends into the ultraviolet. It is unlikely that any potential impacts of light at night could be reduced through spectral means, unless further research identifies behavioral responses similar to the sea turtles (Cheloniidae) in which light that can be seen by the organism (red and yellow for the sea turtles) nevertheless is less disruptive to certain behaviors (Witherington 1992, Witherington and Martin 1996). This conclusion applies to visual responses, but because these turtles likely have menalopsin, pinopsin, vertebrate ancient opsin and neuropsin all contributing to physiological systems, and all of which are sensitive to shorter wavelengths like other vertebrates, the turtles could have less physiologically disruption under longer wavelengths of light, even if their photopic visual system is engaged.

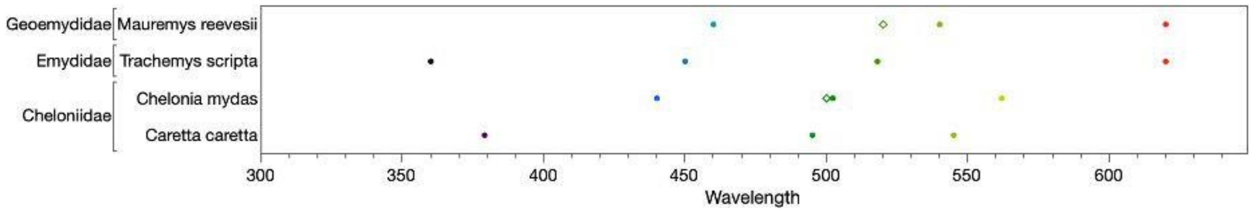

Figure 18. Photoreceptors of turtle species by family. Cones are closed circles and rods are indicated by open diamonds. Results are not exhaustive.

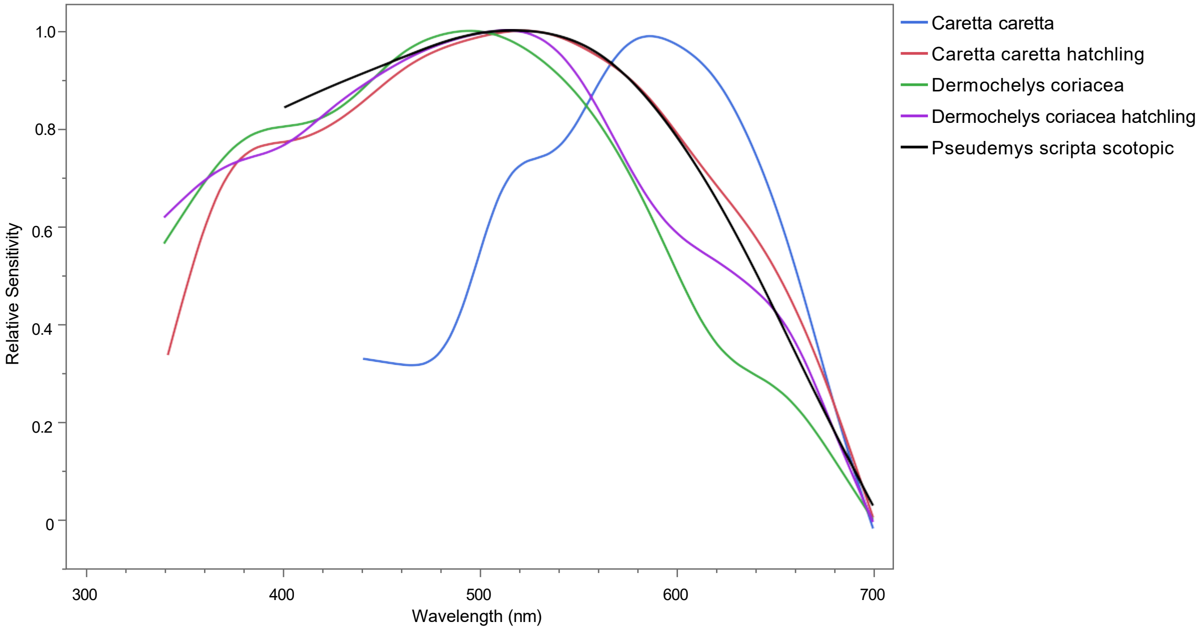

Figure 19. Spectral sensitivity curves for turtle species.

Mohave Ground Squirrel and San Joaquin Antelope Squirrel

Both Mohave Ground Squirrel (*Xerospermophilus mohavensis*) and San Joaquin Antelope Squirrel (*Ammospermophilus nelsoni*) are diurnal species (Kotschwar Logan 2016, Germano et al. 2021) and are not found to be active at night. Photopigments have not been described for them, but other members of the Sciuridae all have a blue cone and a green cone providing dichromatic vision (Figure 20) (Crescitelli and Pollack 1965, 1972). Behavioral studies show that white-tailed antelope squirrels do discern yellow, by using the contrast between the two peak sensitivities, but not red, as a color (Crescitelli and Pollack 1972). Antelope squirrels and presumably Mohave Ground Squirrels have a rod as well (Fisher et al. 1976), which would peak around 500–510 nm.

Spectral response curve for both light- and dark-adapted white-tailed antelope squirrels (*Ammospermophilus leucurus*) have been obtained through ERG. The most closely related genera to these two species are *Callospermophilus* and *Otospermophilus* (Helgen et al. 2009), for which spectral response curves at low light are available as well (Figure 21).

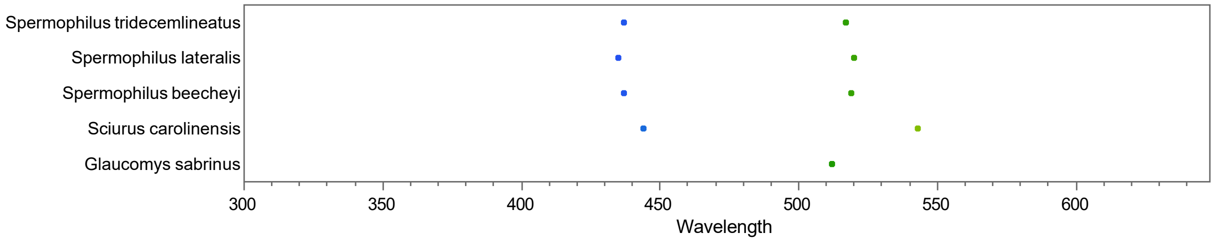

Figure 20. Photopigments of squirrel (Sciuridae) species.

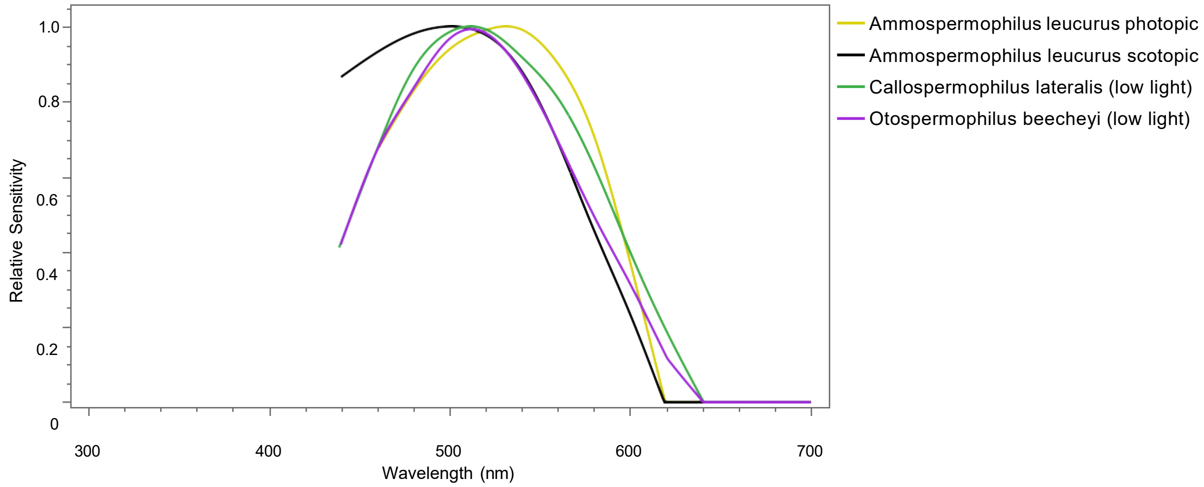

Figure 21. Visual response curves for squirrels in the genera *Ammospermophilus*, *Callospermophilus*, and *Otospermophilus*. For the latter two, individuals were adapted to 0.2 lux (approximately a full moon's illumination) before testing.

For both *A. nelsoni* and *X. mohavensis*, effects of light at night should be minimal as both are nocturnal species, although it is possible that they might extend activity periods under artificial lights as other species have been known to do. If active at night, their sensitivity will be more toward blue than yellow light and orange and red should be relatively dimmer for them.

Giant Garter Snake and Southern Rubber Boa

Giant garter snake (*Thamnophis gigas*; Colubridae) is predominantly diurnal but can be nocturnal in hot weather. Southern rubber boa (*Charina umbratica*; Boidae) is nocturnal and crepuscular. Spectral response curves for snakes have been difficult to locate. For the boids, an ultraviolet cone and ~550 long-wavelength cone have been recorded (Figure 22). For the colubrids, three cones ranging from the ultraviolet to near yellow have been documented. Furthermore, boids can see into the infrared through a different, non-pigment system (Goris 2011).

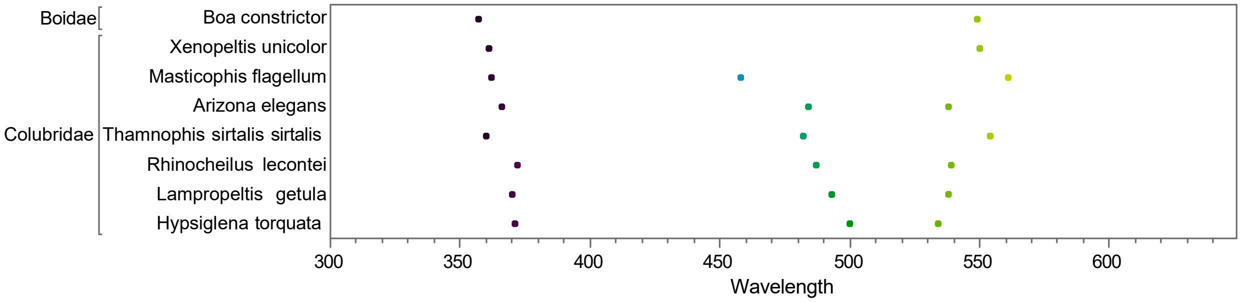

Figure 22. Peak sensitivity of photopigments determined for snake species in the families Boidae and Colubridae. Results are not exhaustive. Rods shown in open diamonds and the remainder are cones.

The vertical pupil of snakes allows high visual sensitivity at night, while producing a more effective means of reducing light input during the day than does a round pupil (Brischoux et al. 2010). Nocturnal species have long wavelength opsins shifted to shorter wavelengths than diurnal species.

From the data available, it is possible that foraging by Rubber Boa is somewhat increased as a result of some increased illumination; some nocturnal snake species show increased activity under the full moon (Lillywhite and Brischoux 2012). Nighttime activity of normally diurnal species is also possible (Perry and Lazell 2000). But decreased activity under increased lighting is also possible, as is seen in lunar cycles for many species (Perry and Fisher 2006, Perry et al. 2008, Weaver 2010). Efforts to mitigate any disruption of natural patterns should focus on reducing the amount of light and even though detailed response curves are not available, the likely visual system has more of a chance of being less sensitive to longer wavelengths than short ones, given the assumed presence of ultraviolet sensitivity.

Swainson's Hawk

Swainson's Hawks (*Buteo swainsoni*) are diurnal, with broad spectral sensitivity arising from four cones and a rod (Figure 23). The only evidence of nocturnal activity is a record of nighttime migration from Costa Rica (Riba-Hern?ndez et al. 2012), which may be widespread in diurnal raptors. Spectral response curves show a Purkinje shift to shorter wavelengths when moving from photopic to scotopic vision, like most species (Figure 24).

Possible effects of roadway lighting on raptors might include extension of hunting period into the night, as observed for Peregrine Falcons hunting migrating passerines (DeCandido and Allen 2006) and Goshawks hunting opportunistically at lights (Rutz 2006). Such behavior, extending foraging activities through dusk and into the night under artificial lights has been documented in a wide range of avian species, including: American Redstart (Bakken and Bakken 1977), Blue Tit (Blackett 1970), Ring-billed Gull (Leck 1971), House Sparrow (Broun 1971, Brooke 1973, Marti 1973), Spotted Flycatcher (King 1967), Pied Wagtail (King and King 1974), Turquoise-browed Motmot (Thurber and Komar 2002), and Northern Mockingbird (Stracey et al. 2014). Another risk of night lighting is the possibility of advancing breeding phenology, which has been shown for passerines (Dominoni et al. 2013).

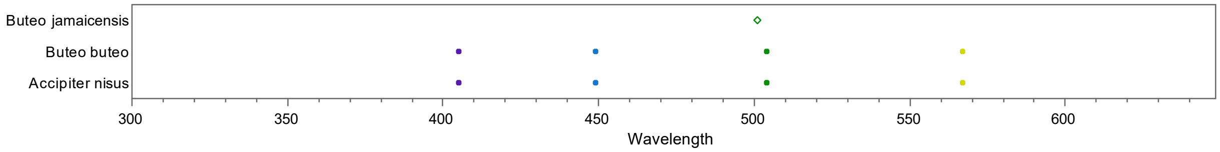

Figure 23. Peak sensitivity of photopigments determined for species in the family Accipitridae. Cones are represented by closed circles; rods are open diamonds. Findings are not exhaustive; Red-tailed Hawk (*Buteo jamaicensis*) also has cones in addition to the rod that has been characterized and the other species have a rod.

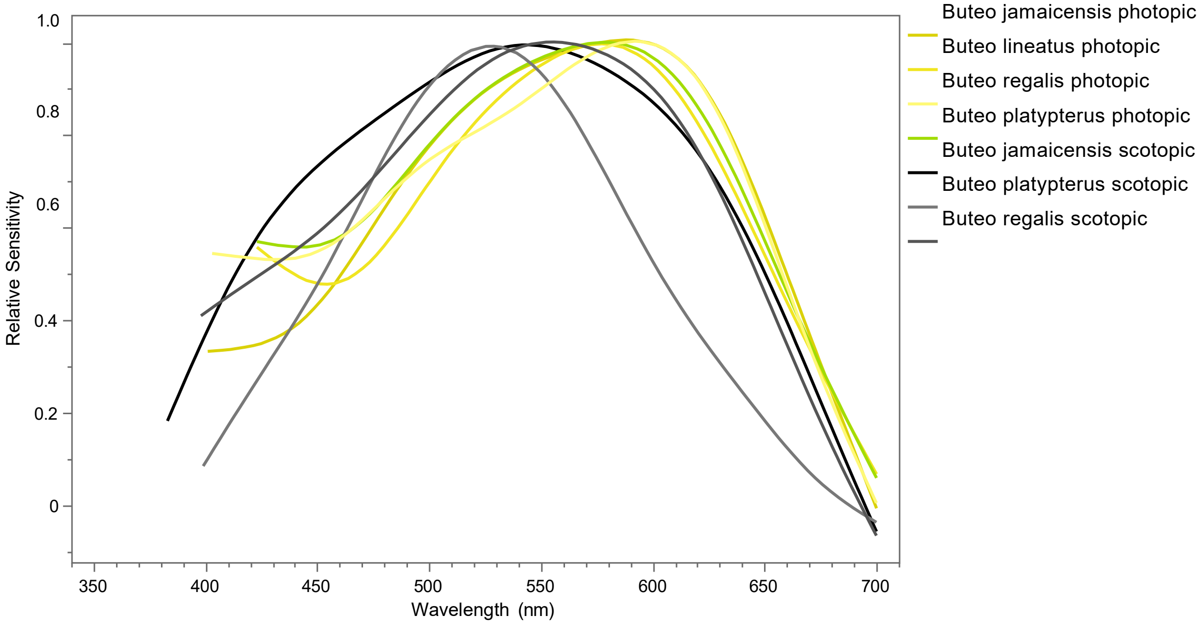

Figure 24. Photopic and scotopic spectral sensitivity curves for *Buteo* species (Krempels 1989).

Foothill Yellow-legged Frog

Rana boylii is a predominantly diurnal frog that can also be active, including calling, at night. It is found in the subgenus Amerana, for which no visual information was found. The closest relative for which visual sensitivity has been measured id *Rana temporaria*, in the subgenus Rana, and *Rana pipiens*, in the subgenus Pantherana. Frog vision is typically dominated by rods, including rods at shorter wavelengths found in other orders, because of the high percentage of nocturnal activity. Rods, being the more sensitive of the forms of cells housing photopigments, therefore dominate. The peak sensitivity of photopigments in *R. temporaria* and *pipiens* are similar, with either rods or cones at 435 nm, 505 nm, and 555–565 nm (Figure 25). For R. pipiens both photopic and scotopic sensitivity curves are available (Figure 26) and show a marked Purkinje shift from a peak near 570 nm during bright conditions to 515 nm during dark conditions. The scotopic response curve for *R. temporaria* has a peak at 500 nm.

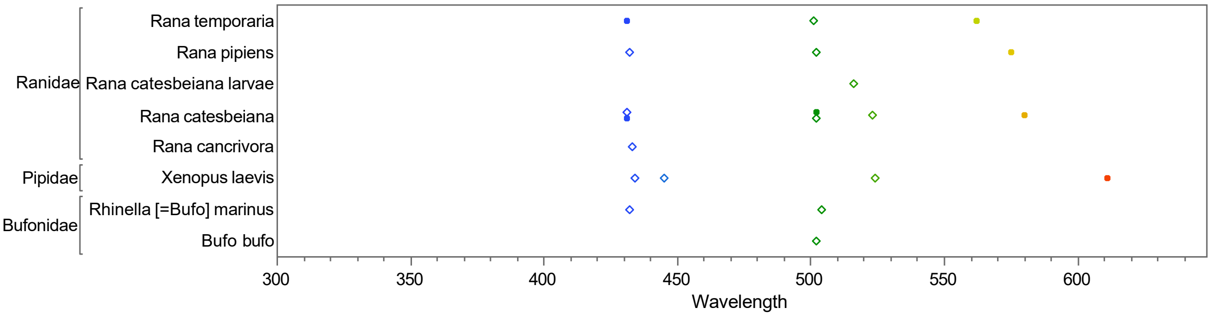

Figure 25. Peak sensitivity for photopigments documented in frogs and toads. Cones are represented by closed circles; rods are open diamonds. Findings are not exhaustive.

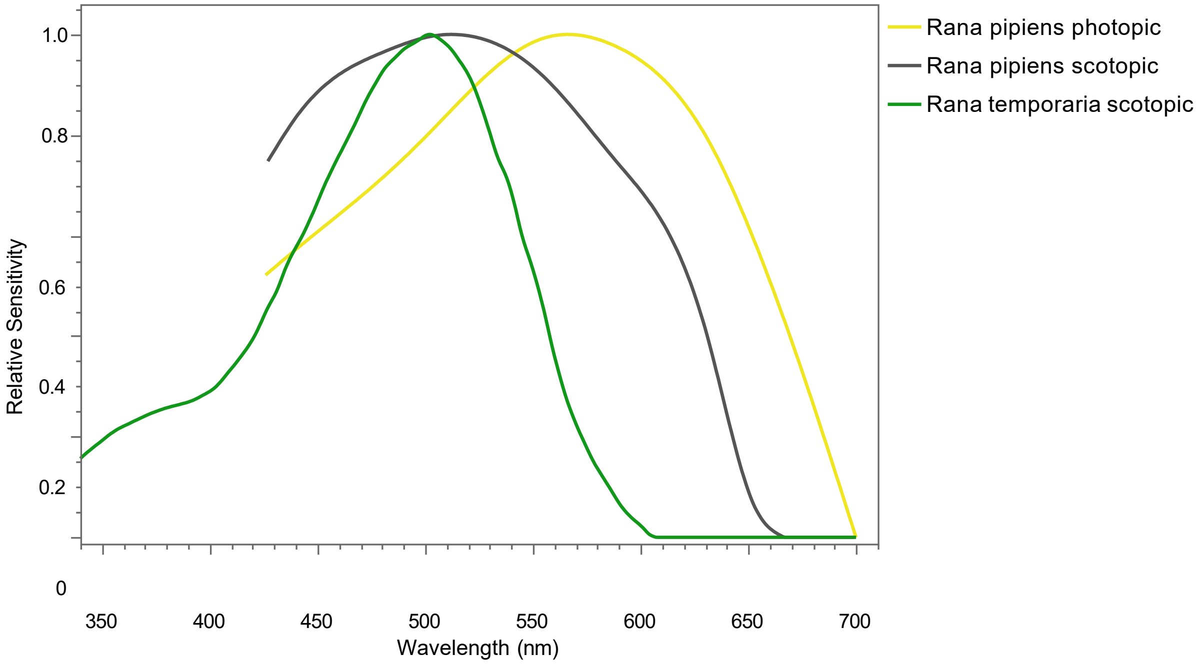

Figure 26. Spectral sensitivity of species in the genus Rana: photopic sensitivity for *Rana pipiens* and scotopic sensitivity for *Rana pipiens* and *Rana temporaria*.

For all the reasons to avoid impacts from artificial light at night on frogs (Buchanan 1993, Baker and Richardson 2006, Buchanan 2006, Hall 2016, May et al. 2019, Forsburg et al. 2021), strategies to do so could exploit the Purkinje shift by using longer wavelengths so long as intensity reaching habitats is low. Frogs have a long refractory time to recover from bleaching when exposed to bright lights during scotophase, so lights should nevertheless be kept dim, distant, or shielded to avoid this.

San Joaquin Kit Fox

Similar to other kit foxes, peak activity of San Joaquin kit fox (*Vulpes macrotis mutica*) is crepuscular and nighttime, but the species can also be active during daylight conditions (Kavanau and Ramos 1975). Like other canids, it will have a rod around 510 nm, a cone at 430–440 nm and a cone at 555 nm (Figure 27). Spectral response curves under photopic conditions for canids show the peak around 555 nm, while scotopic vision has peak sensitivity associated with the 510 nm cone (Figure 28).

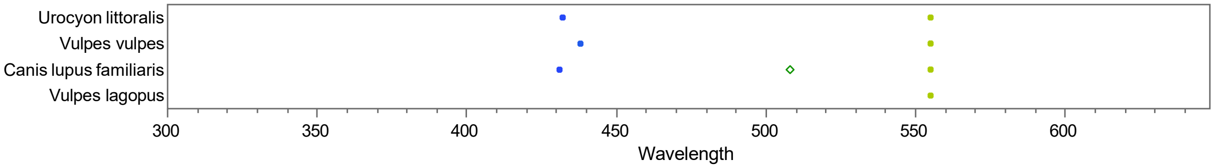

Figure 27. Peak sensitivity of photopigments of canids. Cones are closed circles; rods are open diamonds. Note that findings are not exhaustive; each fox species likely also has the rod at 508 nm and *Vulpes lagopus* would have a short wavelength cone around 400–435 nm (Jacobs et al. 1993b).

