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Better red than dead: Plasticine moths are attacked less under HPS streetlights than LEDs

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ABSTRACT

Anthropogenic light at night is growing exponentially while many insect populations are in decline. Many nocturnal insects provide numerous ecosystem services and are attracted to anthropogenic lights at night resulting in decreased fitness, greater mortality and population declines. During twilight and night, moths are depredated by bats and birds, both of which use vision, among other strategies, to detect and prey upon moths. The visual detection of moths by predators is dependent upon the light environment illuminating the moth's body. Effects of anthropogenic light at night can differ drastically with the color (spectral composition) and intensity of light. Currently, high pressure sodium lamps (HPS) and light emitting diodes (LEDs) are common municipal light sources, and these lights differ spectrally, thus altering the visual scene. Most LEDs are broadband (i.e., white) whereas HPS are long wavelength dominant (i.e., amber); both of these light types can alter color perception of prey. To test if moths are more likely to survive under HPS lighting than LEDs and non-lit poles, we used plasticine clay models. Visual model analyses reveal that HPS lamps rendered moths more cryptic against their background than LEDs or ambient urban lighting, albeit with small differences in contrast that may not be biologically relevant. These results indicate that HPS lighting is the most insect-friendly lighting when considering depredation on insects in comparison to LED.

Introduction

There are an estimated 26 million streetlights in the United States and the number of commercial and public external lights is estimated at 126 million (Smalley, 2012). This artificial lighting at night (ALAN) has resulted in 47% of the continental US having light-polluted night skies, and globally 23 % of Earth's terrestrial surface is light-polluted (Falchi et al., 2016). Unfortunately, light pollution continues to increase and is estimated to be growing approximately 10 % each year since 2011 (Kyba et al., 2023). A main reason for this rapid increase in light pollution is light emitting diode (LED) technology, which requires a fraction of the energy to produce equivalent illuminance compared to older lighting technologies, such as high-pressure sodium (HPS) lamps (Tähkämö et al., 2012; Yoomak et al., 2018). Since the mid 1900s, HPS lamps were the standard for street lighting across the U.S., however, those bulbs are being replaced by LED at a rapid rate. Before 2018, HPS lighting comprised 65 % of all U.S, street lighting, but by 2020 HPS comprised 47 % due to a 20 % increase in LED street lighting (Elliott & Lee, 2020). Furthermore, LED bulbs are predicted to account for 85 % of the global streetlight market by 2028 (Northeast Group LLC, 2019). Overall, this is a step towards sustainable energy consumption as LEDs require less energy and thus have a much lower carbon footprint than HPS lamps (Boyce, 2019). However, this is also concerning because unlike the long wavelength composition (i.e. amber) of HPS lamps, LEDs can be designed to produce light of any wavelength composition and thus, many LEDs are rich in all visible wavelengths resulting in an environment bathed in white light (Grubisic et al., 2019; Seymoure et al., 2019a). Although this enables humans to carry on color-vision

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dependent tasks far into the night, it also results in even more unnatural nocturnal light for the environment and the wildlife within Davies et al. (2013), Seymoure et al. (2019b), Garrett et al. (2020) and McMahon et al. (2022).

The effects of ALAN on wildlife are numerous and diverse, including impacts on organismal phenology, physiology, development, behavior, predation, and survival (Seymoure et al., 2019b; Sanders et al., 2021; Merckx et al., 2023). Debatably, no group of organisms is more affected by ALAN than insects due to insects' flight to light behavior, dependence upon light for development, and many other light-dependent behaviors (Owens et al., 2020; Fabian et al., 2023; Merckx et al., 2023). Recent work has demonstrated that insects are attracted to artificial light at night due to a dorsal-light response, in which a flying insect orients its dorsum to a point source (Fabian et al., 2023). The dorsal-light-response likely evolved due to the sky being the brightest area of an insect's visual field and thus a reliable indicator of which direction is up (Fabian et al., 2023). Eisenbeis et al. (2006) estimated that once a moth begins the dorsal-light-response towards an artificial light source, it has a 33 % chance of mortality that night. There are numerous factors resulting in the mortality of the moth, a main factor being depredation by insectivores including bats and birds (Russ et al., 2015; Schoeman, 2016; Firebaugh & Haynes, 2019). Many insectivorous aerial bats seek out artificial light sources due to their association with high prey abundances (Schoeman, 2016). A bat may eat hundreds of insects near a light source during one night, especially under the broadband white light of LEDs (Stone et al., 2015; Wakefield et al., 2015). Furthermore, insects not only need to be concerned with predation from predators that naturally occupy the same temporal niche, but also from insectivorous birds that now, due to artificial light at night, expand their once twilight restricted hunting behaviors into the night hours (Titulaer et al., 2012; Dominoni & Partecke, 2015; Russ et al., 2015). Thus, insects at night not only have to contend with artificial light sources that result in light-oriented behavior, but both nocturnal and diurnal predators that use artificial light to increase hunting efficacy (Stracey et al., 2014; Russ et al., 2015; Schoeman, 2016).

Nocturnal insects have evolved predator defenses under natural nighttime conditions that have remained consistent for millions of years (Yager, 2012). In the absence of light pollution, ambient light levels drastically change during twilight. The bright broadband conditions of daylight fade to dim purplish light (i.e., short and long wavelengths) that is one million times less bright (Johnsen, 2012). Once twilight ends, the light intensity has decreased yet again by four orders of magnitude and is composed of long wavelengths of light (i.e., amber and red; Johnsen 2012). Nocturnal prey, such as moths, evolved body and wing coloration consisting of many shades of browns that are cryptic at night due to the dim, long wavelength rich light (Frank et al., 2006; Cook et al., 2012). This red-shifted night environment lacks short wavelength light, which reduces the contrast between a moth's brown wings and green vegetation. Leaves absorb long wavelengths of light; therefore, only a small portion of the long wavelength dominant light environment is reflected by the vegetation resulting in a dark background (Cronin et al., 2014). So, although a moth's dull brown coloration is easy to spot when perched against green leaves in broad daylight, it matches the dark colorless vegetative background at night. However, due to artificial lighting at night, moths may no longer be cryptic (Seymoure, 2018). Even though humans have been lighting the night for two hundred years with electric lights, the nighttime environment was still mostly long wavelength dominant due to the amber spectrum of HPS lamps (Elvidge et al., 2010). Now with broadband LED lighting, the nocturnal light environment is growing ever closer to twilight and daylight conditions in both color and light intensity (Spitschan et al., 2016).

As insect populations are putatively in decline worldwide due to ALAN and other factors (Sánchez-Bayo and Wyckhuys 2019, Owens et al. 2020, Wagner et al. 2020, but see Saunders 2019, Thomas et al. 2019, Cardoso et al. 2020, Wagner et al. 2021 for a comprehensive review on the status of global insect declines), and insects provide ecosystem services worth trillions of dollars each year (Noriega et al., 2018), it is imperative to understand how artificial light at night is affecting predation of insects. Here, we ask how predation of army cutworm moths, *Euxoa auxiliaris*, is affected by two common streetlight sources in an urban environment: broadband LED and HPS. We predict that broadband LED streetlights should increase contrast of moths against their background resulting in higher predation rates, whereas HPS streetlights are more chromatic with long wavelengths (i.e., orange and red) and thus will decrease contrast of moths resulting in lower predation rates. Overall, we predict that moth predation will be higher under street lighting due to overall greater light intensity than non-illuminated urban areas. We tested these predictions using plasticine clay models of *Euxoa auxiliaris* in Fort Collins, Colorado, USA under LED and HPS streetlights.

Materials and methods

Site: Fort Collins, CO

We tested our predictions of predation rates on moths illuminated by different streetlights in Fort Collins, Colorado, USA. Fort Collins is a city in northern Colorado east of the Front Range of the Rocky Mountains and can be mostly categorized as the great plains biome. It is approximately 1525 m above sea level, comprises 151 km^2, and during 2018 had a population of 166,401 residents. We collaborated with the city of Fort Collins Utilities office to obtain locations of LED and HPS streetlights within the city limits. The city manages thousands of streetlights, making it possible to test hundreds of moth models for each streetlight type.