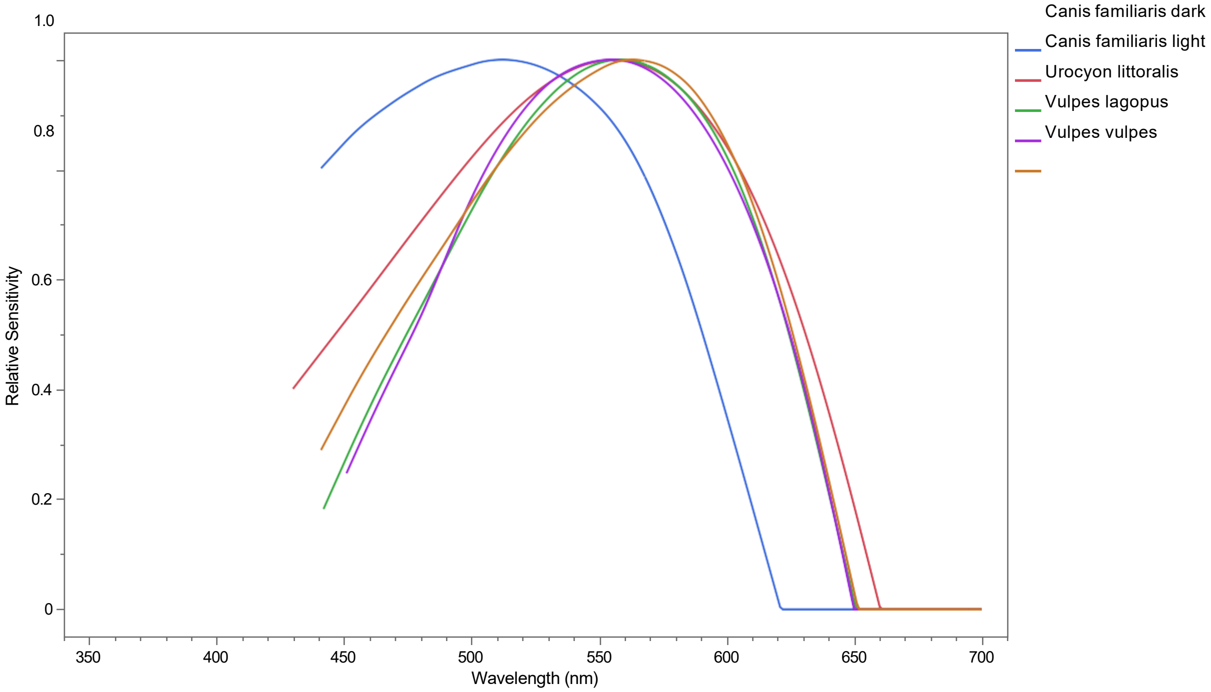

Figure 28. Spectral sensitivity curves determined by electroretinography on live animals in light-adapted conditions for island fox (*Urocyon littoralis*), red fox (*Vulpes vulpes*), Arctic

fox (*Vulpes lagopus*), and domestic dog (*Canis familiaris*), and in dark-adapted conditions for domestic dog.

Avoidance of peak scotopic sensitivity for canids would likely involve using longer wavelengths that provide light above the photopic peak of humans (555 nm). If canids are exposed to higher lighting levels, however, their photopic vision has the same peak sensitivity as humans and they can and will use illuminated areas, even preferentially (De Molenaar et al. 2003). In fact, the use of lights intended to reduce fox predation on a piggery resulted in a 12% increase in fox detections and 23% decline in piglet survival (Hall and Fleming 2021). Use of spectrum for mitigation depends on intensity as experienced by the fox to be within the intensity range of its scotopic vision.

Kangaroo Rats

Kangaroo rats (*Dipodomys* spp.) are considered together because no species-specific information is known about their visual systems. Nocturnally foraging rodents tend to have lower activity on full moon lights (Lockard and Owings 1974, Kaufman and Kaufman 1982, Daly et al. 1992, Upham and Hafner 2013, Prugh and Golden 2014) and in areas with artificial illumination (Kotler 1984, Shier et al. 2020).

The heteromyid rodents, including *Dipodomys*, are a sister group to the Geomyidae, which are likely to have the most similar visual system to them, but comparison to other rodent visual systems is also illustrative. Like most of the nocturnal rodents, geomyids retain a UV-sensitive cone, which combines with single cone sensitive at 500–525 nm and a rod around 500 nm as well (Figure 29). This pattern is repeated in the murid rodents, also mostly nocturnal, and the octodontids, which include both diurnal and nocturnal species. The wholly diurnal groups such as Sciuridae have a blue cone instead of the ultraviolet cone.

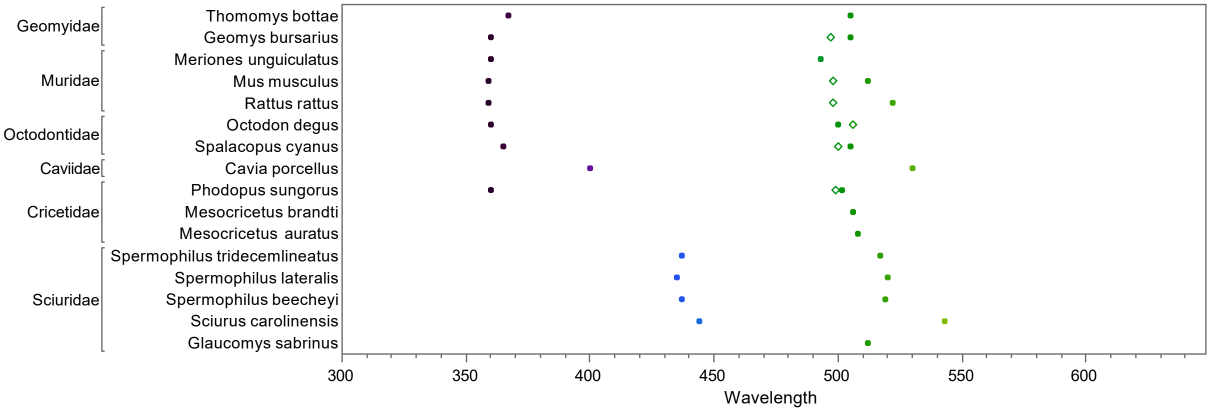

Figure 29. Peak photopigment sensitivity for rodent species by family. Cones are represented by closed circles; rods are open diamonds. Results are not exhaustive.

For spectral response curves, the closest example is for *Thomomys bottae*, Botta's pocket gopher (Figure 30). It shows the greatest sensitivity at short wavelengths (<400 nm), has a peak at 500 nm as would be expected from its second cone pigment, and decreasing sensitivity through the yellow and the orange.

Some field work on *Dipodomys* leaves open the possibility that spectral tuning may contribute to decreased impacts. Shier et al. (2020) set out foraging stations along a transect away from a 6000K LED floodlight, a yellow CFL "bug light," and a control of either moonlight or the new moon. During new moon conditions both the floodlight and bug light reduced foraging by *Didpodomys*, with a greater effect of the floodlight, but the yellow CFL was also substantially dimmer than the floodlight and so the independent contribution of intensity and spectrum could not be inferred. The yellow light had half of its emissions between 500 and 600 nm, so that it still affected foraging is consistent with the significant portion of the *Thomomys* response curve being sensitive to these wavelengths (Figure 30). This result is similar to that found previously with beach mice, where yellow "bug lights" affected foraging less than other full spectrum lights, but still more than control conditions (Bird et al. 2004). Nevertheless, the spectral sensitivity skewed toward shorter wavelengths suggests there would be reduced effects of longer-wavelength light on visually mediated activities, especially for light that is orange and red (>575 nm).

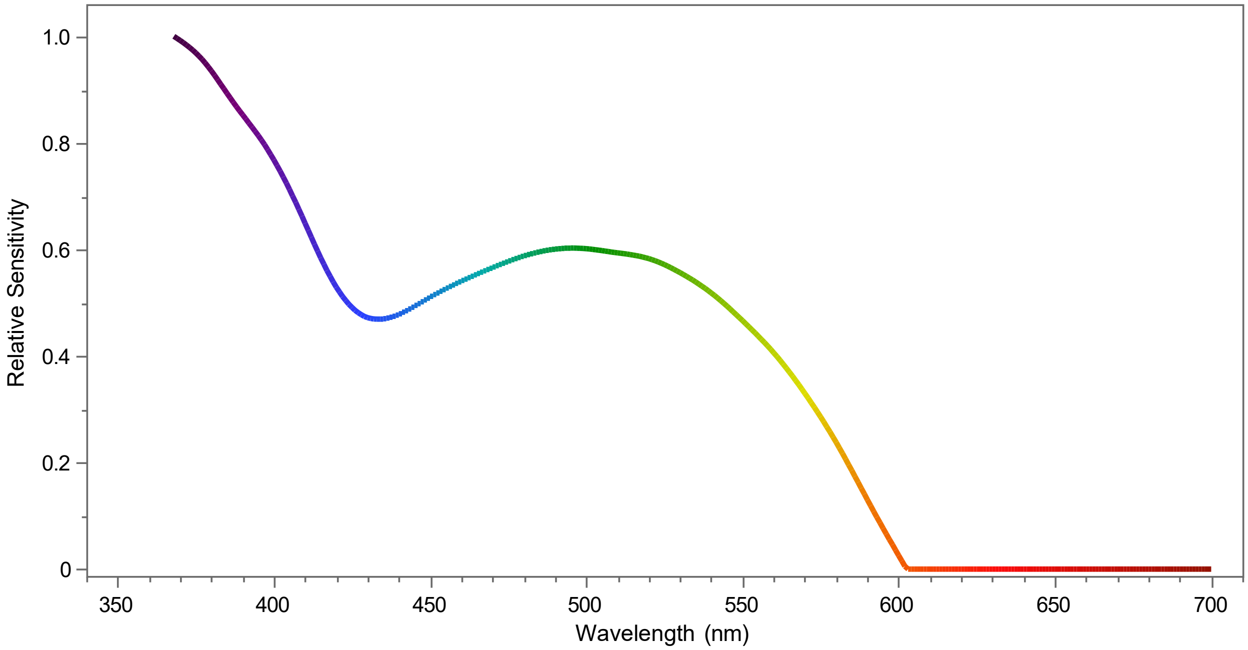

Figure 30. Spectral response curve for *Thomomys bottae*, the closest relative to species in the Heteromyidae for which such information is available.

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 both systems may be implicated when evaluating the potential effects of artificial light at night. The threshold points for conversion from scotopic to photopic vision vary by taxa among the vertebrates so no one threshold can be set to distinguish between the two visual systems when calculation 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 simplistic assumption that species will have a greater response to light that is perceived as being more powerful. 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 it. We do have some studies that show this correlation however (Young et al. 2012). Optical response curves have been correlated with insect phototaxis (Donners et al. 2018) and used to predict outcomes in the field (Deichmann et al. 2021). Firefly mating behavior is suppressed by light at the species' peak sensitivity (Owens and Lewis 2021). There are contradictory studies as well (Pawson and Bader 2014), so more studies 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).

Indeed, more studies confirming behavioral responses 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 glowsticks would have appeared brighter to them (Liebgold and Carleton 2020). Behavioral preferences such as these, associated with a species' ecology may be widespread. The potential of spectral tuning for lighting mitigation is most likely to be realized for impacts where photophobia or 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.

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.

The diversity of visual response systems, despite being evolutionarily conserved, still encompasses large variability. Consequently, there is no "silver bullet" that will provide visual safety for humans while avoiding impacts on other species. Spectral tuning will always be a marginal benefit, to be pursued only when all other mitigation measures have been exhausted, such as controlling light power, restricting operating times, dimming, and controlling light direction (Longcore and 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.

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Appendix A

Index of Species in Peak Photopigment Sensitivity Database

Phylum	Class	Order	Family	Species	References
Arthropoda	Arachnida	Aranae	Araneidae	*Argiope amoena*	(Yamashita and Tateda 1976)
Arthropoda	Arachnida	Aranae	Araneidae	*Argiope bruennichi*	(Yamashita and Tateda 1976)
Arthropoda	Arachnida	Aranae	Ctenidae	*Cupiennius salei*	(Walla et al. 1996)
Arthropoda	Arachnida	Aranae	Salticidae	*Menemerus confusus*	(Yamashita and Tateda 1976)
Arthropoda	Arachnida	Aranae	Salticidae	*Phidippus regius*	(DeVoe 1972)
Arthropoda	Arachnida	Aranae	Salticidae	*Plexippus validus*	(Blest et al. 1981)
Arthropoda	Branchiopoda	Anomopoda	Daphniidae	*Daphnia magna*	(Smith and Macagno 1990)
Arthropoda	Insecta	Blattodea	Blattidae	*Periplaneta americana*	(Mote and Goldsmith 1970, Paul et al. 1986)
Arthropoda	Insecta	Coleoptera	Carabidae	*Carabus auratus*	(Hasselmann 1962)
Arthropoda	Insecta	Coleoptera	Carabidae	*Carabus nemoralis*	(Hasselmann 1962)
Arthropoda	Insecta	Coleoptera	Coccinellidae	*Coccinella septempunctata*	(Lin and Wu 1992)
Arthropoda	Insecta	Coleoptera	Lampyridae	*Bicellonycha wickershamorum*	(Lall et al. 1988)
Arthropoda	Insecta	Coleoptera	Lampyridae	*Photinus collustrans*	(Lall et al. 1988)
Arthropoda	Insecta	Coleoptera	Lampyridae	*Photinus macdermotti*	(Lall et al. 1988)
Arthropoda	Insecta	Coleoptera	Lampyridae	*Photinus marginellus*	(Lall et al. 1988)
Arthropoda	Insecta	Coleoptera	Lampyridae	*Photinus pyralis*	(Lall et al. 1988)
Arthropoda	Insecta	Coleoptera	Lampyridae	*Photinus scintillans*	(Lall et al. 1988)
Arthropoda	Insecta	Coleoptera	Lampyridae	*Photuris frontalis*	(Lall et al. 1988)
Arthropoda	Insecta	Coleoptera	Lampyridae	*Photuris lucicrescens*	(Lall et al. 1988)
Arthropoda	Insecta	Coleoptera	Lampyridae	*Photuris potomaca*	(Lall et al. 1988)
Arthropoda	Insecta	Diptera	Drosophilidae	*Drosophila melanogaster*	(Bernard and Stavenga 1979)
Arthropoda	Insecta	Diptera	Muscidae	*Musca domestica*	(Hardie 1985)
Arthropoda	Insecta	Diptera	Syrphidae	*Eristalis tenax*	(Horridge et al. 1975)
Arthropoda	Insecta	Hemiptera	Notonectidae	*Notonecta glauca*	(Bruckmoser 1968, Bennett and Ruck 1970)
Arthropoda	Insecta	Hemiptera	Notonectidae	*Notonecta insulata*	(Bennett and Ruck 1970)
Arthropoda	Insecta	Hemiptera	Notonectidae	*Notonecta irrorata*	(Bennett and Ruck 1970)
Arthropoda	Insecta	Hemiptera	Notonectidae	*Notonecta undulata*	(Bennett and Ruck 1970)
Arthropoda	Insecta	Hymenoptera	Adrenidae	*Andrena florea*	(Peitsch et al. 1992)
Arthropoda	Insecta	Hymenoptera	Adrenidae	*Anthophora acervorum*	(Peitsch et al. 1992)
Arthropoda	Insecta	Hymenoptera	Adrenidae	*Callonychium petuniae*	(Peitsch et al. 1992)

Arthropoda	Insecta	Hymenoptera	Adrenidae	*Oxea flavescens*	(Peitsch et al. 1992)
Arthropoda	Insecta	Hymenoptera	Apidae	*Apis mellifera*	(Peitsch et al. 1992)
Arthropoda	Insecta	Hymenoptera	Apidae	*Bombus distinguendis*	(Vishnevskaya and Mazokhin-Porshnyakov 1972)

Arthropoda	Insecta	Hymenoptera	Apidae	*Bombus fervidus*	(Bernard and Stavenga 1978)
Arthropoda	Insecta	Hymenoptera	Apidae	*Bombus hortorum*	(Meyer-Rochow 1980)
Arthropoda	Insecta	Hymenoptera	Apidae	*Bombus hypnorum*	(Peitsch et al. 1992)
Arthropoda	Insecta	Hymenoptera	Apidae	*Bombus impatiens*	(Bernard and Stavenga 1978)
Arthropoda	Insecta	Hymenoptera	Apidae	*Bombus jonellus*	(Peitsch et al. 1992)
Arthropoda	Insecta	Hymenoptera	Apidae	*Bombus lapidarius*	(Peitsch et al. 1992)
Arthropoda	Insecta	Hymenoptera	Apidae	*Bombus monticola*	(Peitsch et al. 1992)
Arthropoda	Insecta	Hymenoptera	Apidae	*Bombus morio*	(Peitsch et al. 1992)
Arthropoda	Insecta	Hymenoptera	Apidae	*Bombus terrestris*	(Peitsch et al. 1992)
Arthropoda	Insecta	Hymenoptera	Apidae	*Collectes fulgidus*	(Peitsch et al. 1992)
Arthropoda	Insecta	Hymenoptera	Apidae	*Lestrimelitta limao*	(Peitsch et al. 1992)
Arthropoda	Insecta	Hymenoptera	Apidae	*Melecta punctata*	(Peitsch et al. 1992)
Arthropoda	Insecta	Hymenoptera	Apidae	*Melipona marginata*	(Peitsch et al. 1992)
Arthropoda	Insecta	Hymenoptera	Apidae	*Melipona quadrifasciata*	(Peitsch et al. 1992)
Arthropoda	Insecta	Hymenoptera	Apidae	*Nomada alboguttata*	(Peitsch et al. 1992)
Arthropoda	Insecta	Hymenoptera	Apidae	*Partamona helleri*	(Chittka et al. 1997)
Arthropoda	Insecta	Hymenoptera	Apidae	*Schwarziana sp*	(Peitsch et al. 1992)
Arthropoda	Insecta	Hymenoptera	Apidae	*Trigona spinipes*	(Peitsch et al. 1992)
Arthropoda	Insecta	Hymenoptera	Apidae	*Xylocopa brasilianorum*	(Peitsch et al. 1992)
Arthropoda	Insecta	Hymenoptera	Colletidae	*Formica polyctena*	(Menzel and Knaut 1973)
Arthropoda	Insecta	Hymenoptera	Crabronidae	*Cataglyphis bicolor*	(Paul et al. 1986)
Arthropoda	Insecta	Hymenoptera	Crabronidae	*Philanthus triangulum*	(Peitsch et al. 1992)
Arthropoda	Insecta	Hymenoptera	Formicidae	*Anthidium manicatum*	(Peitsch et al. 1992)
Arthropoda	Insecta	Hymenoptera	Formicidae	*Myrmecia gulosa*	(Lieke 1981)
Arthropoda	Insecta	Hymenoptera	Halictidae	*Lasioglossum albipes*	(Peitsch et al. 1992)
Arthropoda	Insecta	Hymenoptera	Halictidae	*Lasioglossum malachurum*	(Peitsch et al. 1992)
Arthropoda	Insecta	Hymenoptera	Ichneumoidae	*Ichneumon spp.*	(Peitsch et al. 1992)
Arthropoda	Insecta	Hymenoptera	Ichneumoidae	*Ichneumon stramentarius*	(Peitsch et al. 1992)
Arthropoda	Insecta	Hymenoptera	Megachilidae	*Chelostoma florisomne*	(Peitsch et al. 1992)
Arthropoda	Insecta	Hymenoptera	Megachilidae	*Osmia rufa*	(Peitsch et al. 1992)
Arthropoda	Insecta	Hymenoptera	Siricidae	*Urocerus gigas*	(Peitsch et al. 1992)
Arthropoda	Insecta	Hymenoptera	Sphecidae	*Cerceris rybyensis (female)*	(Peitsch et al. 1992)
Arthropoda	Insecta	Hymenoptera	Sphecidae	*Cerceris rybyensis (male)*	(Peitsch et al. 1992)
Arthropoda	Insecta	Hymenoptera	Tenthredinidae	*Tenthredo campestris*	(Peitsch et al. 1992)

Arthropoda	Insecta	Hymenoptera	Tenthredinidae	*Tenthredo scrophulariae*	(Peitsch et al. 1992)
Arthropoda	Insecta	Hymenoptera	Vespidae	*Dolichovespula norwegica*	(Peitsch et al. 1992)
Arthropoda	Insecta	Hymenoptera	Vespidae	*Polistes dominulus*	(Peitsch et al. 1992)
Arthropoda	Insecta	Hymenoptera	Vespidae	*Vespo crabro (female)*	(Peitsch et al. 1992)
Arthropoda	Insecta	Hymenoptera	Vespidae	*Vespo crabro (male)*	(Peitsch et al. 1992)
Arthropoda	Insecta	Hymenoptera	Vespidae	*Vespula germanica*	(Peitsch et al. 1992)