Study organism: army cutworm moth (Euxoa auxiliaris)

As Fort Collins is located where the Great Plains meet the Rocky Mountains, it is directly within the migration path of the army cutworm moth, *Euxoa auxiliaris*, also known as "Miller moths" (Dittemore, 2022). *Euxoa auxiliaris* is a large noctuid moth (*ca.* 45 mm wingspan) that feeds on grains, alfalfa, and canola in the western Great Plains as a larva and then migrates west to high altitudes in the Rocky Mountains as an adult (Kendall et al., 1981; Dittemore, 2022). Being a noctuid, *E. auxiliaris* is highly attracted to lights at night and is known for its large swarms around streetlights that may include thousands of individuals (White et al., 1998; Frank et al., 2006). Due to the migratory nature of *E. auxiliaris*, it builds large fat stores that result in the moth being 80 % body fat as the migration begins (French et al., 1994). Due to its high fat content, *E. auxiliaris* is a key calorie source for carnivores in the Rocky Mountains, including bears, which have been estimated to eat 40,000 moths each day during the summer (French et al., 1994; White et al., 1998). As the army cutworm moth is highly attracted to artificial lights at night like so many Macrolepidoptera, including most Noctuidae, Erebidae, Arctiidae, and Geometridae (Merckx & Slade, 2014), this species is a model system for understanding how moth predation is affected by the different light sources that attract moths.

Moth model construction

We acquired four male *E. auxiliaris* specimens from the C. P. Gillette Museum of Arthropod Diversity at Colorado State University in fall 2017. We then developed artificial models following the methods of Seymoure and Aiello (2015) and Seymoure et al. (2018). As *E. auxiliaris* perch with wings hooded over the abdomen, we scanned the dorsal surface of the moth specimens in perching posture using a Brother MFC-J4510DW Scanner (Brother Industries; Fig. 1). High resolution images of the wings were then printed onto Whatman filter paper with a Brother MFC-J4510DW (Brother Industries) printer. To confirm that the paper wing models of *E. auxiliaris* matched the spectral reflectance of *E. auxiliaris*, we measured both wing and paper model reflectance and

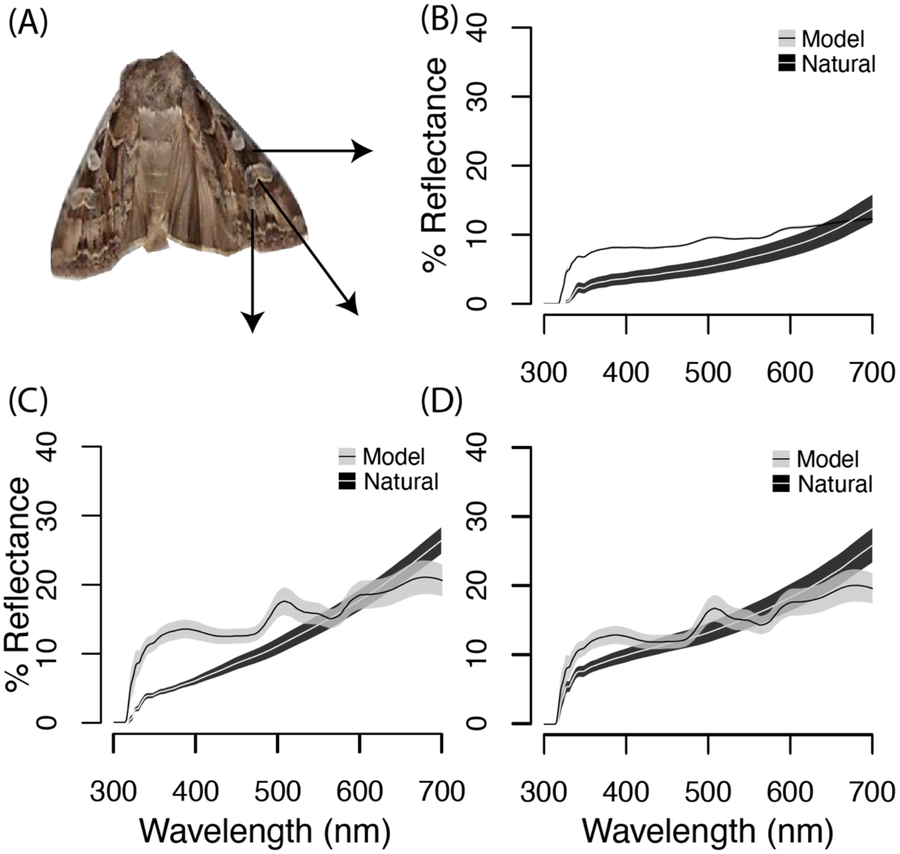

Fig. 1. *Euxoa auxiliaris* wing reflectance compared to moth model reflectance across three different wing patches. (A) The dorsal wings of *E. auxiliaris*. (B–D) Reflectance comparisons between natural moth wings and model moth wings for each respective patch shown in (A).

then compared spectra between the wings and models. We measured the dorsal reflectance of three color patches on the four moth specimens and on the four printed model wings using an Ocean Optics USB4000 spectroradiometer illuminated with an Ocean Optics Deuterium UV/VIS light source. Wing color reflectance was measured as the proportion of a white reference standard (WS-1-SL, Ocean Optics) using a bifurcated reflectance fiber optic (QR400-7, Ocean Optics) and recorded using Spectrasuite (Ocean Optics). We then evaluated reflectances between the moths and paper models using the *Pavo* package (Maia et al., 2019) within R. There are two different visual systems for birds in which the shortest wavelength sensitivity differs between ultraviolet and violet (Vorobyev & Osorio, 1998; Osorio & Vorobyev, 2005). We expected that the main avian predators for these moths would be insectivorous passerines that have the UV cone, and thus we used the ultraviolet sensitive visual system of a blue tit (*Cyanistes caeruleus*; Hart 2001). We applied von Kries transformation to account for receptor adaptation and used the default parameters for Weber's fraction of 0.05, illumination of D65 (irradiance spectrum for standard daylight), background and cone ratios of N1 = 1, N2 = 2, N3 = 2, N4 = 4 (Hart, 2001; Maia et al., 2019). We calculated both chromatic and achromatic just noticeable differences (JNDs) for three comparisons: natural vs. model of patch A, natural vs. model of patch B, and natural vs. model of patch C (Fig. 1).

JNDs represent the ability of a visual system to perceive two colors differently, with JNDs less than one being indistinguishable in ideal conditions (i.e., full spectrum lighting and a highly contrasting visual background) and a JND value of less than three being indistinguishable under natural conditions (Siddiqi et al., 2004). Furthermore, JNDs calculate color contrast (i.e., chromatic contrast, dS) separately from brightness contrast (i.e., achromatic contrast, dL). It is possible for an animal to have low chromatic contrast while also having high achromatic contrast and vice versa; thus, we compared JNDs for both chromatic and achromatic channels. Due to the pigmentary differences between ink and moth pigments, the paper model wings were not identical, but were a close match that resulted in JNDs with averages ranging between less than one and five. Although JND values of five are high for matches between similar colors, when comparing the patches of natural moth wings to other natural moth wings, there were many cases of JNDs higher than five. Thus, although our model wing colors would be discriminable when compared to natural moth colors in ideal conditions, our moth models did match the large variation of coloration found in *E. auxiliaris* (Fig. 1).

We cut paper wing models that matched the wing size of *E. auxiliaris* and then inserted the paper wings into black non-toxic plasticine clay "bodies" using Plastalina clay (Michaels Crafts). Plasticine models of insects, as well as other animals, have been a productive method for measuring predation rates across species, as well as how predation varies with traits and biogeography (Niskanen & Mappes, 2005; Saporito et al., 2007; Roslin et al., 2017). The plasticine clay remains malleable for weeks and thereby allows assessment of beak marks from avian predators as well as teeth marks from mammalian predators (e.g., bats; Merrill et al. 2012, Seymoure and Aiello 2015, Seymoure et al. 2018).

Mortality experiments

We tested the survival of *E. auxiliaris* models within the city limits of Fort Collins, CO from May 29, 2018 to June 30, 2018. This corresponds to the migration of *E. auxiliaris* through the Front Range of Colorado (Dittemore, 2022). Using maps of both LED and HPS streetlights provided by Fort Collins Utilities, we targeted 16 blocks that covered most of the neighborhoods within Fort Collins. We only placed moth models on residential streets to reduce any confounding effects of commercial lighting (e.g., parking lot lights). Moth models were tied around streetlight poles with black thread sewn through both the paper wings and clay body of the moth model. *Euxoa auxiliaris* is attracted to streetlights and will perch near streetlights for the duration of night. We realize that moths perch on other substrates, including vegetation surrounding built structures that may render the moth more cryptic (Kang et al., 2013); however, to standardize the background and orientation of the moth models, we only placed them on street poles. Street poles did differ in coloration and thus each street pole had its color qualified and then a subset of poles for each color category were quantified spectrally after the survival experiments (see *visual models of contrast*).