Arthropoda	Insecta	Hymenoptera	Vespidae	*Vespula vulgaris*	(Peitsch et al. 1992)
Arthropoda	Insecta	Hymenoptera	Xiphydriidae	*Xiphydria camelus*	(Peitsch et al. 1992)
Arthropoda	Insecta	Lepidoptera	Epicopeiidae	*Epicopeia hainesii*	(Eguchi et al. 1982)
Arthropoda	Insecta	Lepidoptera	Geometridae	*Arichanna gaschkevitchii*	(Eguchi et al. 1982)
Arthropoda	Insecta	Lepidoptera	Hepialiidae	*Phassus excrescens*	(Eguchi et al. 1982)
Arthropoda	Insecta	Lepidoptera	Hesperiidae	*Ochlodes venata*	(Eguchi et al. 1982)
Arthropoda	Insecta	Lepidoptera	Hesperiidae	*Parnara guttata*	(Eguchi et al. 1982)
Arthropoda	Insecta	Lepidoptera	Lycaenidae	*Celastrina argiolus*	(Eguchi et al. 1982)
Arthropoda	Insecta	Lepidoptera	Lycaenidae	*Lycaena dorcas*	(Bernard and Remington 1991)
Arthropoda	Insecta	Lepidoptera	Lycaenidae	*Lycaena heteronea*	(Bernard and Remington 1991)
Arthropoda	Insecta	Lepidoptera	Lycaenidae	*Lycaena nivalis*	(Bernard and Remington 1991)
Arthropoda	Insecta	Lepidoptera	Lycaenidae	*Lycaena phlaeas*	(Eguchi et al. 1982)
Arthropoda	Insecta	Lepidoptera	Lycaenidae	*Lycaena rubidus*	(Bernard and Remington 1991)
Arthropoda	Insecta	Lepidoptera	Lycaenidae	*Pseudozizeeria maha*	(Eguchi et al. 1982)
Arthropoda	Insecta	Lepidoptera	Noctuidae	*Anadevidia peponis*	(Eguchi et al. 1982)
Arthropoda	Insecta	Lepidoptera	Noctuidae	*Mamestra brassicae*	(Ichikawa and Tateda 1982)
Arthropoda	Insecta	Lepidoptera	Noctuidae	*Spodoptera exempta*	(Langer et al. 1979)
Arthropoda	Insecta	Lepidoptera	Nymphalidae	*Aglais urticae*	(Steiner et al. 1987)
Arthropoda	Insecta	Lepidoptera	Nymphalidae	*Argynnis ruslana*	(Eguchi et al. 1982)
Arthropoda	Insecta	Lepidoptera	Nymphalidae	*Fabriciana adippe*	(Eguchi et al. 1982)
Arthropoda	Insecta	Lepidoptera	Nymphalidae	*Heliconius erato*	(Weller and Pashley 1995)
Arthropoda	Insecta	Lepidoptera	Nymphalidae	*Heliconius numata*	(Struwe 1972b, a)
Arthropoda	Insecta	Lepidoptera	Nymphalidae	*Heliconius sara*	(Struwe 1972b)
Arthropoda	Insecta	Lepidoptera	Nymphalidae	*Minois dryas*	(Eguchi et al. 1982)
Arthropoda	Insecta	Lepidoptera	Nymphalidae	*Neope goschkevitschii*	(Eguchi et al. 1982)
Arthropoda	Insecta	Lepidoptera	Nymphalidae	*Nymphalis xanthomelas*	(Eguchi et al. 1982)
Arthropoda	Insecta	Lepidoptera	Nymphalidae	*Parage aegeria*	(Paul et al. 1986)
Arthropoda	Insecta	Lepidoptera	Nymphalidae	*Polygonia c-album*	(Eguchi et al. 1982)
Arthropoda	Insecta	Lepidoptera	Nymphalidae	*Vanessa cardui*	(Bernard 1979, Briscoe et al. 2003)
Arthropoda	Insecta	Lepidoptera	Papilionidae	*Atrophaneura alcinous*	(Eguchi et al. 1982)
Arthropoda	Insecta	Lepidoptera	Papilionidae	*Graphium sarpedon*	(Eguchi et al. 1982)
Arthropoda	Insecta	Lepidoptera	Papilionidae	*Papilio achaon*	(Eguchi et al. 1982)
Arthropoda	Insecta	Lepidoptera	Papilionidae	*Papilio aegeus*	(Matic 1983)
Arthropoda	Insecta	Lepidoptera	Papilionidae	*Papilio maackii*	(Eguchi et al. 1982)
Arthropoda	Insecta	Lepidoptera	Papilionidae	*Papilio protenor*	(Eguchi et al. 1982)
Arthropoda	Insecta	Lepidoptera	Papilionidae	*Papilio xuthus*	(Eguchi et al. 1982, Arikawa et al. 1987)
Arthropoda	Insecta	Lepidoptera	Papilionidae	*Papilo bianor*	(Eguchi et al. 1982)
Arthropoda	Insecta	Lepidoptera	Pieridae	*Colias erate*	(Eguchi et al. 1982)
Arthropoda	Insecta	Lepidoptera	Pieridae	*Gonepteryx aspasia*	(Eguchi et al. 1982)
Arthropoda	Insecta	Lepidoptera	Pieridae	*Pieris brassicae*	(Paul et al. 1986, Steiner et al. 1987)

Arthropoda	Insecta	Lepidoptera	Pieridae	*Pieris melete*	(Eguchi et al. 1982)
Arthropoda	Insecta	Lepidoptera	Pieridae	*Pieris rapae*	(Wakakuwa et al. 2010)

Arthropoda	Insecta	Lepidoptera	Pyralidae	*Amyelois transitella*	(Eguchi et al. 1982, Bernard et al. 1984)
Arthropoda	Insecta	Lepidoptera	Pyralidae	*Galleria mellonella*	(Goldman et al. 1975)
Arthropoda	Insecta	Lepidoptera	Saturniidae	*Actias artemis aliena*	(Eguchi et al. 1982)
Arthropoda	Insecta	Lepidoptera	Saturniidae	*Antheraea polyphemus*	(Langer et al. 1986)
Arthropoda	Insecta	Lepidoptera	Saturniidae	*Samia cynthia ricini*	(Eguchi et al. 1982)
Arthropoda	Insecta	Lepidoptera	Sphingidae	*Ampelophaga rubiginosa*	(Eguchi et al. 1982)
Arthropoda	Insecta	Lepidoptera	Sphingidae	*Callambulyx tatarinovii*	(Eguchi et al. 1982)
Arthropoda	Insecta	Lepidoptera	Sphingidae	*Deilephila elpenor*	(Hamdorf et al. 1971, Höglund et al. 1973, Schwemer and Paulsen 1973)
Arthropoda	Insecta	Lepidoptera	Sphingidae	*Macroglossum stellatarum*	(Hasselmann 1962)
Arthropoda	Insecta	Lepidoptera	Sphingidae	*Manduca sexta*	(White et al. 1983)
Arthropoda	Insecta	Lepidoptera	Sphingidae	*Marumba sperchius*	(Eguchi et al. 1982)
Arthropoda	Insecta	Neuroptera	Ascalaphidae	*Libelloides macaronius*	(Gogala 1967, Paul et al. 1986)
Arthropoda	Insecta	Odonata	Aeshnidae	*Aeschna cyanea*	(Autrum and Kolb 1968)
Arthropoda	Insecta	Odonata	Aeshnidae	*Aeshna tuberculifera*	(Chappell and DeVoe 1975)
Arthropoda	Insecta	Odonata	Aeshnidae	*Anax junius*	(Chappell and DeVoe 1975)
Arthropoda	Insecta	Odonata	Aeshnidae	*Libellula pulchella*	(Chappell and DeVoe 1975)
Arthropoda	Insecta	Odonata	Corduliidae	*Hemicordulia tau*	(Yang and Osorio 1991)
Arthropoda	Insecta	Odonata	Libellulidae	*Sympetrum rubicundulum*	(Meinertzhagen et al. 1983)
Arthropoda	Insecta	Orthoptera	Acrididae	*Locusta migratoria*	(Vishnevskaya and Shura-Bura 1990)
Arthropoda	Insecta	Orthoptera	Blattidae	*Gryllus bimaculatus adult*	(Zufall et al. 1989)
Arthropoda	Insecta	Orthoptera	Blattidae	*Gryllus campestris*	(Zufall et al. 1989)
Arthropoda	Insecta	Orthoptera	Romaleidae	*Romalea microptera*	(Bruckler and Williams 1981)
Arthropoda	Malacostraca	Isopoda	Ligiidae	*Ligia exotica*	(Hariyama et al. 1993)
Chordata	Amphibia	Anura	Bufonidae	*Bufo bufo*	(Fyhrquist et al. 1998, Ala-Laurila et al. 2002)
Chordata	Amphibia	Anura	Bufonidae	*Rhinella [=Bufo] marinus*	(H?rosi 1975, Matthews 1983, Sillman 1987, Ala-Laurila et al. 2002)
Chordata	Amphibia	Anura	Pipidae	*Xenopus laevis*	(Witkovsky et al. 1981, Darden et al. 2003)
Chordata	Amphibia	Anura	Ranidae	*Rana catesbeiana*	(Crescitelli 1958, Gordon and Hood 1976, Makino-Tasaka and Suzuki 1984,

					Donner et al. 1990)
Chordata	Amphibia	Anura	Ranidae	*Rana catesbeiana larvae*	(Crescitelli 1958, Donner et al. 1990)
Chordata	Amphibia	Anura	Ranidae	*Rana cracrivora*	(Donner and Reuter 1962, Dartnall 1967)

Chordata	Amphibia	Anura	Ranidae	*Rana pipiens*	(Crescitelli 1958, Liebman and Entine 1968)
Chordata	Amphibia	Anura	Ranidae	*Rana temporaria*	(Koskelainen et al. 1994)
Chordata	Amphibia	Gymnophiona	Dermophiidae	*Geotrypetes seraphini*	(Mohun et al. 2010)
Chordata	Amphibia	Gymnophiona	Ichthyophiidae	*Ichthyophis cf. kohtaoensis*	(Mohun et al. 2010)
Chordata	Amphibia	Gymnophiona	Rhinatrematidae	*Rhinatrema bivittatum*	(Mohun et al. 2010)
Chordata	Amphibia	Gymnophiona	Typhlonectidae	*Typhlonectes natans*	(Mohun et al. 2010)
Chordata	Amphibia	Urodela	Ambystomatidae	*Ambystoma tigrinum larvae*	(Perry and McNaughton 1991, Ma et al. 2001, Isayama et al. 2014)
Chordata	Amphibia	Urodela	Ambystomatidae	*Ambystoma tigrinum aquatic*	(H?rosi 1975, Isayama et al. 2014)
Chordata	Amphibia	Urodela	Ambystomatidae	*Ambystoma tigrinum land*	(H?rosi 1975, Isayama et al. 2014)
Chordata	Amphibia	Urodela	Proteidae	*Necturus maculosus*	(Crescitelli 1958, Liebman 1972, H?rosi 1975)
Chordata	Amphibia	Urodela	Salamandridae	*Cynops orientalis*	(Korenyak and Govardovskii 2013)
Chordata	Amphibia	Urodela	Salamandridae	*Cynops pyrrhogaster*	(Takahashi and Ebrey 2003)
Chordata	Amphibia	Urodela	Salamandridae	*Lissotriton vulgaris*	(Korenyak and Govardovskii 2013)
Chordata	Amphibia	Urodela	Salamandridae	*Pleurodeles waltl*	(Korenyak and Govardovskii 2013)
Chordata	Aves	Accipitriformes	Accipitridae	*Buteo jamaicensis*	(Sillman et al. 1981)
Chordata	Aves	Anseriformes	Anatidae	*Anas platyrhynchos*	(Jane and Bowmaker 1988, Hart and Vorobyev 2005)
Chordata	Aves	Caprimulgiformes	Caprimulgidae	*Caprimulgus europaeus*	(Ödeen and Håstad 2003)
Chordata	Aves	Casuariiformes	Casuariidae	*Dromiceius novae-hollandiae*	(Sillman et al. 1981)
Chordata	Aves	Charadriiformes	Laridae	*Larus atricilla*	(Liebman 1972)
Chordata	Aves	Columbiformes	Columbidae	*Columba livia*	(Bowmaker et al. 1997)
Chordata	Aves	Galliformes	Phasianidae	*Coturnix coturnix*	(Bowmaker et al. 1993, Hart and Vorobyev 2005)
Chordata	Aves	Galliformes	Phasianidae	*Gallus gallus*	(Bowmaker et al. 1993, Hart and Vorobyev 2005)
Chordata	Aves	Galliformes	Phasianidae	*Meleagris gallopavo*	(Crescitelli et al. 1964)
Chordata	Aves	Galliformes	Phasianidae	*Pavo cristatus*	(Hart and Vorobyev 2005, Macedonia et al. 2009)
Chordata	Aves	Passeriformes	Corvidae	*Corvus frugilegus*	(Bowmaker 1979)
Chordata	Aves	Passeriformes	Estrildidae	*Amadina fasciata*	(Hart et al. 2000)
Chordata	Aves	Passeriformes	Estrildidae	*Taeniopygia guttata*	(Bowmaker et al. 1997)
Chordata	Aves	Passeriformes	Fringillidae	*Serinus canaria*	(Das et al. 1999, Hart and Vorobyev 2005)

Chordata	Aves	Passeriformes	Leiothrichidae	*Leiothrix lutea*	(Maier and Bowmaker 1993)
Chordata	Aves	Passeriformes	Paridae	*Parus caeruleus*	(Hart et al. 2000, Hart and Vorobyev 2005)
Chordata	Aves	Passeriformes	Passeridae	*Passer domesticus*	(Hart 2001)

Chordata	Aves	Passeriformes	Passeroidea	*Chloebia gouldiae*	(Hart et al. 2000, Hart and Vorobyev 2005)
Chordata	Aves	Passeriformes	Passeroidea	*Lonchura maja*	(Hart et al. 2000, Hart and Vorobyev 2005)
Chordata	Aves	Passeriformes	Passeroidea	*Neochmia modesta*	(Hart et al. 2000, Hart and Vorobyev 2005)
Chordata	Aves	Passeriformes	Sturnidae	*Sturnus vulgaris*	(Hart et al. 2000, Hart and Vorobyev 2005)
Chordata	Aves	Passeriformes	Turdidae	*Turdus merula*	(Hart et al. 2000, Hart and Vorobyev 2005)
Chordata	Aves	Procellariiformes	Procellariidae	*Puffinus pacificus*	(Hart 2004, Hart and Vorobyev 2005)
Chordata	Aves	Procellariiformes	Procellariidae	*Puffinus puffinus*	(Bowmaker et al. 1997)
Chordata	Aves	Psittaciformes	Psittacidae	*Melopsittacus undulatus*	(Bowmaker et al. 1997)
Chordata	Aves	Rheiformes	Rheidae	*Rhea americana*	(Wright and Bowmaker 2001)
Chordata	Aves	Sphenisciformes	Spheniscidae	*Spheniscus humboldti*	(Bowmaker and Martin 1985)
Chordata	Aves	Strigiformes	Strigidae	*Bubo virginianus*	(Jacobs et al. 1987a)
Chordata	Aves	Strigiformes	Strigidae	*Strix aluco*	(Bowmaker and Martin 1978)
Chordata	Aves	Struthioniformes	Struthionidae	*Struthio camelus*	(Wright and Bowmaker 2001)
Chordata	Aves	Tinamiformes	Tinamidae	*Nothoprocta cinerascens*	(Sillman et al. 1981)
Chordata	Aves	Tinamiformes	Tinamidae	*Nothoprocta perdicaria*	(Sillman et al. 1981)
Chordata	Mammalia	Artiodactyla	Bovidae	*Bos taurus*	(Jacobs et al. 1998)
Chordata	Mammalia	Artiodactyla	Bovidae	*Capra hircus*	(Jacobs et al. 1998)
Chordata	Mammalia	Artiodactyla	Bovidae	*Ovis aries*	(Jacobs et al. 1998)
Chordata	Mammalia	Artiodactyla	Cervidae	*Dama dama*	(Jacobs et al. 1994)
Chordata	Mammalia	Artiodactyla	Cervidae	*Odocoileus virginianus*	(Jacobs et al. 1994)
Chordata	Mammalia	Artiodactyla	Suidae	*Sus scrofa*	(Neitz and Jacobs 1989)
Chordata	Mammalia	Carnivora	Canidae	*Canis lupus familiaris*	(Jacobs et al. 1993b)
Chordata	Mammalia	Carnivora	Canidae	*Urocyon littoralis*	(Jacobs et al. 1993b)
Chordata	Mammalia	Carnivora	Canidae	*Vulpes vulpes*	(Jacobs et al. 1993b)
Chordata	Mammalia	Carnivora	Felidae	*Felis catus*	(Nelson 1977, Ringo et al. 1977, Crocker et al. 1980, Jacobs and Neitz 1986)
Chordata	Mammalia	Carnivora	Mustelidae	*Mustela putorius furo*	(Calderone and Jacobs 2003)
Chordata	Mammalia	Carnivora	Procyonidae	*Nasua nasua*	(Jacobs and Deegan 1992)

Chordata	Mammalia	Carnivora	Procyonidae	*Potos flavus*	(Jacobs and Deegan 1992)
Chordata	Mammalia	Carnivora	Procyonidae	*Procyon lotor*	(Jacobs and Deegan 1992)
Chordata	Mammalia	Chiroptera	Hipposideridae	*Hipposideros speoris*	(Joshi and Chandrashekaran 1985)
Chordata	Mammalia	Chiroptera	Phyllostomidae	*Carollia perspicillata*	(Müller et al. 2009)
Chordata	Mammalia	Chiroptera	Phyllostomidae	*Glossophaga soricina*	(Müller et al. 2009)

Chordata	Mammalia	Chiroptera	Pteropodidae	*Haplonycteris fischeri*	(Wang et al. 2004)
Chordata	Mammalia	Chiroptera	Pteropodidae	*Pteropus dasymallus*	(Wang et al. 2004)
Chordata	Mammalia	Chiroptera	Pteropodidae	*Pteropus samoensis*	(Melin et al. 2014)
Chordata	Mammalia	Chiroptera	Vespertilionidae	*Myotis velifer*	(Wang et al. 2004)
Chordata	Mammalia	Chiroptera	Vespertilionidae	*Myotis lucifugus*	(Feller et al. 2009)
Chordata	Mammalia	Lagomorpha	Leporidae	*Oryctolagus cuniculus*	(Nuboer et al. 1983)
Chordata	Mammalia	Marsupialia	Didelphidae	*Didelphis aurita*	(Hunt et al. 2009)
Chordata	Mammalia	Marsupialia	Didelphidae	*Didelphis virginiana*	(Jacobs and Williams 2010)
Chordata	Mammalia	Marsupialia	Didelphidae	*Monodelphis domestica*	(Hunt et al. 2009)
Chordata	Mammalia	Marsupialia	Didelphidae	*Thylamys elegans*	(Palacios et al. 2010)
Chordata	Mammalia	Marsupialia	Macropodidae	*Setonix brachyurus*	(Arrese et al. 2005)
Chordata	Mammalia	Perissodactyla	Equidae	*Equus caballus*	(Carroll et al. 2001)
Chordata	Mammalia	Primates	Aotidae	*Aotus trivirgatus*	(Jacobs et al. 1993a, Tan and Li 1999, Tan et al. 2005)
Chordata	Mammalia	Primates	Cebidae	*Callithrix jacchus jacchus*	(Travis et al. 1988, Tovée et al. 1992)
Chordata	Mammalia	Primates	Cebidae	*Cebus spp.*	(Jacobs and Deegan II 2003)
Chordata	Mammalia	Primates	Cebidae	*Leontopithecus rosalia rosalia*	(Jacobs and Deegan II 2003)
Chordata	Mammalia	Primates	Cebidae	*Sagiunus midas*	(Jacobs and Deegan II 2003)
Chordata	Mammalia	Primates	Cebidae	*Saguinus fuscicollis*	(Jacobs and Deegan II 2003)
Chordata	Mammalia	Primates	Cebidae	*Saguinus oedipus*	(Jacobs and Deegan II 2003)
Chordata	Mammalia	Primates	Cebidae	*Saimiri sciureus*	(Jacobs et al. 1987b)
Chordata	Mammalia	Primates	Cercopithecidae	*Cercopithecus cephus*	(Bowmaker et al. 1991)
Chordata	Mammalia	Primates	Cercopithecidae	*Cercopithecus diana*	(Bowmaker et al. 1991)
Chordata	Mammalia	Primates	Cercopithecidae	*Cercopithecus petaurista*	(Bowmaker et al. 1991)
Chordata	Mammalia	Primates	Cercopithecidae	*Chlorocebus aethiops*	(Bowmaker et al. 1991)
Chordata	Mammalia	Primates	Cercopithecidae	*Erythrocebus patas*	(Bowmaker et al. 1991)
Chordata	Mammalia	Primates	Cercopithecidae	*Macaca fascicularis*	(Baylor et al. 1984, Nunn et al. 1984, Baylor et al. 1987)
Chordata	Mammalia	Primates	Cercopithecidae	*Macaca mulatta*	(Bowmaker et al. 1991)
Chordata	Mammalia	Primates	Cercopithecidae	*Miopithecus talapoin*	(Bowmaker et al. 1991)
Chordata	Mammalia	Primates	Cercopithecidae	*Papio papio*	(Bowmaker et al. 1991)
Chordata	Mammalia	Primates	Cheirogaleidae	*Cheirogaleus major*	(Tan and Li 1999)
Chordata	Mammalia	Primates	Cheirogaleidae	*Cheirogaleus medius*	(Tan and Li 1999)
Chordata	Mammalia	Primates	Cheirogaleidae	*Microcebus murinus*	(Tan and Li 1999)
Chordata	Mammalia	Primates	Cheirogaleidae	*Mirza coquereli*	(Tan and Li 1999, Carvalho et al. 2012)
Chordata	Mammalia	Primates	Daubentoniidae	*Daubentonia madagascariensis*	(Tan and Li 1999, Hunt et al. 2009, Carvalho et al.

2012)

Chordata	Mammalia	Primates	Galagidae	*Galago senegalensis*	(Zhou et al. 1997, Tan and Li 1999)
Chordata	Mammalia	Primates	Galagidae	*Otolemur crassicaudatus*	(Deegan and Jacobs 1996, Tan and Li 1999)
Chordata	Mammalia	Primates	Galagidae	*Otolemur garnettii*	(Zhou et al. 1997, Tan and Li 1999)

Chordata	Mammalia	Primates	Hominidae	*Homo sapiens*	(Dartnall et al. 1983)
Chordata	Mammalia	Primates	Indriidae	*Avahi laniger*	(Tan et al. 2005)
Chordata	Mammalia	Primates	Lemuridae	*Eulemur fulvus fulvus*	(Jacobs and Deegan 1993)
Chordata	Mammalia	Primates	Lemuridae	*Lemur catta*	(Jacobs and Deegan 1993)
Chordata	Mammalia	Primates	Lepilemuridae	*Lepilemur ruficaudatus*	(Tan and Li 1999, Tan et al. 2005)
Chordata	Mammalia	Primates	Lorisidae	*Loris tardigradus*	(Tan and Li 1999, Kawamura and Kubotera 2004)
Chordata	Mammalia	Primates	Pitheciidae	*Pithecia pithecia*	(Jacobs and Deegan II 2003)
Chordata	Mammalia	Primates	Tarsiidae	*Carlito syrichta*	(Tan and Li 1999, Tan et al. 2005)
Chordata	Mammalia	Primates	Tarsiidae	*Cephalopachus bancanus*	(Tan and Li 1999, Tan et al. 2005)
Chordata	Mammalia	Proboscidea	Elephantidae	*Elephas maximus*	(Yokoyama et al. 2005)
Chordata	Mammalia	Proboscidea	Elephantidae	*Loxodonta africana*	(Yokoyama et al. 2005)
Chordata	Mammalia	Rodentia	Caviidae	*Cavia porcellus*	(Parry and Bowmaker 2002)
Chordata	Mammalia	Rodentia	Cricetidae	*Mesocricetus auratus*	(Calderone and Jacobs 1999, Williams and Jacobs 2008)
Chordata	Mammalia	Rodentia	Cricetidae	*Mesocricetus brandti*	(Williams and Jacobs 2008)
Chordata	Mammalia	Rodentia	Cricetidae	*Phodopus sungorus*	(Calderone and Jacobs 1999)
Chordata	Mammalia	Rodentia	Geomyidae	*Geomys bursarius*	(Williams et al. 2003)
Chordata	Mammalia	Rodentia	Geomyidae	*Thomomys bottae*	(Williams et al. 2005)
Chordata	Mammalia	Rodentia	Muridae	*Meriones unguiculatus*	(Jacobs and Neitz 1989, Jacobs and Deegan II 1994a)
Chordata	Mammalia	Rodentia	Muridae	*Mus musculus*	(Jacobs et al. 1991, Jacobs 1993)
Chordata	Mammalia	Rodentia	Muridae	*Rattus rattus*	(Jacobs et al. 1991, Jacobs 1993)
Chordata	Mammalia	Rodentia	Octodontidae	*Octodon degus*	(Ch?vez et al. 2003)
Chordata	Mammalia	Rodentia	Octodontidae	*Spalacopus cyanus*	(Peichl et al. 2005)
Chordata	Mammalia	Rodentia	Sciuridae	*Glaucomys sabrinus*	(Jacobs 1993, Carvalho et al. 2006)
Chordata	Mammalia	Rodentia	Sciuridae	*Sciurus carolinensis*	(Blakeslee et al. 1988)
Chordata	Mammalia	Rodentia	Sciuridae	*Otospermophilus beecheyi*	(Jacobs et al. 1985)
Chordata	Mammalia	Rodentia	Sciuridae	*Callospermophilus lateralis*	(Kraft 1988)
Chordata	Mammalia	Rodentia	Sciuridae	*Ictidomys [=Spermophilus] tridecemlineatus*	(Jacobs et al. 1985)
Chordata	Mammalia	Scandentia	Tupaiidae	*Tupaia glis*	(Bowmaker et al. 1991)
Chordata	Reptilia	Crocodilia	Alligatoridae	*Alligator mississippiensis*	(Sillman et al. 1991)

Chordata	Reptilia	Squamata	Agamidae	*Ctenophorus ornatus*	(Barbour et al. 2002)
Chordata	Reptilia	Squamata	Chamaeleonidae	*Chamaeleo dilepis*	(Bowmaker et al. 2005)
Chordata	Reptilia	Squamata	Chamaeleonidae	*Furcifer pardalis*	(Bowmaker et al. 2005)
Chordata	Reptilia	Squamata	Colubridae	*Boa constrictor*	(Sillman et al. 2001)
Chordata	Reptilia	Squamata	Colubridae	*Masticophis flagellum*	(Macedonia et al. 2009)

Chordata	Reptilia	Squamata	Colubridae	*Python regius*	(Sillman et al. 1999, Davies et al. 2009)
Chordata	Reptilia	Squamata	Colubridae	*Thamnophis sirtalis sirtalis*	(Sillman et al. 1997)
Chordata	Reptilia	Squamata	Colubridae	*Xenopeltis unicolor*	(Davies et al. 2009)
Chordata	Reptilia	Squamata	Colubridae	*Lampropeltis getula*	(Simoes et al. 2016)
Chordata	Reptilia	Squamata	Colubridae	*Arizona elegans*	(Simoes et al. 2016)
Chordata	Reptilia	Squamata	Colubridae	*Rhinocheilus lecontei*	(Simoes et al. 2016)
Chordata	Reptilia	Squamata	Colubridae	*Hypsiglena torquata*	(Simoes et al. 2016)
Chordata	Reptilia	Squamata	Gekkonidae	*Cyrtopodion caspium*	(Govardovskii et al. 1984)
Chordata	Reptilia	Squamata	Gekkonidae	*Cyrtopodion fedtschenkoi*	(Govardovskii et al. 1984)
Chordata	Reptilia	Squamata	Gekkonidae	*Cyrtopodion kotschyi*	(Govardovskii et al. 1984)
Chordata	Reptilia	Squamata	Gekkonidae	*Gekko gekko*	(Loew 1994)
Chordata	Reptilia	Squamata	Gekkonidae	*Hemidactylus frenatus*	(Loew et al. 1996)
Chordata	Reptilia	Squamata	Gekkonidae	*Hemidactylus garnotii*	(Loew et al. 1996)
Chordata	Reptilia	Squamata	Gekkonidae	*Hemidactylus platyurus*	(Crescitelli et al. 1977)
Chordata	Reptilia	Squamata	Gekkonidae	*Hemidactylus turcicus*	(Loew et al. 1996)
Chordata	Reptilia	Squamata	Gekkonidae	*Ptychozoon lionotum*	(Crescitelli et al. 1977)
Chordata	Reptilia	Squamata	Iguanidae	*Anolis bahorucoensis*	(Loew et al. 2002)
Chordata	Reptilia	Squamata	Iguanidae	*Anolis carolinensis*	(Kawamura and Yokoyama 1998)
Chordata	Reptilia	Squamata	Iguanidae	*Anolis conspersus*	(Loew et al. 2002)
Chordata	Reptilia	Squamata	Iguanidae	*Anolis cristatellus*	(Loew et al. 2002)
Chordata	Reptilia	Squamata	Iguanidae	*Anolis evermanni*	(Loew et al. 2002)
Chordata	Reptilia	Squamata	Iguanidae	*Anolis extremus*	(Loew et al. 2002)
Chordata	Reptilia	Squamata	Iguanidae	*Anolis grahami*	(Loew et al. 2002)
Chordata	Reptilia	Squamata	Iguanidae	*Anolis gundlachi*	(Loew et al. 2002)
Chordata	Reptilia	Squamata	Iguanidae	*Anolis krugi*	(Loew et al. 2002)
Chordata	Reptilia	Squamata	Iguanidae	*Anolis lineatopus*	(Loew et al. 2002)
Chordata	Reptilia	Squamata	Iguanidae	*Anolis pulchellus*	(Loew et al. 2002)
Chordata	Reptilia	Squamata	Iguanidae	*Anolis sagrei*	(Loew et al. 2002)
Chordata	Reptilia	Squamata	Iguanidae	*Anolis stratulus*	(Loew et al. 2002)
Chordata	Reptilia	Squamata	Iguanidae	*Crotaphytus dickersonae*	(Macedonia et al. 2009)
Chordata	Reptilia	Squamata	Iguanidae	*Platysaurus broadleyi*	(Fleishman et al. 2011)
Chordata	Reptilia	Squamata	Phyllodactylidae	*Tarentola chazaliae*	(Roth and Kelber 2004)
Chordata	Reptilia	Squamata	Sphaerodactylidae	*Teratoscincus scincus*	(Loew et al. 1996)
Chordata	Reptilia	Testudines	Chelonidae	*Chelonia mydas*	(Liebman and Granda 1971)
Chordata	Reptilia	Testudines	Cheloniidae	*Caretta caretta*	(Gocke 2003)
Chordata	Reptilia	Testudines	Emydidae	*Trachemys scripta*	(Baylor and Hodgkin 1973)

Chordata	Reptilia	Testudines	Geoemydidae	*Mauremys reevesii*	(Ohtsuka 1985)

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Appendix B

Index of Species in Spectral Response Curve Database

Class	Species	Type	Condition	Reference
Amphibia	*Agalychnis callidryas*	ERG	Dark	(Liebau et al. 2015)
Amphibia	*Agalychnis callidryas*	ERG	Light	(Liebau et al. 2015)
Amphibia	*Ambystoma mexicanum*	ERG		(Deutschlander and Phillips 1995)
Amphibia	*Ambystoma tirgrinum*	Optical Density	Dark	(Cornwall et al. 1984)
Amphibia	*Hyla cinerea*	Behavior	Dark	(King et al. 1993)
Amphibia	*Hylas regilla*	ERG	Light	(Wente and Phillips 2005)
Amphibia	*Lithobates pipiens*	ERG	Dark	(Kennedy 1957)
Amphibia	*Lithobates pipiens*	ERG	Light	(Kennedy 1957)
Amphibia	*Rana temporaria*	ERG	Dark	(Govardovskii and Zueva 1974)
Amphibia	*Salamandra salamandra*	Behavior	Light	(Przyrembel et al. 1995)
Arachnida	*Lycosa baltimoriana anterior median eye*	ERG	Dark	(DeVoe 1972)
Arachnida	*Menemerus confusus*	ERG	Dark	(Yamashita and Tateda 1976)
Arachnida	*Plexippus validus*	ERG	Light	(Blest et al. 1981)
Arachnida	*Vejovis spinigerus* *Centruoides sculpturatus* *Opisthacanthus validus*	ERG	Light	(Machan 1968)
Aves	*Anous minutus*	ERG	Dark	(Reed 1986)
Aves	*Anous stolidus*	ERG	Dark	(Reed 1986)
Aves	*Columba livia*	ERG	Dark	(Blough 1957) See also (Remy and Emmerton 1989)
Aves	*Columba livia*	Behavior	Light	(Remy and Emmerton 1989)
Aves	*Coturnix japonica*	ERG	Dark	(Kawamuro et al. 1997)
Aves	*Gallus domesticus*	ERG	Dark	(Armington and Thiede 1956)
Aves	*Gygis alba*	ERG	Dark	(Reed 1986)
Aves	*Larus argentatus/fuscus*	Behavior	Light	(Thompson 1971)
Aves	*Larus argentatus/fuscus juv.*	Behavior	Light	(Thompson 1971)
Aves	*Leiothrix lutea*	Behavior	Low light	(Maier 1992)
Aves	*Phoebastria immutabilis*	ERG	Dark	(Reed 1986)
Aves	*Phoebastria nigripes*	ERG	Dark	(Reed 1986)
Aves	*Pterodroma hypoleuca*	ERG	Dark	(Reed 1986)
Aves	*Pterodroma phaeopygia*	ERG	Dark	(Reed 1986)
Aves	*Puffinus newelli*	ERG	Dark	(Reed 1986)
Aves	*Strix aluco*	Behavior	Dark	(Martin 1977)
Aves	*Sturnus vulgaris*	Behavior	Dark	(Hart 2001)
Aves	*Sula nebouxii*	ERG	Dark	(Reed 1986)
Aves	*Sula sula*	ERG	Dark	(Reed 1986)
Aves	*Sula variegata*	ERG	Dark	(Reed 1986)
Aves	*Buteo jamaicensis*	ERG	Light	(Krempels 1989)
Aves	*Buteo jamaicensis*	ERG	Dark	(Krempels 1989)
Aves	*Buteo lineatus*	ERG	Light	(Krempels 1989)
Aves	*Buteo regalis*	ERG	Light	(Krempels 1989)
Aves	*Buteo regalis*	ERG	Dark	(Krempels 1989)
Aves	*Buteo platypterus*	ERG	Light	(Krempels 1989)
Aves	*Buteo platypterus*	ERG	Dark	(Krempels 1989)
Crustacea	*Talorchestia longicornis*	Behavior	Night	(Cohen et al. 2010)

Insecta	*Aedes aegypti*	ERG	Dark	Combined (Goldman 1972, Muir et al. 1992)
Insecta	*Aeshna tuberculifera*	ERG	Dark	(Chappell and DeVoe 1975)
Insecta	*Aglais io*	ERG	Dark	(Eguchi et al. 1982)
Insecta	*Aleochara bilineata*	ERG	Unk	https://cronodon.com/BioTech/Insect_Vision.html
Insecta	*Amyelois transitella*	Optical	Dark	(Bernard et al. 1984)
Insecta	*Anax junius*	ERG	Dark	(Chappell and DeVoe 1975)
Insecta	*Argyronome ruslana*	ERG	Dark	(Eguchi et al. 1982)
Insecta	*Arichanna gaschkevitchii*	ERG	Dark	(Eguchi et al. 1982)
Insecta	*Ascalaphus macaronius*	ERG	Unk	(Gogala 1967, Paul et al. 1986)
Insecta	*Atrophaneura alcinous*	ERG	Dark	(Eguchi et al. 1982)
Insecta	*Bibio marci (main and ventral)*	ERG	Light	(Burkhardt and de la Motte 1972)
Insecta	*Bicellonycha wickershamorum*	ERG	Dark	(Lall et al. 1988)
Insecta	*Bombus hortorum*	ERG	Light	(Meyer-Rochow 1980)
Insecta	*Caliothrips phaseoli*	Behavior	Dark	(Mazza et al. 2010)
Insecta	*Calliphora vicinia*	Optical	Dark	(McCann and Arnett 1972, Bernard and Stavenga 1979)
Insecta	*Cataglyphis bicolor*	ERG	Unk	(Paul et al. 1986)
Insecta	*Cephonodes hylas*	ERG	Dark	(Eguchi et al. 1982)
Insecta	*Cerapteryx graminis*	ERG	Dark	(Mikkola 1972)
Insecta	*Chlorops sp.*	Optical	Dark	(Bernard and Stavenga 1979)
Insecta	*Colias erate*	ERG	Dark	(Eguchi et al. 1982)
Insecta	*Conistra vaccinii*	ERG	Dark/Day	(Mikkola 1972)
Insecta	*Conistra vaccinii*	ERG	Dark/Night	(Mikkola 1972)
Insecta	*Culex pipiens*	ERG	Dark	(Peach et al. 2019)
Insecta	*Delia antiqua*	ERG	Unk	https://cronodon.com/BioTech/Insect_Vision.html
Insecta	*Dielepila elpenor*	ERG	Dark	(Höglund et al. 1973)
Insecta	*Dimecoenia spinosa*	Optical	Dark	(Bernard and Stavenga 1979)
Insecta	*Drosophila melanogaster*	Optical	Dark	(Bernard and Stavenga 1979)
Insecta	*Ephoron virgo*	Behavior	Dark	(Mész?ros et al. 2021)
Insecta	*Eristalis sp.*	ERG	Dark	(Burkhardt and de la Motte 1972)
Insecta	*Fulgeochlizus bruchii*	ERG	Dark	(Lall et al. 2010)
Insecta	*Glossina morsitans*	ERG	Light	(Hardie et al. 1989) R1-6
Insecta	*Gonepteryx aspasia*	ERG	Dark	(Eguchi et al. 1982)
Insecta	*Haematobia irritans*	ERG	Light	(Agee and Patterson 1983)
Insecta	*Heliconius erato*	ERG	Light	(Struwe 1972b)
Insecta	*Heliconius sara*	ERG	Light	(Struwe 1972b)
Insecta	*Hepialus ganna*	ERG	Dark	(Mikkola 1972)
Insecta	*Hydraecia fucosa*	ERG	Dark/Day	(Mikkola 1972)
Insecta	*Hydraecia fuscos*	ERG	Dark/Night	(Mikkola 1972)
Insecta	*Hydroecia micacea*	ERG	Dark	(Mikkola 1972)
Insecta	*Laothoe populi*	ERG	Dark	(Mikkola 1972)
Insecta	*Lutzomyia longipalpis*	ERG	Dark	(Mellor et al. 1996)
Insecta	*Lycaena phlaeas*	ERG	Dark	(Eguchi et al. 1982)
Insecta	*Minois dryas*	ERG	Dark	(Eguchi et al. 1982)
Insecta	*Musca autumnalis*	ERG	Light	(Agee and Patterson 1983)
Insecta	*Musca domesticus*	Optical	Dark	(Bernard and Stavenga 1979)
Insecta	*Neope goschkevitschii*	ERG	Dark	(Eguchi et al. 1982)
Insecta	*Notonecta sp.*	Behavior	Dark	(Bennett and Ruck 1970)
Insecta	*Ochlodes venata*	ERG	Dark	(Eguchi et al. 1982)
Insecta	*Panorpa cognata*	ERG	Light	(Burkhardt and de la Motte 1972)

Insecta	*Papilio maackii*	ERG	Dark	(Eguchi et al. 1982)
Insecta	*Papilio machaon*	ERG	Dark	(Eguchi et al. 1982)
Insecta	*Papilio xuthus*	ERG	Light	Ave of eye parts (Arikawa et al. 1987)
Insecta	*Papilio xuthus*	ERG	Dark	(Eguchi et al. 1982)
Insecta	*Parantica sita*	ERG	Dark	(Eguchi et al. 1982)
Insecta	*Parnara guttata*	ERG	Dark	(Eguchi et al. 1982)
Insecta	*Periplaneta americana*	ERG	Unk	(Paul et al. 1986)
Insecta	*Pharmacis fusconebulosus*	ERG	Dark	(Mikkola 1972)
Insecta	*Photinus collustrans*	ERG	Dark	(Lall et al. 1988)
Insecta	*Photinus macdermotti*	ERG	Dark	(Lall et al. 1988)
Insecta	*Photinus marginellus*	ERG	Dark	(Lall et al. 1988)
Insecta	*Photinus pyralis*	ERG	Dark	(Lall et al. 1988)
Insecta	*Photinus scintillans*	ERG	Dark	(Lall et al. 1988)
Insecta	*Photuris lucicrescens*	ERG	Dark	(Lall et al. 1982)
Insecta	*Phryganea grandis*	ERG	Dark	(Mikkola 1972)
Insecta	*Pieris brassicae*	ERG	Light	(Steiner et al. 1987)
Insecta	*Pieris melete*	ERG	Dark	(Eguchi et al. 1982)
Insecta	*Plusia chrysitis*	ERG	Dark	(Mikkola 1972)
Insecta	*Poecilocampa populi*	ERG	Dark	(Mikkola 1972)
Insecta	*Pseudozizeeria maha*	ERG	Dark	(Eguchi et al. 1982)
Insecta	*Pyrearinus termitilluminans*	ERG	Dark	(Lall et al. 2010)
Insecta	*Pyrophorus divergens*	ERG	Dark	(Lall et al. 2010)
Insecta	*Pyrophorus punctatissimus*	ERG	Dark	(Lall et al. 2010)
Insecta	*Romalea microptera*	ERG	Dark	(Bruckler and Williams 1981)
Insecta	*Simuliid*	ERG	Light	(Kirschfeld and Vogt 1986)
Insecta	*Stomoxys calcitrans*	ERG	Light	(Agee and Patterson 1983)
Insecta	*Tabanus nigrovittatus*	ERG	Light	(Allan et al. 1991)
Mammalia	*Aotus trivirgatus*	ERG	Dark	(Jacobs et al. 1993a)
Mammalia	*Carollia perspicillata*	ERG	Mesopic	(Müller et al. 2009)
Mammalia	*Carollia perspicillata*	ERG	Mesopic	(Müller et al. 2009)
Mammalia	*Cavia porcellus*	ERG	Dark	(Jacobs and Deegan II 1994b)
Mammalia	*Ctenomys magellanicus*	ERG	Light	(Schleich et al. 2010)
Mammalia	*Ctenomys talarum*	ERG	Light	(Schleich et al. 2010)
Mammalia	*Cynomys ludovicianus*	ERG	Dark	(Jacobs 1978)
Mammalia	*Dama dama*	ERG	Dark	(Jacobs et al. 1994)
Mammalia	*Equus caballus*	ERG	Light	(Carroll et al. 2001)
Mammalia	*Felis catus*	ERG	Light	(Jacobs and Neitz 1986)
Mammalia	*Glossophaga soricina*	ERG	Mesopic	(Müller et al. 2009)
Mammalia	*Glossophaga soricine*	ERG	Mesopic	(Müller et al. 2009)
Mammalia	*Lemur catta*	ERG	Dark	(Jacobs and Deegan 1993)
Mammalia	*Meriones unguiculatus*	ERG	Light	(Jacobs et al. 1991)
Mammalia	*Mesocricetus auratus*	ERG	Light	(Williams and Jacobs 2008)
Mammalia	*Mesocricetus brandtii*	ERG	Light	(Williams and Jacobs 2008)
Mammalia	*Mus musculus*	ERG	Light	(Jacobs and Williams 2007, Rocha et al. 2016)
Mammalia	*Mustela putorious furo*	ERG	Dark	(Calderone and Jacobs 2003)
Mammalia	*Nasua nasua*	ERG	Light	(Jacobs and Deegan 1992)
Mammalia	*Octodon bridgesi*	ERG	Dark	(Ch?vez et al. 2003)
Mammalia	*Octodon degus*	ERG	Dark	(Ch?vez et al. 2003)
Mammalia	*Octodon lunatus*	ERG	Dark	(Ch?vez et al. 2003)

Mammalia	*Odocoileus virginianus*	ERG	Dark	(Jacobs et al. 1994)
Mammalia	*Oryctolagus cuniculus*	Behavior	Light	(Nuboer and Moed 1983)
Mammalia	*Otospermophilus beecheyi*	ERG	Dark	(Jacobs 1978, Jacobs et al. 1985)
Mammalia	*Phoca vitulina*	ERG	Light	(Crognale et al. 1998)
Mammalia	*Phodopus sungorus*	ERG	Dark	(Calderone and Jacobs 1999)
Mammalia	*Procyon lotor*	ERG	Dark	(Jacobs and Deegan 1992)
Mammalia	*Rattus norvegicus*	ERG	Light	(Jacobs et al. 1991)
Mammalia	*Saguinus fuscicollis*	Behavior	Light	(Jacobs et al. 1987b)
Mammalia	*Sciurus carolinensis*	ERG	Dark	(Blakeslee et al. 1988)
Mammalia	*Sciurus carolinensis*	Behavior	Dark	(Arden and Silver 1962)
Mammalia	*Sciurus niger*	Behavior	Dark	(Jacobs 1974)
Mammalia	*Ammospermophilus luecurus*	ERG	Dark, Light	(Fisher et al. 1976)
Mammalia	*Callospermophilus lateralis*	ERG	Dark	(Jacobs 1978)
Mammalia	*Ictidomys [=Spermophilus] mexicanus*	ERG	Dark	(Jacobs 1978)
Mammalia	*Ictidomys [=Spermophilus] tridecemlineatus*	ERG	Dark	(Jacobs 1978)
Mammalia	*Thomomys bottae*	ERG	Light	(Jacobs et al. 1991, Williams et al. 2005)
Reptilia	*Anolis sagrei*	ERG	Dark	(Fleishman et al. 2011)
Reptilia	*Caretta caretta*	ERG	Light	(Levenson et al. 2004)
Reptilia	*Carretta carretta* hatchling			(Horch et al. 2008)
Reptilia	*Chelonia mydas*	ERG	Light	(Levenson et al. 2004) (Granda and O'Shea 1972)
Reptilia	*Dermochelys coriacea*	ERG	Dark	(Gocke 2003)
Reptilia	*Dermochelys coriacea* hatchling	ERG	Dark	(Horch et al. 2008)
Reptilia	*Platysaurus broadleyi*	ERG	Dark	(Fleishman et al. 2011)
Reptilia	*Tiliqua rugosa*	ERG	Light	(Nagloo 2016)
Mammalia	*Canis familiaris*	ERG	Dark, Light	(Jacobs et al. 1993b)
Mammalia	*Urocyon littoralis*	ERG	Light	(Jacobs et al. 1993b)
Mammalia	*Vulpes vulpes*	ERG	Light	(Jacobs et al. 1993b)
Mammalia	*Alopex lagopus*	ERG	Light	(Jacobs et al. 1993b)
Reptilia	*Pseudemys scripta*	ERG	Dark	(Baylor and Hodgkin 1973)
Reptilia	*Pseudemys scripta*	ERG	Dark	(Granda and Stirling 1966)

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Chapter 4. Assessing and Mitigating Taxon-Specific Light Pollution Impacts from Roadway Lighting Projects

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Executive Summary

Predicting the adverse effects of light at night is necessary to do thorough environmental impact analysis and to ensure compliance with laws and regulations that protect species. Frequently, the lighting assessments provided for environmental review are not at a sufficient level of sensitivity – they may only resolve to 1 lux illumination, when light two orders of magnitude is biologically relevant – and do not account for different visual systems of the diverse organisms impacted.