In total, 500 moth models were placed at distances of at least 100 m from each other. Models were placed so that they were directly illuminated by the streetlight. Two hundred models were placed under LED lamps, 100 that were 73 W and 100 that were 10 W. Two hundred models were placed under HPS lamps, 100 that were 70 W and 100 that were 150 W. Although the LEDs had lower wattage, they had similar total illuminance as they require less energy to produce light and were broad spectrum. We placed 100 models on unilluminated poles as a control. These poles were not streetlight poles nor were they directly illuminated by nearby lights. They consisted mostly of street sign poles, sport poles (e.g., volleyball net posts), and fence posts. Models were placed during daylight and then checked during both dawn and dusk for 72 h. No precipitation occurred during the moth survival trials. As we were concerned with predation events occurring when the models were illuminated by streetlights, we only counted predation events that happened between dusk and dawn (i.e., at night). If a model was attacked during the day, the model was replaced during the dusk check, whereas if a model was attacked at night, the model was removed from the experiment and was recorded as attacked during the dawn check. Models were categorized as attacked if beak marks or teeth marks were noticeable on the clay body. Models that went missing were not counted as attacked and were instead censored (Hurlbert, 1984; Seymoure et al., 2018). After a model had survived for 72 h, it was removed from the streetlight.

Differences in survival probabilities after 72 h between light types (LED, HPS, control) and wattages were analyzed using Kaplan–Meier survival analysis with the log-rank test ‘survival’ package (Therneau et al., 2015) in R Team (2017). We restricted our survival analysis to only attacks and missing models that occurred at night. Missing models were incorporated into the Kaplan–Meier survival analysis as censored individuals (Seymoure & Aiello, 2015).

Visual models of contrast

We predicted that predation events on moth models would be explained by the contrast of a moth model illuminated by its respective light source (i.e., LED, HPS, or ambient light on a non-lit pole) against its respective light pole. To test this, we measured reflectance of a subset of poles that represented the different pole colors used in this study as well as the irradiance of a subset of LED lights, HPS lights, and ambient control sites. Due to the very low light levels of the ambient control sites and limitations of the spectroradiometric equipment, we measured the irradiance of two sites for the ambient control where attacks on models had occurred during the experiment. We quantified the reflectance of three different streetlights for each light type and wattage. We also quantified the reflectance of at least two different street poles within each color category except for “yellow”, which was the color of only one pole in the study. For each streetlight and street pole, we averaged three irradiance and reflectance measurements, respectively. Due to the large number of poles and intensive labor required to quantify streetlight irradiance and pole reflectance, our quantification of contrasts for each moth model is only a small sample of the poles and lighting environment in our predation study.

Irradiance of light sources was measured using a cosine corrected probe attached *via* a 1000 µm fiber optic cable (F1000-UVVis-SR-1; StellarNet) to a highly sensitive spectroradiometer (SILVER-Nova-TEC-X2; StellarNet). Each light source was measured three times with the cosine corrected probe oriented perpendicular to the ground (i.e., directly up at the light source). The cosine corrected probe was held in place with a tripod and the tripod was moved approximately 10 cm between each of the three irradiance measurements to incorporate variation in the lighting field. Using Spectrawhiz software (StellarNet), we recorded irradiance in energy flux in watts/cm^2/second/nm and then converted it to photon flux (photons/cm^2/second/nm; Johnsen 2012).

Pole reflectance was measured similarly to moth and model reflectance (see above), except that instead of measuring it in a laboratory setting, we measured pole reflectance *in situ* using an Ocean Optics reflectance probe holder (RPH-1; Ocean Optics). The reflectance probe holder was set directly onto the street pole, blocking all environmental light from reaching the reflectance fiber. As in the reflectance measurements above, we used an Ocean Optics USB4000 spectroradiometer illuminated with an Ocean Optics Deuterium UV/VIS light source. Pole color reflectance was measured as the proportion of a white reference standard (WS-1-SL, Ocean Optics) using a bifurcated reflectance fiber optic (QR400-7, Ocean Optics) and recorded using Spectrasuite (Ocean Optics).