Using two recent Caltrans projects as examples, a methodology for creating maps to assess and mitigate the impacts of roadway lighting on a sensitive species was developed and demonstrated. The method involves calculation of vertical and horizontal illuminance using the lighting design software AGi32 at a higher precision than usually done for design work (0.001 lux resolution) importing those values into a geographic information system (GIS; ArcGIS Pro) and then reclassifying values based on the relative sensitivity of the relevant organism, either California tiger salamander or San Bernardino Merriam's kangaroo rat. The resulting maps of illumination are in units of "equivalent moonlight lux", meaning that the illumination is as bright as the same amount of moonlight would appear to the organism, once the spectral sensitivity of the organism is considered. To demonstrate the effectiveness of changing spectral composition on light impact area, maps were made comparing the as-built lamps (3000 K LEDs) to Low Pressure Sodium, PC Amber LEDs, High Pressure Sodium, 2266 K LEDs, and 4310 K LEDs. To demonstrate the mitigative potential of commercially available shields, a second set of calculations was done using off-the-shelf shielding available for the lamps used by Caltrans at each location. Thresholds for impacts at 0.01 and 0.1 equivalent moonlight lux were set for analysis.

Implementation of this workflow revealed current challenges with using lighting engineering software for environmental assessment, namely difficulties in doing full radiosity calculations (including reflections) on larger study areas, and pointing to a need for innovation that integrates GIS with lighting calculations in a manner that can be deployed over large geographic areas.

Spectral control reduced the impact area for both species, with greater potential for benefits for the kangaroo rat because of its high sensitivity to short wavelengths of light. Shielding reduced the impact area for one case study by focusing light more closely on the roadways to be illuminated, but for the other site the design of the available shields increased forward facing light emissions in at 80–90? above nadir and thereby increased the area illuminated at >0.01 and >0.1 lux surrounding the newly lighted area and extending further into endangered species habitat.

The magnitude of benefits from spectral tuning was 8–19% decrease in area >0.01 lux for the California tiger salamander site and 21–25% for the kangaroo rat site. The magnitude of benefits for shielding was greater than the potential benefits from spectral tuning for the lamps that had shields that controlled light emitted forward at high angles, but had no benefits when shields redirected light into this portion of the emissions distribution.

The results demonstrate a feasible approach to calculate and mitigate the impacts of new lights introduced into habitat of a sensitive species. The different results depending on detailed specifications of the lamps used and their available shields strongly indicate a need to do such assessments and propose mitigation before projects are installed. Spectral tuning is available as an approach but its effectiveness depends on the visual system of the particular species impacted. With these results, one can conclude that the most effective mitigation would be ensuring first that light does not substantially exceed the recommended minimum illumination levels for safety, then evaluating other approaches with detailed information about proposed equipment, shields, and affected species.

Introduction

Environmental assessment and mitigation planning for roadway lighting projects necessarily takes place in a virtual world of maps and diagrams that describe the spatial configuration of existing conditions and the probable future conditions to predict the outcomes for sensitive resources. Feasibly integrating concerns about impacts to wildlife and potential mitigations with lighting engineers requires a means to translate between the different graphical, analytical, and measurement tools used in lighting design as compared with wildlife ecology. For example, lux (or foot-candles) is used as the measurement unit for illumination in lighting design, yet these measurements reflect the sensitivity of the human eye only. Because humans are largely diurnal species with comparatively poor night vision, the dynamic range of lighting design maps frequently is only resolved to 1 lux, which is on the order of 10 times brighter than the illumination from a full moon (Kyba et al. 2017). Lighting design maps showing future illumination rounded to 1 lux are utterly insufficient to map the extent of alteration of natural conditions, which may be several orders of magnitude darker. Lighting design software can be used to map vertical lux, which may be useful information but is insufficient to calculate, for example, whether a new light will be visible as a glare source to an organism on the ground (a foraging rodent, for example) or in a water body below the roadway plane. Lighting practice, however, generally does have information about the spectral power distribution of lighting products being proposed and this information can be used to convert the modelled illumination in lighting design programs to the predicted visibility or behavioral responses of any target species for which behavioral action spectra are available (Longcore et al. 2018).

Environmental impact analysis and mitigation practice depends largely on assessing the adverse impacts that could be expected for individual species, either in terms of direct demographic effects (e.g., mortality) or adverse impacts to the species habitat. Mitigation programs often take the place of offsetting demographic impacts to a population, such as captive breeding and release to make up for the loss of adult California Condors, or the protection, restoration, or enhancement of habitat to make up for the impacts to suitable habitats ("compensatory mitigation") (Allen and Feddema 1996). Evaluation of the effects of light pollution in the environmental review process (e.g., under the National Environmental Policy Act, California Environmental Quality Act) has historically only been part of the evaluation of aesthetic impacts, where a set of criteria are in use that address human-centered visual impacts. For example, such analyses may assess the distribution of direct glare, or set illumination criteria at property boundaries that are thought to reduce visual impacts. Often, the evaluation of impacts on wildlife is treated in a superficial manner unless specific impacts of light pollution on the species in question are well known. Mitigation measures developed for human visual impacts are often referenced as if they were relevant to evaluating impacts to other species. They are not, because the spectral and dynamic sensitivity of light-detecting systems in other species differs dramatically from humans.

Project proponents and agency personnel need detailed information about the spatial extent of lighting impacts to properly evaluate and mitigate them. Even for phenomena that can result in death for affected individuals (e.g., attraction of insects or juvenile seabirds to lights), depictions of the impact zone are a necessary step to establish mitigation actions and potential mitigation ratios for impacted habitat. In this report, we develop a method to map the impact zones from two real world lighting projects, each of which affects a listed species, as a demonstration of how existing lighting engineering calculations combined with information about wildlife developed as part of this project can be deployed. The general approach is first to use conventional lighting design software to map horizontal and vertical illuminance from the designed lighting systems at a higher precision (i.e., 0.001 lux) than is conventionally done. Then, the illuminance is converted to a species-specific metric that compares it to how the species would perceive a standard amount (0.1 lux) of light from the moon, yielding a map of areas that are in terms of the percent brightness of 0.1 lux of moonlight as experienced by the species, given the spectral characteristics of the light. Finally, alterations to the lighting design are explored that change shielding and color characteristics to demonstrate changes in impact areas. Once a threshold for impacts for the species is chosen (expressed as a percentage of moonlight) impact maps can be made and compared that can then be used in typical mitigation approaches (e.g., to set mitigation ratios).

Setting of thresholds for impacts on nocturnal species will probably be most effective if related to illumination levels in the natural environment without light pollution. Many species exhibit lunar cycles (Hauenschild 1960, Gliwicz 1986), which are driven by considerations of safety from predators (Nelson 1989, Prugh and Golden 2014) and visibility of prey and forage items at natural illumination levels (Upham and Hafner 2013, San-Jose et al. 2019). Some species increase activity with lunar illumination (Lillywhite and Brischoux 2012), while others decrease activity (Prugh and Golden 2014), both of which would be adverse impacts when induced by artificial illumination out of cycle with natural patterns. There is a common tendency to think that impact thresholds might be related to full moon illumination, however, full moon conditions occur only during a very limited period of the month and illumination from the moon increases exponentially, not linearly, to its peak (Figure 31). Based on lunar cycles, time of moonrise and moonset, and lunar angle, nighttime light conditions from the moon are below 10% of its maximum a full 90% of the time (Śmielak 2022). Full moon illumination can, under ideal conditions near the equator, approach 0.4 lux (Brown 1952, Krisciunas and Schaefer 1991), but a more typical illumination is 0.1 lux (Kyba et al. 2017). It is dimmer at higher latitudes because of the angle of incidence and the amount of atmosphere traversed (Horvath 1993), and is also affected by elevation (Green 1992).

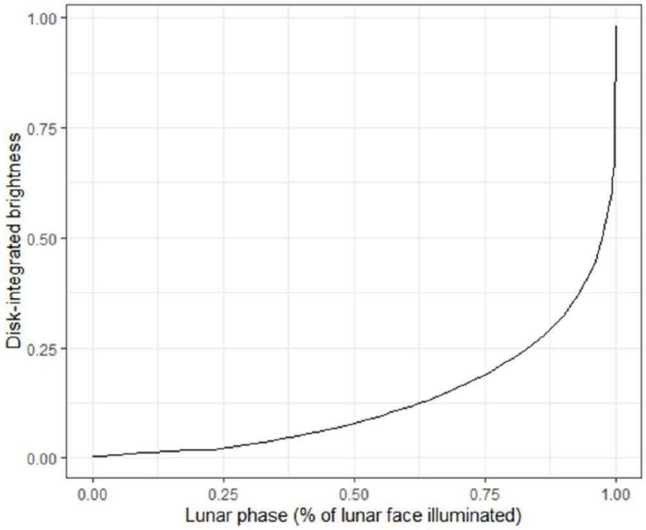

Figure 31. Relationship of moon brightness as proportion of maximum and lunar phase (Śmielak 2022).

Incorporation of spectrum into impact analysis is built on the premise that impacts are proportional to the brightness of light sources within the visual system of organisms. That is, the presumption is that light of colors that appear dimmer to the organisms will have lesser impacts. This approach has been presented and developed in a series of papers (Saunders et al. 2008, van Grunsven et al. 2014, Longcore et al. 2015, Longcore et al. 2018, Seymoure et al. 2019), and validated with field and laboratory data for some organisms (Longcore et al. 2015, Donners et al. 2018, Deichmann et al. 2021, Longcore et al. 2022). Availability of spectral response curves has limited application of this approach save for instances where response curves for higher taxonomic classifications have been developed (Donners et al. 2018). A database of >170 response curves digitized from the physiological literature has been completed as part of the current project and provides the basis to characterize visual responses at the Order or Family level for most wildlife species (Longcore 2022).

This report documents the use of species-specific assessment of light intensity from two case study projects to evaluate impact area of as-built roadway lighting installations and to demonstrate potential reductions in impact area that would result from deploying readily available mechanical shielding and use lamps with different spectral compositions currently available in the marketplace. These examples provide a roadmap for the analysis of such impacts during the environmental review process and examples of mitigation techniques that could be adopted during the review process, in addition to calculating area of impacts that might require off-site mitigation.

Methods

Case Study Locations

Study locations were suggested by Caltrans for sites that were: 1. New lighting projects in an area with little surrounding artificial light, 2. Affecting at least one state or federally listed species, and 3. For which data on the as-built lighting systems was available. Two sites were selected for analysis in consultation with the project advisory panel.

State Route 12/State Route 113 Intersection Improvement Project

The State Route 12/State Route 113 Intersection project added a roundabout and lighting to an existing intersection in Solano County, California. It is in an open grassland habitat with a creek running through the vicinity, known as "The Big Ditch." Habitat for California Tiger Salamander (*Ambystoma californiense*) is in the vicinity. Because few other lights are in the vicinity, and the project represented the first street and area lighting into a relatively dark landscape, it is well suited for this demonstration.

Figure 32. Aerial photograph of completed roundabout at intersection of State Route 12 and State Route 113.

Route 79 and Gilman Springs Road

This site has a completed installation of LED roadway lighting associated with an intersection between a divided highway (Route 79) and a two-lane road (Gilman Springs Road). The lighting along the highway and interchange is immediately adjacent to critical habitat for San Bernardino Merriam's Kangaroo Rat. Riparian habitat suitable for sensitive avian species is nearby. The landscape is open, so light will propagate unimpeded, and the site offers some topographic complexity without being so unique that the analysis would be driven most strongly by the topography. As work on this site proceeded, we found it was too large to be analyzed all at once by the lighting engineering software, so effort was focused on the two intersections of the offramps from SR-79 with Gilman Springs Road (Figure 33).

Figure 33. Illustration of Route 79 and Gillman Springs Road. The two intersections of the on/off ramps with Gillman Springs Road were illuminated. Critical habitat for San Bernardino Kangaroo Rat is found to the southeast of the intersection.

Lighting Scenario Development

For each site, we developed two lighting scenarios using the commercial lighting software AGi32. First, as-built lighting plans for each site were obtained from Caltrans to develop the baseline scenario. IES files were obtained for the fixtures used in the project and the as-built condition was modeled. Then, a shielded scenario was developed by using off-the-shelf shielding products available for the lamps used in the project to focus light on the roadway and reduce off-roadway spill. The steps in creating these two scenarios follow.

Terrain Mesh

A terrain mesh was needed to do the lighting calculations in AGi32. AutoCAD was used in conjunction with two plugins (CADEarth and PlexiEarth) along with Google Earth to obtain topographical information. A polygon was drawn to capture the area limits in Google Earth. The

“Insert terrain mesh from Google Earth” function was used in CADEarth. This function received the polygon in Google Earth to create a terrain mesh in AutoCAD that was georeferenced to that specific area,

Once the terrain mesh was imported into AutoCAD through CADEarth, PlexiEarth was used to obtain an image of the area. To obtain the image, PlexiEarth had to be georeferenced correctly and a pin location was placed in Google Earth. The “Create Mosaic” function in PlexiEarth was used to create the final image.

Once the image and terrain mesh were in AutoCAD, all the terrain meshes were exploded. The roadway and terrain surface areas were separated into two different layers. This makes the layers easier to group them once they are imported into AGi32. The terrain mesh from AutoCAD was imported into AGi32 in a .DWG file format.

Lighting Calculations

All surfaces were grouped and assigned approximate reflectance properties for the roadway and terrain surfaces. A reflectance value of 0.5 was used for roadway surface, while 0.2 was used for terrain surfaces. All surfaces were set to be single-sided. Luminaires were then located by referencing the as-built lighting plans. The PDF plans were scaled to the size of the AGi model, and the x and y coordinates were identified. The approximate Z-coordinates were identified on the terrain mesh elevations. All luminaires were mounted at 34 feet above grade, based on Caltrans luminaire specification standards. All calculation grids were set to be calculated in lux with a precision of 0.001 lux. Horizontal illuminance was calculated for both locations, and vertical illuminance was calculated for the 112/13 location. The study area of the SR-79/Gilman Springs Road site was too large for the AGi32 software to analyze vertical illuminance.

Horizontal Calculation

The horizontal calculation grids were placed with the automatic calculation grid applied to the grouped roadway and ground surfaces. The calculation points were assigned on a 10 by 10 ft. grid spacing. For horizontal illuminance, the meter is aimed up toward the zenith, instead of being aimed perpendicular (default) to the sloped surfaces in the terrain mesh. All illuminance data were exported to a .DWG file format.

Vertical Calculation

The vertical calculations were imported into separate files from the horizontal calculation. This was done to improve the calculation speed of AGi32. Like the horizontal calculation grid, the calculation grids were assigned with the automatic calculation grid placement on a 10 by 10 ft. grid spacing. The grouped surfaces were moved vertically up the Z-axis by three inches to approximate the sightline of the California Tiger Salamander. Five calculations were run to capture data with the illuminance points aimed to the center of the installation and each cardinal direction.

For the 112/13 site, one calculation was run with all the vertical vantage points aimed at one central point in the middle of that roundabout using the “Variable Meter” option within the calculation grid menu. This method could also be used for calculating intersections and other clusters of luminaires. The central point should be placed at the elevation of the luminaires (elevation of the luminaire location plus pole height).

When calculating luminaires in the approach zone to the roundabout, the calculation points were set using the “Fixed Orient/Tilt” option from the calculation menu for each cardinal direction (Table 3). For each cardinal direction, a new file was created.

Table 3. Cardinal direction inputs used in AGi32 calculations.

	North	East	South	West
Orient	-90	180	90	0
Tilt	90	90	90	90

A batch calculation was run for all calculation files using full radiosity. It is recommended to run a direct-only calculation on a file to check for any anomalies or errors. The calculation data was exported to AutoCAD in a .DWG file format.

Shielding Calculations

A shielding study was performed to study the effects of using house-side shields, front-side shields, and cul-de-sac shields. This was done by replacing the IES files with IES files from luminaires that have shields built into the photometry. The same process was followed to export the calculation grids to AutoCAD in a .DWG file format.

Maps of horizontal illuminance were produced for each scenario, measured in millilux, at a point 3 inches above the ground surface to indicate the perspective of small ground dwelling vertebrates (California Tiger Salamander and San Bernardino Kangaroo Rat). Vertical illuminance was calculated for the surface mesh across the 112/13 study area, with values taken in the four cardinal directions and pointing directly to the center of the light installation area. These illumination maps were exported to GIS for further analysis.

Adjustment for Wildlife Visual Systems

Once the as-built and shielded scenarios were developed, the results were in lux at a 0.001 lux resolution. To analyze further, we imported the results into ArcGIS Pro and located them within the proper coordinate system at each study location. A raster with 3-ft. resolution was then created from the points, using a kriging approach. For the 112/13 site, six rasters were created for each location, representing horizontal illuminance, vertical illuminance (N, S, E, W), and vertical illuminance directed toward the center of the lighted zone. We then took the maximum value of these six rasters to represent the peak exposure within each cell, which was used for subsequent maps, consistent with environmental impact analysis practices of evaluating the "worst case" for the purpose of predicting and mitigating impacts.

A number of steps were then needed to account for the visual systems of each target species (Longcore et al. 2018). The approach taken was to compare the illumination levels from the as-built spectral power distribution (SPD) of the lamp to perception of brightness of the full moon by the organism. Because roadway lighting differs in spectral content from moonlight, both the spectral power distribution of the lighting and of the moonlight must be known. Moonlight spectral composition is red-shifted from sunlight (Sweeney et al. 2011) and varies with phase angle, libration (caused by its inclined and non-circular orbit and its angle in space), and atmospheric conditions (Kieffer and Stone 2005). Although future work might account for these variations, we used the spectral power distribution of the full moon as a standard against which to compare the lamps in the example installations.

For species sensitivity, we used spectral response curves documented in Longcore (2022) to develop reasonable assumptions for the sensitivity of California Tiger Salamander and San Bernardino Merriam's Kangaroo Rat. For the salamander, two curves of species within the genus *Ambystoma* are available, so we used a spline fit between the two. For the kangaroo rat, the closest species taxonomically, and most likely to share a visual system, is Botta's pocket gopher (*Thomomys bottae*) and this curve was used as a stand-in for the *Dipodomys* visual system.

Using the two visual response curves, we used the technique described in Longcore et al. (2018) to create a conversion factor between a series of lamp types and the resulting brightness relative to the moon (instead of relative to D65 as done in Longcore et al. 2018). Then these conversion factors were multiplied by the illumination rasters to obtain maps that estimate species-specific illuminance. These conversions were made for the as-built condition (3000 K LED lamps) along with the following sources: Low pressure sodium, High pressure sodium, 1717 K LED (PC Amber), 2266 K LED (Amber White), and 4200 K LED (Cool White). Spectral power distributions of these sources were not obtained for the actual as-built lamps but rather typical sources on file were used. By multiplying the conversion factor by the illuminance rasters for the as-built and shielded scenarios, resulting values represent the organism-specific brightness relative to if the light had been from moonlight. That is, a value of 0.1 of "moonlight adjusted lux" for a species would represent the brightness to the organism equivalent to 0.1 lux of moonlight, even if the actual illuminance (to the human eye) were 0.12 lux.

Impact Thresholds

The next step is to map those areas where light from the installation exceeds, to the organism, thresholds that would be considered to cause a significant environmental impact. We elected to use thresholds associated with the natural brightness of moonlight during the lunar cycle (Table 4). Given the known effects of lunar cycles on species, the full moon is one logical threshold. The brightness of the full moon dimmer at higher latitudes because of the angle of incidence and the amount of atmosphere traversed (Horvath 1993), and is also affected by elevation (Green 1992). It also varies with whether the moon is above the horizon and how high. Although calculations for all of these conditions can be made and empirically calibrated (Śmielak 2022), we elected instead to consider 0.1 lux as a full moon, and set this as the threshold over which adverse impacts would be assumed to be present.

Table 4. Illumination from lunar phases, showing maximum possible values (which would be under clear conditions at the equator and high elevation).

	Phase Angle	**Brown (1952) (lux)**	**(Krisciunas & Schaefer 1991) (lux)**
Full 100% illuminated	0?	0.37	0.423
Gibbous 75% illuminated	60?	0.10	0.071
First and Last Quarter 50% illuminated	90?	0.043	0.028
Crescent 25% illuminated	120?	0.013	0.008

Although many may think that lunar illuminance varies linearly through its cycle, it does not (Figure 31). The brightness of the moon increases exponentially toward the full moon, and, moving away from the full moon, the waxing moon goes down before the night is over and the waning moon does not rise until later in the night, meaning that through much of the month, illumination is far less than the full moon maximum. In fact, 82% of each month, illumination levels are at <1% of that produced by the full moon (Śmielak 2022). Only 0.7% of the time is illumination more than 0.05 lux (assuming a 0.1 lux maximum). Brightness of moon also varies by season, and can be less than half of brightest moon in summer at high latitudes. It is reasonable to describe 0.01 lux as a “normal” condition, while any illumination >0.001 would indicate that the lamp is visible and could affect orientation even if scene brightness were negligible. We therefore mapped the areas of each study site where each organism would be exposed to the equivalent of <0.001, 0.001–0.01, 0.01–0.1, 0.1–1, 1–10, and >10 lux. Knowing the natural variation of lunar illumination, >0.01–0.1 lux (adjusted for organismal vision) can be considered unnatural and potentially a significant adverse impact, while >0.1 lux implies that lunar cycles are erased completely and would definitely constitute a significant adverse impact.

Results

The comparison of as-built conditions with the different scenarios illustrated the potential for strategies such as shielding and spectrum to mitigate light impacts on the example species. To be able to set thresholds for potential impacts, the conversion factors were first necessary.

Lamp Conversion Factors

We tested the conversion factors derived from the two spectral response curves for *Ambystoma* and *Thomomys* (as a stand-in for *Dipodomys*) with 25 spectral power distributions used in previous investigations (Longcore et al. 2018), using the percentage of moonlight intensity as the reference (Figure 34). For *Ambystoma*, values ranged from 0.48 for a low-pressure sodium lamp to 1.26 for daylight (D65). For *Thomomys*, values ranged from 0.20 for a custom filtered LED with almost no blue (Anna's light, see Longcore et al. 2018) to 1.42 for daylight (D65). These conversion factors correlated with correlated color temperature (CCT) of the lamps both highly (0.83 for *Ambystoma* and 0.87 for *Thomomys*) and significantly (p<0.001). For lamps under consideration in the scenarios, these relationships suggest that for *Ambystoma*, a low-pressure sodium lamp could be almost twice as bright as moonlight when measured in human-centered lux and still seem the same intensity as 0.1 lux of moonlight to the salamander. For *Thomomys*, a low-pressure lamp could be three times as bright as 0.1 lux of moonlight for humans but seem to be of equal brightness to the rodent.

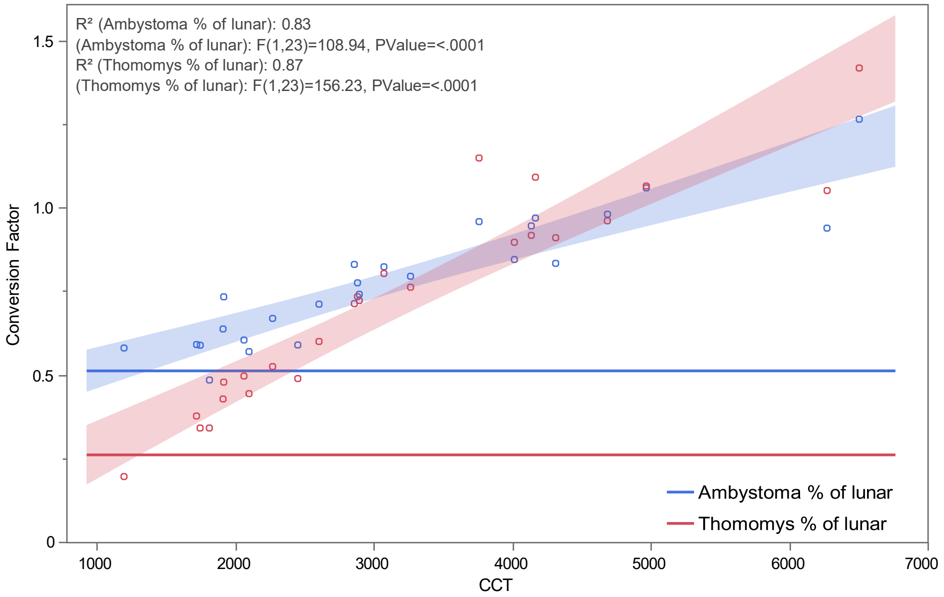

Figure 34. Relationship of Correlated Color Temperature (CCT) with visual conversion factor for *Ambystoma* and *Thomomys*. This regression uses 25 lamp spectra of commercially available lamps plus sunlight and moonlight. The steeper slope of the curve for *Thomomys* means that reduction of impacts using spectrum should be more effective for organisms with this visual system compared with a visual system like *Ambystoma*.

Effectiveness of Shielding

Illuminance maps of the as-built and shielded scenarios for 112/13 show a large difference in the area affected by light at >0.001, 0.001–0.01, and 0.01–0.1 lux. For the as-built scenario, light exceeds 50 lux (human) at the roundabout, which is substantially higher than recommended by good lighting practices. With appropriate shielding of the as-built lights, the maximum was reduced to 33 lux, and the area exceeding 1.0 lux was reduced substantially (Figure 35). With the shielding, two corners of the study area, approximately 600 feet from the roundabout, were at illumination <0.001 lux (salamander) and probably would be minimally affected by the lights. In the as-built condition, light >0.1 lux (salamander) extended >200 feet outward from the approach areas of the roads into what presumably was endangered salamander habitat.

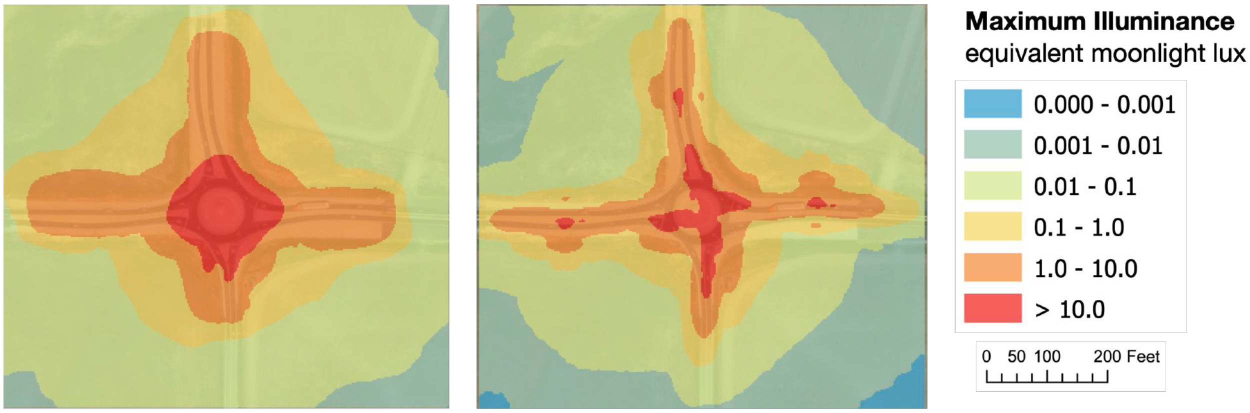

Figure 35. Comparison of maximum illuminance (vertical or horizontal) in as-built and shielded lighting systems for the 112/13 intersection in lux.

At the second site, reflectivity was not computationally feasible to calculate so the effects of the shielded scenario, while still apparent, are less dramatic (Figure 36). Similarly, vertical lux were not calculated, reducing the apparent impact of the lights at greater distances. The intersections were not lit as brightly as the 112/13 site overall and the shielding similarly reduce the area of >10 lux horizontal illuminance. We found that with these horizontal-only measurements and excluding reflectivity, the shielded scenario appears not to be as effective at reducing the area of impacts at the <0.01 lux level. This difference arises in part because the house-side shields available for the lights used at this location reduced the amount of light behind the luminaire and reduced overall lumen output, but increased the throw of light in front of the luminaire in the 80–90? angle. As a result, while the hotspots of maximum illumination were somewhat reduced, the use of these house-side shields increased the area illuminated >0.01 by two acres, a 16% increase.

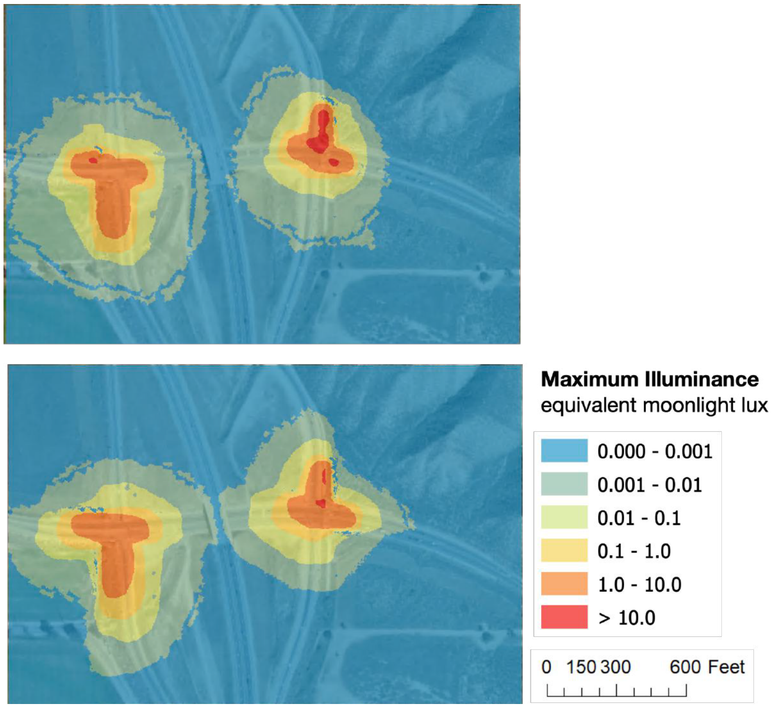

Figure 36. Comparison of as-built and shielded lighting systems for the SR-79/Gilman Springs Road intersection in lux.

Effectiveness of Spectral Control

Spectral control reduced the area impacted at each threshold for both shielded and unshielded scenarios at both sites, as follows from the nature of the calculations (Figure 37 and Figure 38). For the 112/13 site, the total area illuminated >0.01 lux decreased from 16.4 acres to 15.1 acres in the as-built scenario (8% decrease) and from 12.4 acres to 10.1 acres in the shielded scenario (19% decrease) with the use of a Low Pressure Sodium lamp (Figure 39). Similarly, use of LPS would reduce the area illuminated to >0.1 lux from 7.2 to 5.9 acres in the as-built scenario (18% decrease) and 5.2 to 4.5 acres in the shielded scenario (13% decrease). Together, converting to LPS and shielding from the as-built condition would reduce the area >0.01 lux by 38% as perceived by a salamander. LPS lamps are no longer commercially available, but a ~1700K LED plus shielding would reduce the >0.01 lux area to a salamander 33%.

No reliably comparable numbers are available for SR-79/Gilman Spring Road because of the computational limitations, but based on horizontal illuminance alone with no reflectivity, the area exposed to >0.01 lux to a nocturnal rodent could be reduced by 21–25% for shielded and unshielded scenarios and the area exposed to >0.1 reduced by 12–17%, both by converting from a 3000 K LED to LPS lamp, or nearly exactly that much by using a ~1700 K LED in lieu of the LPS.

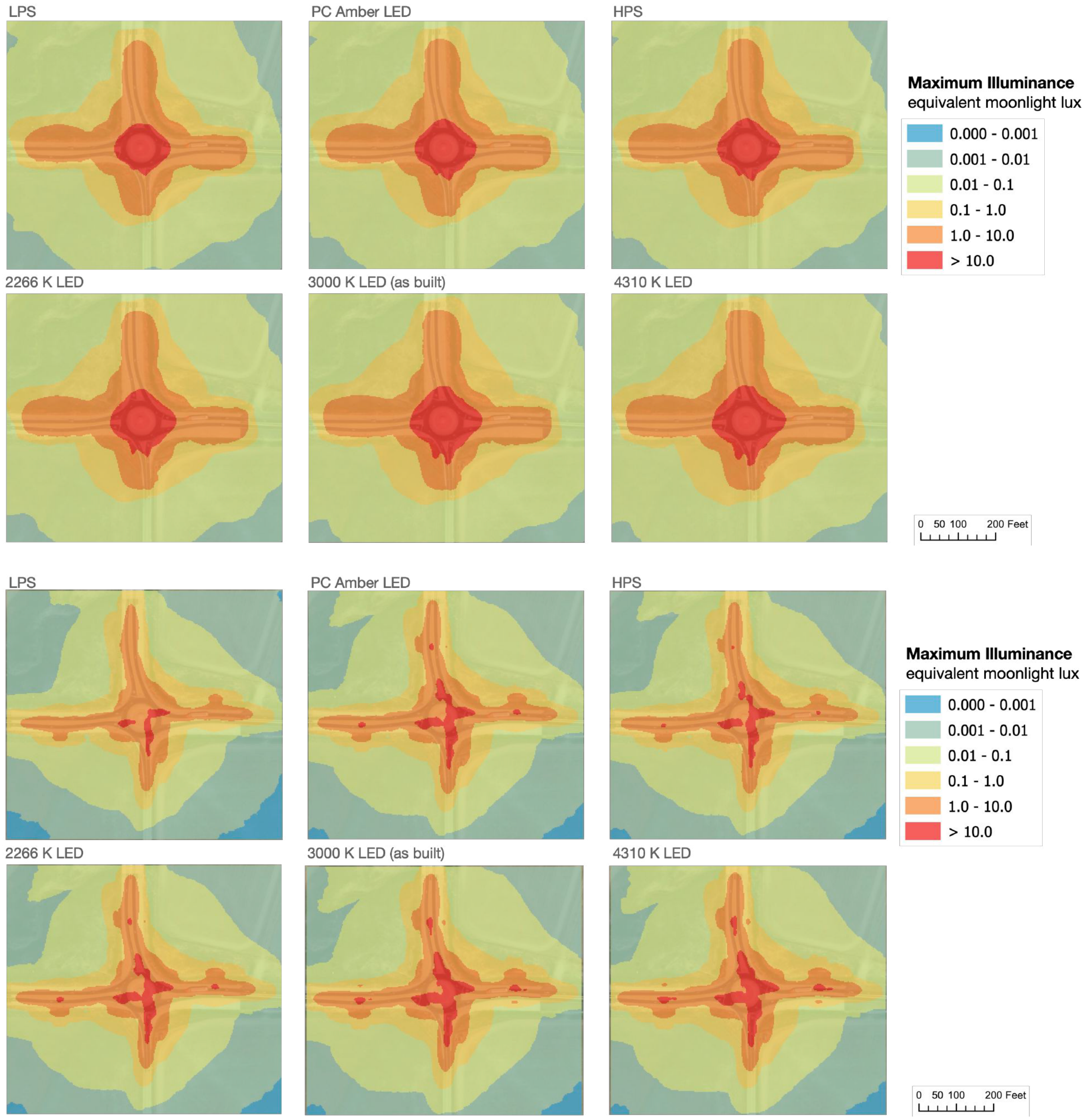

Figure 37. Maximum illumination (vertical or horizontal at 3-inches above ground) from 112/13 intersection as perceived by *Ambystoma* salamanders for different spectra of lights, if the lights were modified with off-the-shelf shielding available from the manufacturer. A measurement of 0.1 lux means *Ambystoma* would perceive the brightness equivalent to 0.1 lux of light with the same spectrum as the full moon. Top: Unshielded. Bottom: Shielded.

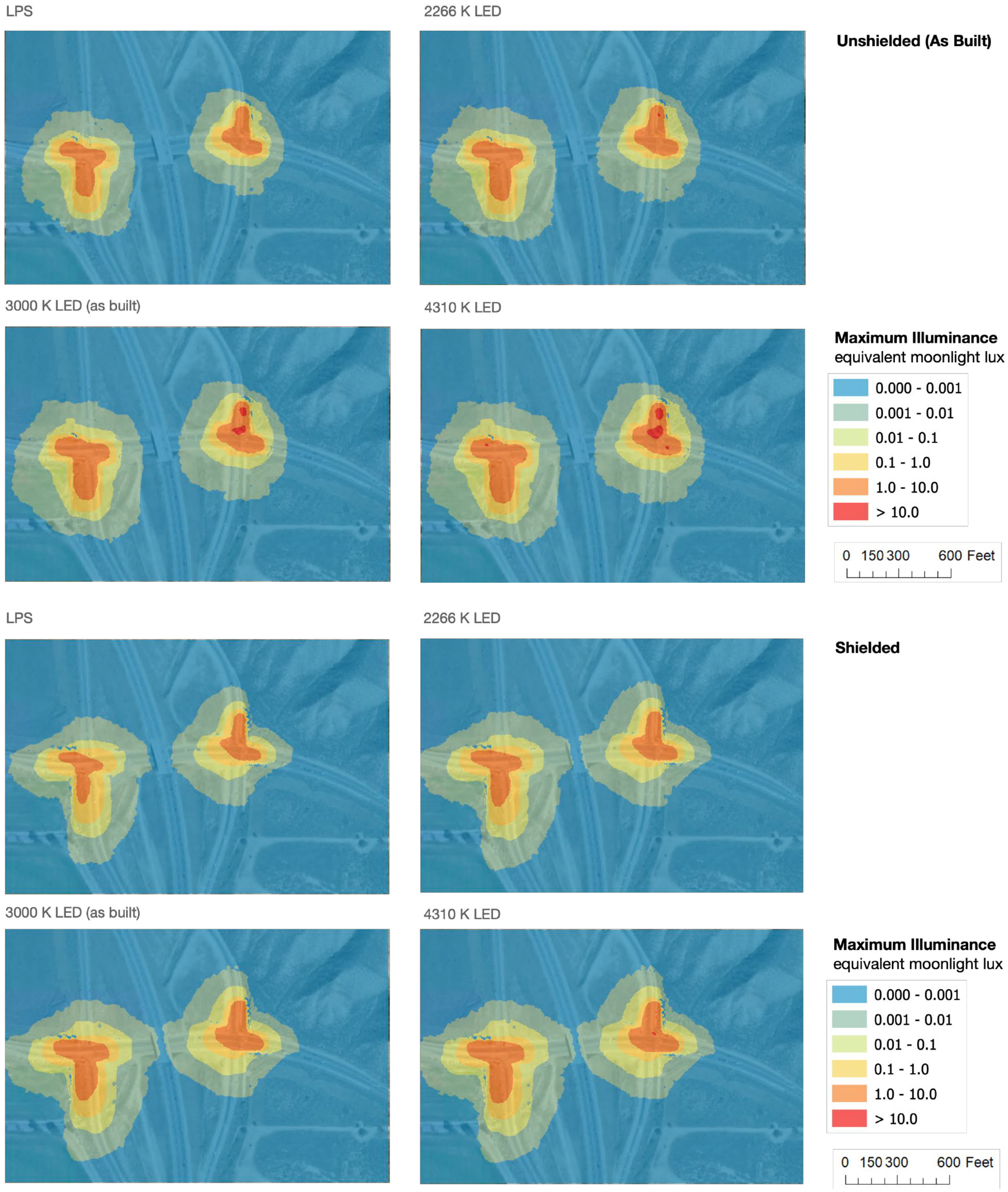

Figure 38. Horizontal illumination from 112/13 intersection as perceived by a rodent with a similar visual system to *Thomomys bottae*. A measurement of 0.1 lux means *Thomomys* would perceive the brightness equivalent to 0.1 lux of light with the same spectrum as the full moon. Top: Unshielded, Bottom: Shielded.

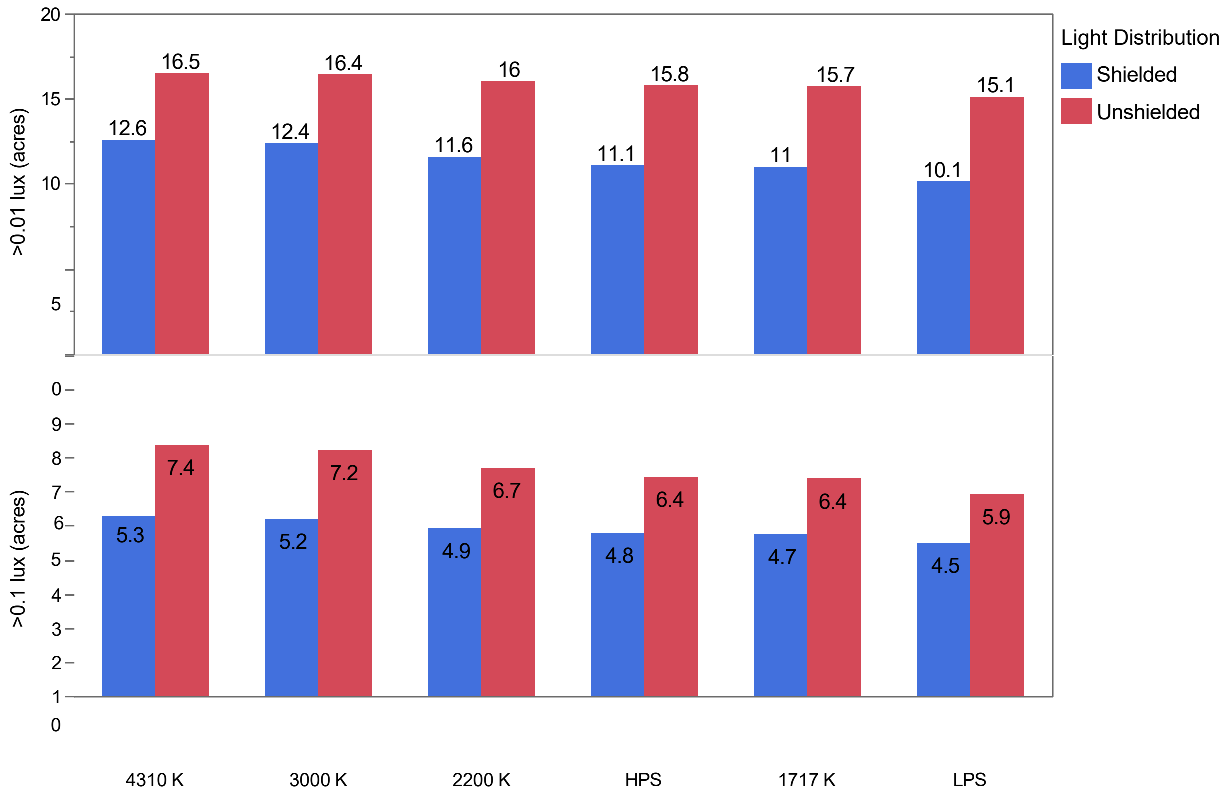

Figure 39. Acres illuminated at the salamander equivalent of >0.01 and >0.1 lux of moonlight for unshielded and shielded fixtures and a range of color correlated temperature lamps. The as-built condition is unshielded and 3000 K.

Discussion

The methods developed here demonstrate an approach that could be used in the project development and environmental impact process to calculate and mitigate adverse impacts from lighting associated with roadways. Each element of the methods could be improved, and the assumptions needed to ultimately produce estimates of areas impacted are not perfect. The approach is, however, a vast improvement on qualitative mitigation approaches that do not map impact zones, and presents an opportunity for improvement through implementation. As agencies discuss such methods for future projects, some topics merit consideration.

With the exception of accounting for animal visual systems, this approach could be implemented using human-centered illumination measurements of lux, given agreement on impact thresholds. Lighting engineers typically provide outputs in foot-candles to a resolution of perhaps 0.1 fc, which is roughly equivalent to 1 lux. They can, however, be asked to provide output in lux and at a precision of 0.001 lux within off-the-shelf lighting software such as AGi32. It is also possible to request vertical illumination in addition to horizontal illumination, and to ask that the orientation be toward the nearest light to investigate the worst-case scenario for wildlife, as described in this report. The transfer of light software outputs to GIS for further analysis and intersection with, for example, endangered species habitat areas, is currently problematic and requires innovation either in the lighting engineering software or development of GIS-resident lighting engineering software. The latter is in process, but not available except as a service, in the form of GIS-native lighting calculations in ArcGIS Pro (see evarilux.com; Figure 40 through Figure 42).