Using the irradiance of each light treatment (i.e., HPS, LED, ambient control), reflectance of the three wing patches, and pole reflectance, we calculated the contrasts for each possible condition that occurred during the experiment. Similar parameters were used for calculating JNDs as were used for the JND calculations between moth wings and model wings, except that von Kries transformation was not applied and we used the quantum catch photoreceptor model to better estimate for the effects of absolute photon intensity (Thurman & Seymoure, 2016). Again, we calculated both chromatic and achromatic JNDs using the blue tit visual system with the double cone sensitivity for achromatic contrast.

To determine if light type and pole color affected the chromatic and achromatic contrast of the moth models, we ran a linear mixed model on both the chromatic and achromatic JND data with patch (i.e., a, b, or c) and moth model (i.e. 1–4) as repeated subjects using the lmerTest package in R (Bates et al., 2015). We then applied the Sattertwaite method through an ANOVA on our mixed model to find significant differences between light types and pole color (Kuznetsova et al., 2017). We visually checked that both the chromatic and achromatic JND data met the assumptions of linear mixed models by plotting residuals vs fitted values and examining QQ plots and residuals vs leverage.

Results

Within 72 h of moth model deployment on streetlights and control poles, 14.4 % (72 of 500) of the models had been attacked, 71 by birds and 1 by a mammal, and another 4.0 % were missing (20 of 500). Most of these attacks occurred at night (56 out of 500, 11.2 %, with 55 avian attacks and 1 mammalian attack at night), whereas more models went missing during the day than at night (11 vs 9; Table 1).

When restricting survival probability to nighttime hours, light type affected survival (Log-rank, $X^2 = 9.7$, $p = 0.008$) with control poles having 15 % (15/100) of moths attacked and LED lights having 14.5 % (29/200) of moths attacked (Table 1). Only 6 % (12/200) of models under HPS lighting were attacked (Table 1B and Fig. 2). When including wattage as a categorical factor nested within light type, there was a significant difference (Log-rank, $X^2 = 10.7$, $p = 0.03$). HPS lights with 150 W had 7 % (7/100) of moth models attacked, HPS with 70 W had 5 % (5/100) of the models attacked, LED with 10 W had 16 % (16/100) of the models attacked, and LED with 73 W had 13 % (13/100) of the models attacked.

Light type significantly affected the chromatic contrast of the moth models ($F_{4,166} = 5.10$, $p < 0.001$), but did not affect their achromatic contrast ($F_{4,1326} = 0.0172$, $p = 0.999$). HPS lighting created the lowest chromatic and achromatic contrasts, while the control poles had the

Table 1
The number of events for each light type recorded during the daytime (A) and nighttime (B).

(A)				
Treatment	Missing	Avian attack	Mammalian attack	Total events
HPS 70W	2	4	0	6
HPS 150W	3	3	0	6
LED 10W	2	6	0	8
LED 73W	3	0	0	3
Ambient control	1	3	0	4
Total	11	16	0	27
(B)				
Nighttime	Missing	Avian attack	Mammalian attack	Total events
HPS 70W	2	5	0	7
HPS 150W	3	7	0	10
LED 10W	2	16	0	18
LED 73W	1	13	0	14
Ambient control	1	14	1	16
Total	9	55	1	65

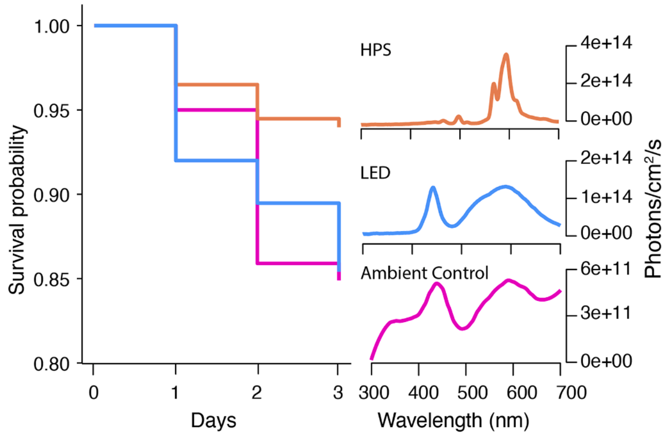

Fig. 2. Moth model survival plot and irradiance spectra for each light source. The colors of survival curves match the color of spectra lines for each light treatment. Note that the axes for the irradiance spectra vary to enable comparison of shapes across the three light types. Spectra lines represent the average spectrum for each respective light type.

highest contrasts (Table 2; see Appendix A). However, when comparing the estimated contrast values of only attacked moth models, there was an effect of light type on both chromatic ($F_{2,38} = 14.10, p < 0.001$) and achromatic ($F_{4,1326}= 0.0172, p = 0.999$) contrasts. Furthermore, pole color greatly affected both chromatic ($F_{9,64}= 148.39, p < 0.001$) and achromatic ($F_{2,57} = 6.03, p = 0.004$) contrasts of moth models (see Appendix A).