Figure 40. Example of GIS-native calculation of light volumes at 0.1, 1, and 10 lux (horizontal) for the 12/113 roundabout, produced by EvariLux.

Figure 41. Three-dimensional visualization of 0.1, 1, and 10 lux (horizontal) light volumes for SR-79 and Gilman Springs Road, calculated native in a specialized GIS environment by EvariLux.

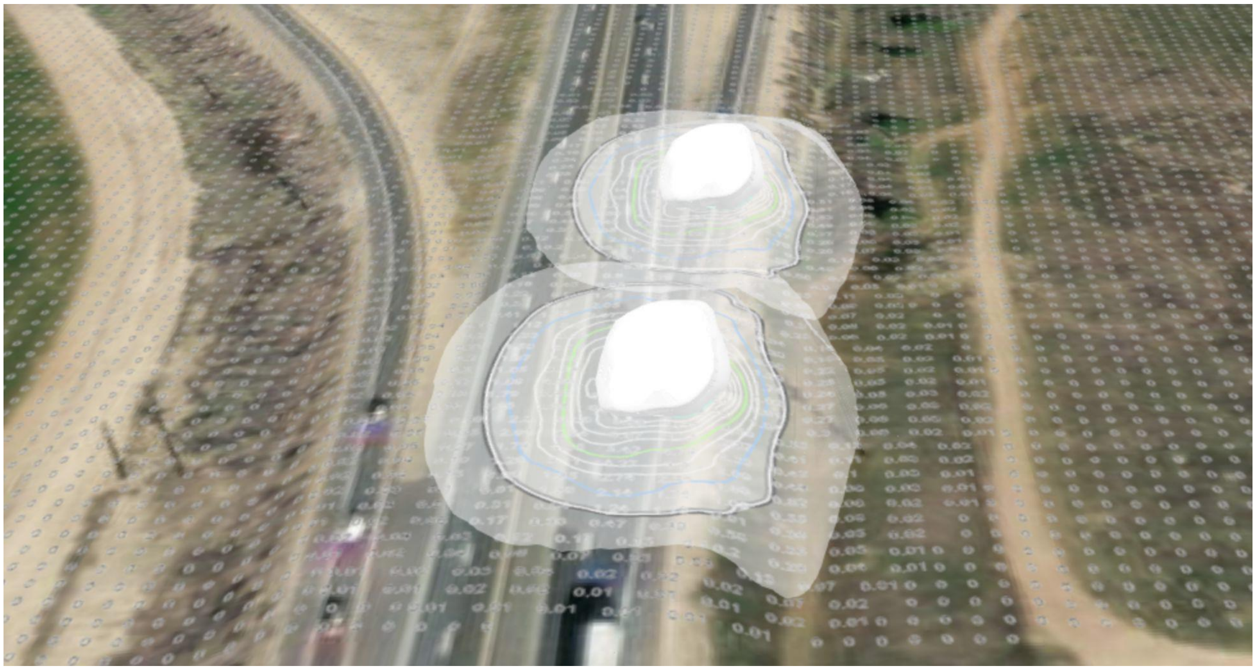

Figure 42. Demonstration of GIS-native calculation of illumination from southern lights at SR-79 and Gilman Springs Road. Illuminations to 0.01 are gridded on the surface and volumes of 0.1, 1, and 10 lux are visualized. As the grid extends, a value of "0" means "<0.01" lux.

Alternate approaches such as EvariLux, however, do not yet provide a 0.001 lux resolution and only provide illumination at the angle of incidence with the topography and at ground level. Notwithstanding the current state of the system, it is a promising development for incorporation into workflows for environmental impact analysis.

Improved software environments to incorporate all elements of analysis into larger products are necessary. Using AGi32, we were unable to calculate full radiosity, incorporating reflective surfaces, into what would be a modestly sized study area from the perspective of environmental impact analysis. A full radiosity calculation considers the light reflected off surfaces that is then incident on the calculation point, which requires surface characteristics, and therefore requires a greater computational effort. Direct-only calculations only consider the component of illuminance the point is directly receiving, that is why the values are going to be lower than reality. There is not a large amount of illuminance lost from the indirect component due to the low reflectance of the terrain coupled with flatter topography studied in SR-79 example, but it has the potential to affect especially the lower illumination thresholds studied.

Light distribution is directly affected by shielding, and direct-only calculations are informative in capturing how the light distribution is reduced. Therefore, direct-only calculations can determine impact reduction of mitigations strategies such as reducing total lumen output and shielding, but ideally, software would be able to do these calculations incorporating reflections at scales of 10s of acres at a time.

Upper limits on roadway illumination should also be considered in the course of impact analysis and mitigation discussion. Current industry guidelines (e.g., IES 2021) specify minimum but not maximum luminance and illuminance values. The center of the roundabout at the 112/13 site was over 52 lux, which is ten times brighter than the recommended minimum and far, far greater than necessary for roadway safety at this location. The maximum illumination of the lighted locations at SR-79/Gilman Springs Road was, in contrast, 22 lux. In areas with sensitive habitat, lighting engineers could minimize costs associated with mitigation of adverse impacts on wildlife by using good design and shielding to keep illumination levels close to the recommended values recommended by the profession.

Somewhat contradictory results were found from the shielding scenarios. In both instances, shields redirected light and increased the evenness of the light coverage on the roadway. For the 12/113 site, for which full radiosity modeling was feasible, shielding substantially reduced the area surrounding the intentionally lighted roadway targets that was illuminated to >0.1 and >0.01 lux. In this example, shielding reduced the areas exceeding these thresholds more than any potential controls on spectrum. For the other site, lacking full radiosity measurements, the available shields for the lamps reduced the maximum illumination values, but moved some of that light into areas further away from the luminaires in the other direction. So although the overall illumination was lower, it was distributed differently and the areas at >0.01 lux and >0.1 lux increased substantially (16% for the area exposed to >0.01 lux and 38% for >0.1 lux). These results suggest some guidance for environmental review. First, full radiosity modeling is needed so that impacts are not underestimated. Second, the results of shielding may depend on the specific lights being used and the shields available for them. Most roadway lamps have front side, house side, and cul-de-sac shields, but how they direct the light may vary by manufacturer, so working through mitigation strategies during project development and in environmental review is recommended lest the addition of shields result in unintended consequences. Third, depending on the visual system of sensitive species at a site, shielding may provide more or less benefit than changing spectrum of lamps. Together, these results indicate the need for both development of modeling platforms for easier assessment of shielding options and to approach each case individually to investigate the specific equipment and shielding that can be used.

This research also provides a workflow by which animal visual systems can be incorporated into assessment of impacts of lighting systems. It depends on agreement over what lighting level should be considered to be a significant impact — we have presented an argument for 0.01 lux equivalent and certainly 0.1 lux equivalent — and on whether the available visual response curves are adequate. To the latter question, only further research will reveal whether the spectral response curves compiled in this project (Longcore 2022) are adequate and even whether visual response curves can be further shown to correlate with adverse outcomes in the field, building on existing empirical work available for some taxa (Longcore et al. 2015, Rodr?guez et al. 2017, Donners et al. 2018, Deichmann et al. 2021). Using available curves of the closest related species is a better alternative than not incorporating spectral concerns at all, but is probably most appropriate to situations where consultations are needed to assess impacts on individual listed species and estimates of areal impacts are needed to calculate mitigation requirements. In such instances, the default could be to use lux to map impacts, with adjusting impact areas downward through changes in lamp type an option when spectral responses are well-known.

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Chapter 5. Guidance for Evaluating and Mitigating Impacts to Sensitive Species from Artificial Light at Night in Caltrans Projects

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Introduction

As outdoor lighting technology has changed, the characteristics intrinsic in different lamp types have raised questions about environmental impacts and how to mitigate them. Introduction of light emitting diode (LED) lamps has transformed lighting practice and brings both risks of adverse impacts and enabling technologies to reduce those risks. As a result of their luminous efficacy, LEDs have become the most widely used source for street and area lighting and are likely to remain so until further developments in solid state technology come to fruition.

The shift to LEDs influences assessment of potentially adverse environmental impacts in three ways. First, LEDs first on the market for outdoor lighting were based on a phosphor-coated blue LED and tended to be full-spectrum light sources with high blue content. Although other spectral compositions are now available, much of the perception of LEDs and their environmental consequences arises from their spectral content. Second, LEDs may flicker at rates that are imperceptible to humans but are visible to other species (Inger et al. 2014, Barroso et al. 2017). Little research has been done on this topic. Third, because of the higher energy efficiency of LEDs, humans have a tendency to use more light, in a human behavioral phenomenon known as Jevons Paradox (Bar? 2013). While keeping these differences in mind, guidance for assessing and mitigating unintended adverse consequences of LEDs in street and roadway lighting is substantially similar to that for other technologies, and certain characteristics of LEDs make them more amenable to mitigation approaches than legacy technologies.

This report summarizes the general categories of potential adverse impacts of street and roadway lighting on terrestrial wildlife, presents a toolbox of approaches to mitigate those potential impacts, and provides discussion of considerations for the listed species for which Caltrans has the most inter-agency consultations.

The focus in this report is on the project scale for roadway lighting, so some mitigation tools that may be used in dark sky ordinances at the municipal level are not included. For example, some light pollution ordinances designed to mitigate sky glow or wildlife impacts include area-based limits on lumens produced in a project. Decision on minimum lighting for street and area lighting projects by an agency such as Caltrans are likely to be governed by internal policies and referenced national standards (e.g., from the Illuminating Engineering Society), so introduction of a lumen limit might come into conflict with required lighting levels. It is worth noting, however, that such national and international standards represent consensus views from industry participants and have not historically been supported by robust empirical evidence (Fotios and Gibbons 2018).

Categories of Adverse Effects from Artificial Light at Night

As reviewed in Chapter 1 of this report, artificial light at night can affect terrestrial wildlife in many ways. In order of the evidence available for LEDs and these responses, they are: movement, development, reproduction, gene expression, ecological interactions, stress and fear, sleep and daily rhythms, immune function, and visual function.

Movement in response to light is well-known and studied for many groups of organisms. Attraction to or repulsion from light is inherent in the biology of many organisms and can result in both direct mortality (e.g., insects attracted to and incinerated at a hot light) and indirect impacts (nocturnally migrating birds attracted to suboptimal stopover habitat by lights). Attraction and repulsion affects species community composition and influences ecological interactions (discussed more below).

From a mitigation perspective, the goal is to avoid this type of impact to the maximum extent possible because it could only be considered to be a positive impact in the instance of dissuading species from encountering a greater harm (e.g., using lasers to keep waterfowl from landing in contaminated ponds of wastewater or encountering power lines or aircraft) (Adams et al. 2021, Baasch et al. 2022). The scale that influences on movement may occur depends on the species and situation. For nocturnal migrants, birds may be attracted to lights from kilometers away (Van Doren et al. 2017). Insects may be attracted from hundreds of meters (Frank 2006) or even kilometers (Tinkham 1938, Tielens et al. 2021). Because orientation often involves a species detecting contrasts in light on the horizon, even small amounts of light that would not appreciably increase local scene brightness are important. This phenomenon is understandable as a human in terms of imagining seeing a single match illuminated at a 100 m or greater distance. It would not provide enough light to illuminate one's immediate surroundings but it would certainly be sufficient to orient and move toward or away from the light.

While the effects of artificial light at night on movement and orientation may extend considerable distances (kilometers), effects on **organismal development** are associated with chronic illumination from nearby sources. For many of the studies showing influences on egg or larval development, the recorded illumination levels tend to range upward from 3–5 lux and consequently would be found in the immediate vicinity of lights themselves, not at a distance. For sensitive nocturnal species, such as amphibians, exposure to light <1 lux can have an impact on development and these levels are comparable to those experienced in a wetland with nearby street lights (Wise 2007).

Reproductive state of organisms can be affected by exposure to light at night. Here, light of 0.3 lux, 0.5 lux and higher can influence the sexual organ status of songbirds. Such conditions could be produced in the vicinity of roadway lighting. Effects on reproduction also include intraspecific communication in bioluminescent organisms locating mates (Owens and Lewis 2021, Van den Broeck et al. 2021). Similarly, **gene expression** can be altered under artificial light at night, which provides evidence of the physiological mechanisms that underly other measurable outcomes, such as development and behavior.

Changes in movement and visibility arising from light at night can influence **ecological interactions**. These include predator-prey dynamic, pollination, and other interspecific interactions. Changes in these interactions may have substantial secondary consequences, such as elimination of a species from an area where lighting has altered its relationship with either its prey or predators. Key examples of these include foraging of bats on insects at streetlights (Voigt et al. 2018), interruption of pollination mutualisms (Knop et al. 2017, Giavi et al. 2020), and avoidance of illuminated areas by vulnerable prey species (Rotics et al. 2011).

Chemical and behavioral markers of **stress** and **fear** are sometimes also found in wildlife exposed to light at night. Such findings are not, however, universal. The impact of such stress may be evident only in secondary outcomes, such as longer infectivity periods for disease, as was found for birds with West Nile Virus (Kernbach et al. 2019).

Artificial light at night affects **sleep** and **circadian rhythms** in wildlife, although techniques to research sleep in free-ranging wildlife are only now being more widely deployed (Robert et al. 2015, Aulsebrook et al. 2020). Light can affect daily rhythms by altering and degrading sleep as well as by extending activity patterns of diurnal species into crepuscular and nocturnal periods. Depending on the species group, thresholds for disruption of circadian rhythms as measured by the nocturnal hormone melatonin vary from 5 lux downward to <0.01 lux (Grubisic et al. 2019).

Other documented effects of light at night on wildlife species include altered **immune responses** and potential impacts to **vision**. The effects on vision are unlikely to occur in the normal deployment of street and area lighting, but the concentrated point-source nature of LEDs could pose a risk if not properly managed.

Mitigation Toolbox

Mitigation of the unintended adverse effects of light at night should be considered with the realization that there is no "safe" level under which anthropogenic light will both be beneficial to human vision *and* have no effects on ecological systems. Circadian rhythms of wildlife can be synchronized at illumination levels below the threshold for human vision. Mitigation is therefore an exercise in providing light necessary for human safety and needs without exceeding that amount.

Conversion to LEDs as the dominant source of outdoor lighting has raised concerns among light pollution advocates from ecological and astronomical perspectives. These concerns arise from three characteristics of LEDs that make them different. First, historically the spectrum of commercially viable LEDs was more weighted toward blue wavelengths to be energy efficient. Technological innovation has reduced the economic need for this spectral tendency, but most LEDs continue to produce broad-spectrum light that is more ecologically damaging than historical sources such as High Pressure Sodium lamps. Second, there might be some different effects from flicker and the point-source nature of the light. This topic deserves more research. Third, people use more light because it is less expensive, a phenomenon known as Jevons Paradox (Bar? 2013). This tendency has not abated and remains a substantial challenge to reducing light pollution.

Another important piece of information to contextualize mitigation efforts is the knowledge that the lighting recommendations for minimum levels used as standards are not based on robust empirical evidence, but rather reflect consensus within the lighting industry (Fotios and Gibbons 2018). The decisionmaking process for the Illuminating Engineering Society (IES), which produces the guidelines that most agencies follow, is one of consensus, where a single member of a committee tasked with developing a "recommended practice" can hold up that document until a demand for a higher (or lower) illumination level recommendation is met. It is therefore possible for agencies and government bodies to deviate from the IES recommended practices and standards if supported by good reasons for doing so, such as balancing different environmental and safety considerations. For example, the Street Lighting Master Plan for Salt Lake City, states "Salt Lake City lighting standards are based on IES recommendations with allowances for adaptive standards that encourage dimming strategies relating to pedestrian activity, community engagement, wildlife and dark skies lighting" (Salt Lake City, UT, Street Lighting Master Plan, 2020, Volume 1, p. 14). Governments have the capacity to devise and implement reasonable and scientifically supported deviations from IES recommendations without undue increase in liability.

Within this context, principles have been adopted for responsible outdoor lighting, having been jointly developed by the Illuminating Engineering Society and the International Dark-Sky Association. They are:

- All light should have a clear purpose;
- Light should be directed only where needed;
- Light should be no brighter than necessary;
- Light should be used only when it is useful; and
- Use warmer colored lights where possible.

We consider each of these in some additional detail and relevant to the findings of this project. Techniques to follow these principles become the toolbox for mitigation of lighting impacts.

All Light Should Have a Clear Purpose

Not all roadway lighting increases safety. To avoid adverse unintended consequences, careful consideration should be given whenever lighting is proposed to ensure that the decision is supported by solid empirical evidence of a specific benefit. Caltrans does not currently have a policy of providing continuous roadway lighting, which is an excellent choice because continuous lighting provides little to no benefits to traffic safety. As an overall policy issue, responsible lighting practice recommends that roadways not be lighted unless there is a proven benefit, especially given the increasing intensity and throw of onboard vehicle lighting.

Light Should Be Directed Only Where Needed

As demonstrated in two cases studies (Chapter 4), shields are available for roadway lighting that can direct light where it is needed. As demonstrated, these shields can direct light more precisely onto roadway surfaces and adjacent approach zones while reducing impacts elsewhere.

Not all shields operate the same, however, and as demonstrated in Chapter 4, a shield can move light around. In one of our examples, the shield reduced the light thrown behind the pole, but reflected that light into the 80–90? region in front of the pole, resulting in an overall greater footprint of light extending outward from the installation. Care must be taken to calculate the light patterns from each installation in a sensitive location to ensure that such conditions are avoided.

It should always be the case that no light is emitted directly upward from roadway lighting. This is usually referred to as “full cut-off” lighting and is essential to reduce impacts to dark skies through sky glow. However, for ecological impacts in areas surrounding the installation, it is equally important that light not be emitted at 80–90? from the vertical, because light emitted at these angles from the height of a roadway lamp is thrown for large distances across what may be sensitive habitat. Although conventional illumination maps from lighting engineers will not show this impact, our analysis (Chapter 4), shows how this light can cause large areas to be subjected to highly unnatural light conditions each lunar cycle. In fact, reducing light to the degree possible in the 60–80? zone would also be beneficial, especially behind and in front of the fixture (backlight and frontlight) once the roadway is adequately illuminated for the purpose of the installation.

Attention should also be paid to lighting associated with signs. Often, Caltrans signs are illuminated by floodlights that are at the bottom of the sign and directed upward. These designs cause substantial off-site spill and glare. Reflective signs are far preferred (no light) or signs with interior illumination rather than floodlights.

Light Should Be No Brighter Than Necessary

Guidance for roadway lighting provides minimum illumination levels and frequently specifies the desired ratio between the maximum and minimum illumination. Lighting engineers are used to designing systems that meet these criteria. To achieve this goal of responsible lighting, however, it is necessary to limit maximum illumination, which is not covered in the recommended practice documents that are used to set illumination standards. Although future guidance documents may specify maximums, depending on the underlying lighting zone where a project is located, they are not currently set.

Our example of the SR 12/113 roundabout intersection (Chapter 4) demonstrates the need to set illumination maximums. At that site, the as-built lighting exceeds 50 lux in the middle of the roundabout, which is about ten times brighter than is recommended for this type of roadway feature. As a result, the area surrounding the intersection is exposed to far greater light than is necessary. During environmental review, routing mitigations could be put in place that limit maximum roadway illumination to reasonable levels (e.g., no more than double the minimum levels).

Lighting designers and engineers should keep in mind that the thresholds for impacts of light at night on other species are orders of magnitude below the outputs of typical outdoor lighting, so any reduction in intensity that can be achieved while meeting design requirements will be beneficial to other species. Careful attention to all of the normal determinants of lighting levels is required (road type, pedestrian conflict level, lighting zone) to balance needed function of the lighting system with its adverse impacts.

Light Should Be Used Only When It Is Useful

One of the potential benefits of LED lamps is that they are easily controlled, turned on and off and dimmed, without any energetic cost. The lighting industry provides and integrates such controls into outdoor lighting systems as off-the-shelf components. As a result it would be possible for roadway and associated transportation lighting systems to be designed to be dimmed, extinguished, or otherwise limited when they are not needed. Such efforts have a long history as “dynamic roadway lighting” in Europe, wherein lights are dimmed after peak traffic hours for environmental reasons, with no unacceptable increase in collision rates (Hasson and Lutkevich 2002, De Molenaar et al. 2006). Although dynamic roadway lighting has been forecast, is technically feasible, and would save significant energy as implemented with LEDs, it has not yet had widespread adoption in the United States. This principle could be adopted for roadway lighting in California in a manner that reduced energy consumption, reduced adverse impacts, and maintained roadway safety if attention were turned to this approach.

Use Warmer Colored Lights Where Possible

The responsible lighting principles specify "warmer" lighting as preferable, which means light sources that have more yellow, orange, and red light compared with blue, violet, and ultraviolet (although UV light is rarely discussed). The reasons for this advice are several.

First, shorter wavelengths (blue, violet) scatter more in the atmosphere as an inherent physical property and therefore contribute more to skyglow when they escape. Astronomers and anyone who appreciates seeing the stars in a dark sky therefore prefer that longer wavelengths be used. The ideal is that a single long wavelength (or very narrow range of wavelengths) be used so that it can be filtered out of astronomical observations, such as that produced by Low Pressure Sodium lamps (no longer on the market) or Narrow Band Amber LEDs.

Second, the peak sensitivity to light for the circadian system for most species of organisms, including humans, is in the blue region of the spectrum at 479 nm. Avoiding light in this spectrum will reduce its circadian impact on humans and other species with circadian sensitivity to light at lower intensity thresholds than humans.

Third, across most groups of wildlife, visual responses are more sensitive at shorter wavelengths than at longer wavelengths, especially when compared with human photopic vision. Humans have a peak sensitivity for photopic vision, which is primarily in use for most outdoor lighting situations such as driving, at 555 nm. Humans also see well into the yellow and red region of the spectrum, which some other species do not. These sensitivities were compiled and summarized in Chapter 3.

The use of the term "warmer" therefore encompasses a qualitative description of light that it be more heavily weighted to the longer yellow, orange, and red wavelengths. Several options for quantitative description of these characteristics are available.

The most useful way to describe spectrum is to simply provide the **spectral power distribution** (SPD) for a light source, which gives the relative power output in 1 nm bins across the electromagnetic spectrum. With SPD and total energy within the visible spectrum any other metrics can be calculated.

The most common semi-quantitative method to describe light spectrum is **correlated color temperature** (CCT). This number is the temperature, in Kelvin, of a black body that would have a hue most similar to the source in question (Galad?-Enr?quez 2018). Although the overarching premise that low CCTs will appear more yellow and high CCTs will appear more blue, the same CCT can describe many different combinations of light wavelengths. It is a "far from perfect descriptor" of spectrum but does have widespread use across the lighting industry.

Other metrics sometimes used to provide a single number to describe the spectral characteristics of light are the percent of the light that is less than a certain threshold, such as <500 nm or <530 nm.

Another assessment of spectrum is the degree to which a lamp influences the melanopic system (peaking at 479 nm) compared with the standard of daylight. This becomes a measurement of 0 to 1 with 0 indicating no overlap with the melanopic system and 1 indicating equal overlap as the D65 daylight standard. Related, the ratio of melanopic to photopic light from a lamp can be calculated as the "M/P ratio."

Although deciding on an ideal index to describe the spectral characteristics of light currently garners attention in the lighting profession, from a practical perspective all of the current metrics are quite similar. For example, given a database of real-world lamps, the values for CCT, melanopic response, M/P ratio, and % under 530 nm all correlate highly and significantly (r ⎬ 0.9; p < 0.0001). The percent light under 500 nm also correlates highly but not quite as well.

To illustrate the potential to mitigate adverse impacts on different groups of organisms, composite visual response curves were developed for each order for which information was available (see Chapter 3). Then the intersection between a set of 30 real-world illumination sources and these visual response curves was calculated following Longcore et al. (2018), in which each source is compared with daylight (D65) as the standard. Each of these values was then plotted relative to the summary metrics of spectrum—CCT, melanopic response, % light <500 nm, % light < 530 nm (Figure 43).

Across all classes of organisms and all summary metrics, light sources with lower blue emissions are predicated to have lower visual apparency to wildlife. The potential magnitude of such mitigation by class is predicted by the slope of the regression lines across each row — steeper slopes indicate a greater potential to reduce impacts. The greatest potential is for insects, arachnids, and mammals, while the least potential is for reptiles and birds. But for all groups, predicted impacts decrease with decreasing CCT, decreasing light < 500 nm or 530 nm, and decreasing intersection with the melanopic response curve.

These new results are consistent with the responsible outdoor lighting guidelines to use warmer colored lights whenever possible. Caltrans has specifications requiring that lighting meet a particular Color Rendering Index (CRI). CRI usually increases with CCT, but the relationship is highly variable and the goal for reducing light pollution impacts should be to use the lowest possible CCT while meeting the required CRI, which can be done even for low CCTs (e.g., <1750).

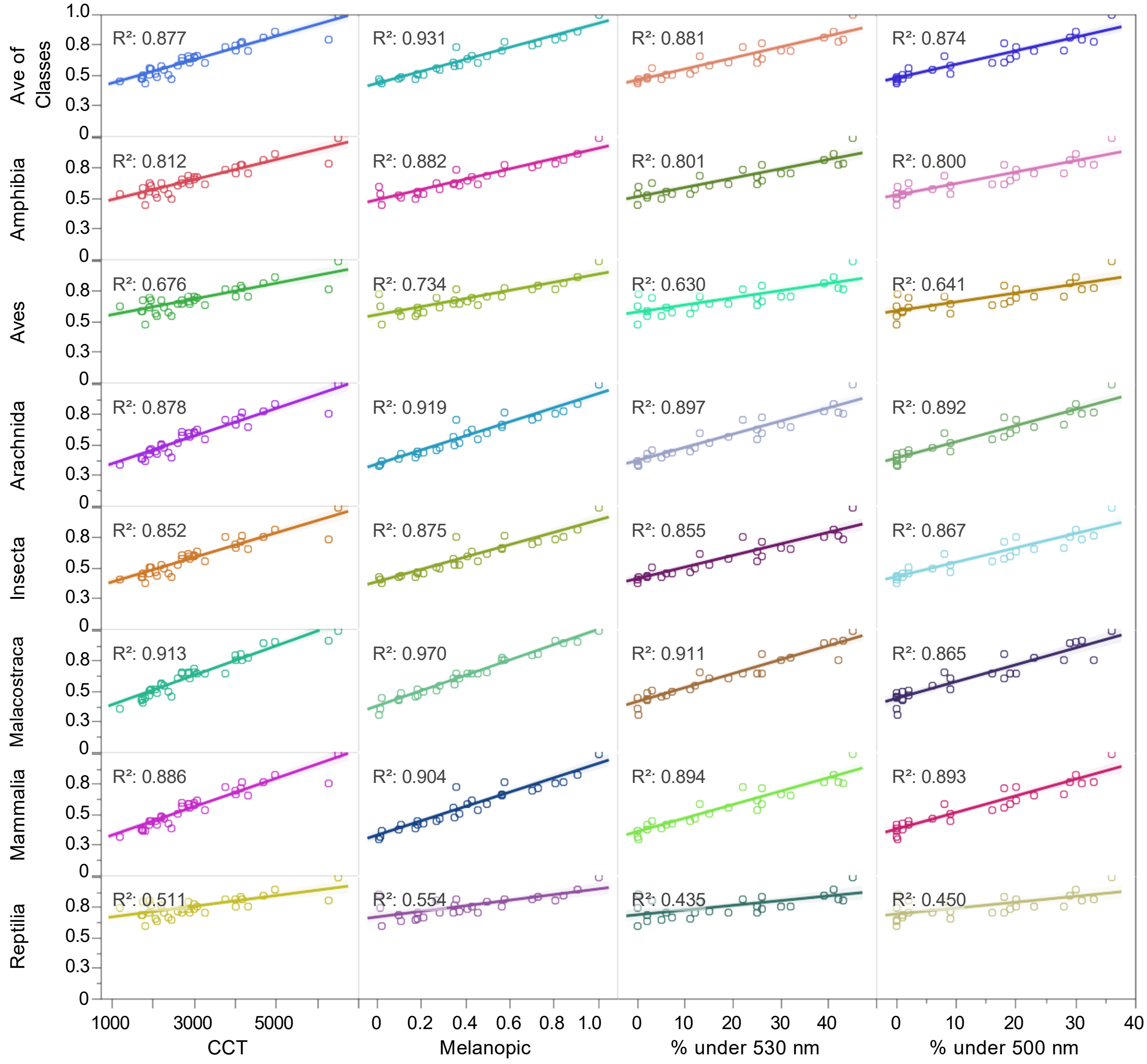

Figure 43. Class-level assessment of potential impacts of different light types.

Notwithstanding the attention paid to spectrum in this report and in currently in the lighting industry more broadly, the most important approach to mitigation is to reduce the amount of light reaching sensitive receptors, not to change its color. As demonstrated in the laboratory (Chapter 2), if light levels are low enough, no adverse impacts are found. This can be achieved by first reducing intensity, controlling direction and duration, and only then looking to spectrum to reduce remaining impacts.

With this toolbox of strategies, adverse impacts from new or retrofitted LEDs can be reduced. Then, remaining impact areas can be mapped in a manner responsive to wildlife visual systems

Species-Specific Considerations

To aid Caltrans in its consultations regarding listed species, the following sections summarize the ecology and relevant knowledge about nocturnal behavior, visual systems, and potential impacts of light at night on the species most commonly addressed in such consultations.

1. California Tiger Salamander
2. Desert Tortoise
3. Mohave Ground Squirrel and San Joaquin Antelope Squirrel
4. Giant Garter Snake and Southern Rubber Boa
5. Swainson's Hawk
6. Foothill Yellow-legged Frog
7. San Joaquin Kit Fox
8. Kangaroo Rats

California Tiger Salamander

California tiger salamander (*Ambystoma californiense*) is largely nocturnal and, like other salamander species, is susceptible to a range of impacts from exposure to light at night (Wise and Buchanan 2006, Wise 2007, Perry et al. 2008). These include alterations to foraging time arising from photophobia, potential effects on development, misorientation under different light conditions, and a range of physiological responses. Phototaxis is also documented (Liebgold and Carleton 2020). Salamanders and newts have extraocular photoreceptors that contribute to their magnetic orientation, which can be disrupted by the wavelength and intensity of light present (Phillips et al. 2001).

Salamanders are susceptible to disruption in melatonin production, which has the follow-on effects of affecting skin coloration, thermoregulation, and ability to visually adapt to darkness (Gern et al. 1983).

Artificial lighting can affect habitat and substrate choice in salamanders, drawing them to use areas in lighted conditions that they would not normally select (Feuka et al. 2017).

Some light, at natural levels of 0.001 lux, increases visual foraging (Wise and Buchanan 2006), while bright lights (under a 100 W incandescent bulb) increased activity but reduced foraging success in a salamander species (Placyk and Graves 2001). Chronic exposure to light at night has potential to limit foraging opportunities, which could reduce growth, survival during inactive periods, population size, and distribution (Wise 2007). Even "low" levels of light (~0.01 lux) are sufficient to affect nighttime foraging behavior of salamanders in a forest environment (Perry et al. 2008).

Artificial light at night influences other physiological and developmental responses. Tail regeneration was studied in the salamander *Plethodon cinereus* and showed slower rates of growth at 0.1 and 100 lux compared to 0.0001 and 1 lux (Wise et al. 2022). The presumed mechanism of this influence is through influence on melatonin production, which should be consistent across salamander species.

Visual sensitivity for California Tiger Salamander should be high across the human visual spectrum, although with decreasing sensitivity to longer wavelengths (see Chapter 3). As nocturnal species, salamanders are adapted to an environment where variation between 0.0001 and 0.1 lux is typical, and studies confirm that these light levels elicit behavioral responses. It is therefore not unreasonable to establish an impact threshold of 0.01 lux of moonlight and to use spectral tuning in addition to reduce potential impacts further.

Desert Tortoise

Desert tortoises are almost exclusively diurnal, except perhaps for emergence from burrows at night during rare rainstorms (Luckenbach 1982). Tortoises spend most nights in burrows (Bulova 1994), which would protect them from artificial light, but some do spend the night in shrubs at the surface (Bulova 1994), which could expose them to both natural and artificial light at night. An extensive camera trap study found only 23 instances of nocturnal activity of 993 trapping events (2.3%) (Agha et al. 2015). Looking to other turtle species, the Red-eared Slider (*Trachemys scripta elegans*) has 91% cones and 9% rods, meaning that it is heavily daytime adapted (Grötzner et al. 2020).

Desert tortoise visual systems are not described, but presumably are similar to other turtles, with a rod in the 500–520 nm range, and red, green, blue, and ultraviolet cones (Katti et al. 2019). As a heavily diurnal species, desert tortoises are most likely to see color across the human visual spectral range and also see ultraviolet.

Mitigation of light pollution in desert habitats of Desert Tortoises should probably focus on reducing impacts on the habitat as a whole, such as disruption of pollination mutualisms for the plants that make up the habitat or promotion of expansion of light-exploiting species that could pose direct threats to Desert Tortoise survival. Tortoises underneath dusk-to-dawn lighting could be susceptible to circadian impacts through extra-ocular photoreceptors characteristic of all non-mammalian vertebrates that are not yet fully understood (Peirson et al. 2009).

Mohave Ground Squirrel and San Joaquin Antelope Squirrel

Both Mohave Ground Squirrel (*Xerospermophilus mohavensis*) and San Joaquin Antelope Squirrel (*Ammospermophilus nelsoni*) are diurnal species (Kotschwar Logan 2016, Germano et al. 2021). These species are not at all crepuscular and are rarely seen until well after sunrise, as documented in the historical literature (Grinnell and Dixon 1918, Hawbecker 1953). More recent radiotracking of a wild Antelope squirrels similarly shows a limit in activity period to the daylight hours (Karasov 1981, DeCoursey et al. 1997).

The natural history of these squirrels, with the use of a burrow at night and almost exclusively diurnal activity patterns, should reduce the direct effects of artificial light at night on them. It is possible that their activity period could be extended under light at night, but this has not been demonstrated. Antelope squirrels can become active at night when their suprachiasmatic nucleus in the brain is lesioned experimentally, so they are physiologically capable of nighttime activity if their circadian system is altered to allow it (DeCoursey et al. 1997). The physiology of diurnal rodents in general can be affected by exposure to light at night (Mas?s-Vargas et al. 2019), but it is difficult to construe a scenario where this would occur in the field for burrowing species.

For both *A. nelsoni* and *X. mohavensis*, effects of light at night should be minimal as both are diurnal species, although it is possible that they might extend activity periods under artificial lights as other species have been known to do. If active at night, their sensitivity will be more toward blue than yellow light and orange and red should be relatively dimmer for them.

Giant Garter Snake and Southern Rubber Boa

Giant Garter Snake (*Thamnophis gigas*; Colubridae) is predominantly diurnal but can be nocturnal in hot weather, similar to other garter snakes (Heckrotte 1975). Southern Rubber Boa (*Charina umbratica*; Boidae) is nocturnal and crepuscular. It is possible that foraging by Rubber Boa is somewhat increased as a result of some increased illumination; some nocturnal snake species show increased activity under the full moon (Lillywhite and Brischoux 2012). Some snakes, when active nocturnally, show a decrease in foraging during the full moon, which may be a strategy to avoid detection by visually hunting predators (Clarke et al. 1996). This behavior is reflected in patterns of encounter of nocturnally active snakes (Klauber 1939). Furthermore, complementary evidence shows predation risk from snakes on their prey items is at a maximum during new moon conditions (Bouskila 1995) and snakes change their ambush sites depending on the moon phase (Bouskila 2001).

The flexibility of some snake species to transition from diurnal to nocturnal activity patterns is seen in the structure of the eye. The vertical pupil of snakes allows high visual sensitivity at night, while producing a more effective means of reducing light input during the day than does a round pupil (Brischoux et al. 2010). Boids see in the ultraviolet and green, while for colubrids, three cones ranging from the ultraviolet to near yellow have been documented. Additionally, boids can see into the infrared through a different, non-pigment system (Goris 2011).

The potential for both species to be active nocturnally, combined with knowledge of strong influence of lunar cycles on nocturnal snake foraging suggest that disruptions to natural lunar illumination patterns would affect these species. Artificial light at night also affects prey species and their behavior at similar illumination levels.

Swainson's Hawk

Swainson's Hawks (*Buteo swainsoni*) are diurnal, with broad spectral sensitivity arising from four cones and a rod (Potier et al. 2020). The only evidence of nocturnal activity is a record of nighttime migration from Costa Rica (Riba-Hern?ndez et al. 2012), which may be widespread in diurnal raptors, but diurnal activity and foraging is the rule and supported by the Swainson's Hawk visual system.

In addition to visual responses, birds have two types of melanopsin, with peak sensitivity around 490 nm (Dominoni 2015). A light-detecting pigment is also located in the pineal gland (like other vertebrates except for mammals), which has a spectral sensitivity peak around 460–470 nm (Dominoni 2015). Increasing daylength affects melatonin production, which in turn affects reproductive state. Another risk of night lighting is the possibility of advancing breeding phenology, which has been shown for passerines (Dominoni et al. 2013).

Possible effects of roadway lighting on raptors might include extension of hunting period into the night, as observed for Peregrine Falcons hunting migrating passerines (DeCandido and Allen 2006) and Goshawks hunting opportunistically at lights (Rutz 2006). This may result in unexpected temporal overlaps and competition among raptor species (Almpanidou et al. 2020). More broadly, lighting may affect prey availability, but Swainson's Hawks are versatile in their prey selection, consuming invertebrates and small animals (Giovanni et al. 2007). Although light at night may influence concentration and distribution of prey species for raptors (Sumasgutner et al. 2021), we have little evidence yet of this for Swainson's Hawks. Burrowing Owls are attracted to areas with higher insect concentrations and their burrows in an urban setting are found closer to streetlights (Rodr?guez et al. 2021).

For a highly mobile and large-range predatory species such as Swainson's Hawk, the most focus should be on nesting sites and the quality of habitat overall for the species and its prey. Notwithstanding potential "benefits" in terms of prey aggregation, standard steps to minimize light spill and intensity are recommended.

Foothill Yellow-legged Frog

Rana boylii is a predominantly diurnal frog that can also be active, including calling, at night. Recent metamorphs are reported to be more numerous and easily detected at night (Alvarez et al. 2022). Aside from information about visual systems in other frog species, we know little about the vision of *R. boylii* (Chapter 3). It is likely to have a Purkinje shift from longer to shorter wavelength sensitivity when shifting from photopic to scotopic vision. For all the reasons to avoid impacts from artificial light at night on frogs (Buchanan 1993, Baker and Richardson 2006, Buchanan 2006, Hall 2016, May et al. 2019, Forsburg et al. 2021), strategies to do so could exploit this Purkinje shift by using longer wavelengths so long as intensity of light reaching habitats is low. Frogs have a long refractory time to recover from bleaching when exposed to bright lights during scotophase, so lights should nevertheless be kept dim, distant, and shielded to avoid this.

Tadpoles, metamorphs, and adults of *R. boylii* are vulnerable to predation by snakes and small mammals and eggs and larvae are vulnerable to predation by aquatic invertebrates and fish. To the degree artificial light at night influences these species, they could have spillover effects on *R. boylii*.

San Joaquin Kit Fox

Similar to other kit foxes, peak activity of San Joaquin kit fox (*Vulpes macrotis mutica*) is crepuscular and nighttime, but the species can also be active during daylight conditions (Kavanau and Ramos 1975). They are predators of nocturnal kangaroo rats and jackrabbits. Some research with foxes suggests that additional light is associated with greater activity (Kavanau 1970). This appears to be consistent with some field data; use of lights intended to reduce fox predation on a piggery resulted in a 12% increase in fox detections and 23% decline in piglet survival (Hall and Fleming 2021).

We have no research that describes whether light exposure has impacts on sleep, reproduction, stress, or other aspects of kit fox biology. The visual system is dichromatic, with two cones at 555 nm (same as humans) and 430–435 nm, and a rod at 508 nm (Jacobs et al. 1993). Avoidance of peak scotopic sensitivity for canids (508 nm) would involve using longer wavelengths that provide light above the photopic peak of humans (555 nm). Use of spectrum for mitigation depends on intensity as experienced by the fox to be within the intensity range of its scotopic vision.

Lighting may affect foraging success and distribution of prey species. In urban areas, hunting and foraging is opportunistic and includes prey species known to be influenced by lighting distribution, such as Burrowing Owls (Rodr?guez et al. 2021) and Opossum (Bliss-Ketchum et al. 2016). Lack of food is not one of the major threats to San Joaquin Kit Fox (rather, habitat loss, disease, predation and competition are), so additional light that might aid in nocturnal foraging should not be seen as a benefit or necessary and standard responsible lighting practices should apply in their habitat.

Kangaroo Rats

Kangaroo rats (*Dipodomys* spp.; Heteromyidae) are considered together because no species-specific information is known about their visual systems. Nocturnally foraging rodents tend to have lower activity on full moon nights (Lockard and Owings 1974, Kaufman and Kaufman 1982, Daly et al. 1992, Upham and Hafner 2013, Prugh and Golden 2014) and in areas with artificial illumination (Kotler 1984, Shier et al. 2020). This is not universally true, however, and species that rely on visual detection of predators may see no effects of moonlight on activity levels (Goetze et al. 2008, Prugh and Brashares 2010). Heteromyids may also switch their foraging habitat from open to shrubby areas during moonlight to manage predation risk (Randall 1993).

The heteromyid rodents, including *Dipodomys*, are a sister group to the Geomyidae, which are likely to have the most similar visual system to them. Like most of the nocturnal rodents, geomyids retain a UV-sensitive cone, which combines with single cone sensitive at 500–525 nm and a rod around 500 nm as well. Some field work on *Dipodomys* leaves open the possibility that spectral tuning may contribute to decreased impacts. Shier et al. (2020) set out foraging stations along a transect away from a 6000K LED floodlight, a yellow CFL "bug light," and a control of either moonlight or the new moon. During new moon conditions both the floodlight and bug light reduced foraging by *Didpodomys*, with a greater effect of the floodlight, but the yellow CFL was also substantially dimmer than the floodlight and so the independent contribution of intensity and spectrum could not be inferred. The yellow light had half of its emissions between 500 and 600 nm, so that it still affected foraging is consistent with the visual sensitivity of the most closely related rodent species for which visual sensitivity is known. This result is similar to that found previously with beach mice, where yellow "bug lights" affected foraging less than other full spectrum lights, but still more than control conditions (Bird et al. 2004). Other studies show on foraging of nocturnal rodents under artificial light draw attention to other elements of foraging than the total amount of food consumed, such as vigilance during foraging or search efficiency (Zhang et al. 2020). Lighting may provide both positive and negative effects on foraging, with the net effect usually being negative (Zhang et al. 2020).

There is evidence of decreased survival in nocturnal rodents exposed to habitats with artificial light at night (3–6 lux of blue, yellow, or white light) compared with a 0.1 lux control (Vardi-Naim et al. 2022). This is evidence potentially of physiological stress of lighting, combined with competition between species. The control, however, at 0.1 lux was quite high relative to natural conditions.

Mitigation of light pollution impacts on sensitive heteromyid species should focus on avoiding disruption of lunar patterns of illumination, combined with using light sources with lower content of blue and shorter wavelengths.

Discussion

Implementing best practices to assess and mitigate the adverse effects of LED lights on wildlife likely will require a combination of actions that can be taken immediately and others that will require new policies, procedures, or technologies.

In this project, we compiled the information about the effect of LEDs on terrestrial wildlife, demonstrating that the impacts will depend on the character of the light produced, similar to other sources. If not controlled, artificial light at night has the potential to affect the physiology of organisms, their behavior, and their interactions with other species.

We demonstrated the relative influence of light intensity and spectrum in a laboratory setting with a nocturnal rodent. The amount of light was more important than its spectral content in suppressing nocturnal activity, but at lights are brighter, spectrum becomes more important.

We compiled a dataset of the visual responses of over 170 species of wildlife to light across the visual spectrum from decades of published studies. These curves confirm the current consensus that outdoor light at night should avoid the shorter wavelengths in the visual spectrum because the maximum utility for humans with the least disruption for other species comes from light in the yellow to red wavelengths.

We developed a method to map the area affected by a lighting installation that reports biologically relevant illuminance levels and adjusts them based on the visual sensitivity of an organism of concern. Development of this approach revealed a need for technical innovation software that does lighting calculations and its interoperation with geographic information systems. Even with off-the-shelf tools, however, agency staff can obtain estimates of the habitat area that will exceed biologically important illuminance thresholds as a result of lighting projects.

Finally, in this chapter, we reviewed the industry and advocacy approved guidance for reducing the unintended adverse effects of artificial light at night and provided available insights specific to the species most commonly affected by Caltrans projects.

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