Discussion

Light pollution is a main contributor to global insect declines, which alter species interactions and trophic structures (Owens et al., 2020; Grubisic & van Grunsven, 2021; Seymoure et al., 2023). Understanding the mechanisms underlying insect declines and altered food webs is crucial as Lepidopteran abundance has declined by 35 % in 40 years (Dirzo et al., 2014). Here we show that predation rates on a common moth species in an urban setting is affected by streetlight type with HPS streetlights leading to higher survival than LED streetlights, and surprisingly, higher survival than no direct street lighting. Furthermore, we found that predation rates were highest at night and that avian predators were the main nocturnal predators on the sedentary moth models, confirming previous research demonstrating that insectivorous birds are foraging at night under the influence of ALAN (Titulaer et al., 2012; Stracey et al., 2014). However, as the moth models in our experiment were sedentary and tethered to streetlight poles, we are reluctant to state that avian predators play a greater role in nocturnal depredation of moths. As many insectivorous bats rely upon both echolocation and eyesight for detecting prey (Boonman et al., 2013), it is likely that avian predators were better at detecting the sedentary prey against streetlight poles.

Table 2
Means and standard errors of the mean of chromatic and achromatic contrast for each light type.

Light type	Chromatic contrast (dS)	Achromatic contrast (dL)
HPS 70W	1.91 ± 0.06	5.42 ± 0.25
HPS 150W	1.77 ± 0.06	5.42 ± 0.25
LED 10W	1.92 ± 0.07	5.43 ± 0.25
LED 73W	1.94 ± 0.06	5.43 ± 0.25
Ambient control	2.06 ± 0.07	5.47 ± 0.25

We found limited support for our prediction that avian predation rates would be enhanced by light conditions that increase visual contrast of moth models (see Briolat et al. 2021 and McMahon et al. 2022 for theoretical models of conspicuousness under ALAN). The chromatic contrasts of moths against pole backgrounds were highest for ambient control and LED lighting and lowest for HPS lighting. Although the differences in chromatic JNDs between the three light conditions were statistically significant, they were small enough (all within 1 JND) that they may not have been biologically meaningful (Siddiqi et al., 2004; Langmore et al., 2011). Furthermore, we found high achromatic contrast of moth models against their respective background regardless of the different light treatments including the ambient control without direct streetlighting. Although control moth models were not directly under streetlights, all moth models were placed in a suburban/urban area with high levels of light pollution from both skyglow and distant light sources. The direct light sources result from both residential and commercial lighting with similar spectral composition to broadband LEDs (Fig. 2). Thus, it is likely that avian predators were using achromatic contrast to detect moth models at night. However, this does not explain why survival rates differed between light treatments. We propose that the difference in moth survival between light conditions is likely due to avian foraging behavior under different light conditions.

Previous research shows mixed effects of ALAN intensity and spectra on predation and predator behaviors. Sanders et al. (2021) revealed through a meta-analysis of 23 studies that ALAN affected predation rates, although the specific predation effects are nuanced and context-dependent. There is overwhelming evidence that predators, ranging from *Anoles* lizards to jumping spiders to insectivorous birds, extend foraging activity into the night under ALAN (Frank, 2009; Titulaer et al., 2012; Maurer et al., 2019). However, the influence of light spectra and proximity to direct lighting as explanatory variables for predation rates are less clear. For example, McMunn et al. (2019) found increased predation rates on tethered *Drosophila* under ALAN (4200K LEDs), whereas Eckhartt and Ruxton (2022) found that predation rates on insect-containing birdfeed increased with distance from LED sources, although they did not report the LED spectra. Furthermore, bat predation on moths increased under LEDs even though moth abundance decreased (Minnaar et al., 2015). However, Rydell (1992) and Acharya and Brock Fenton (1999) found that bats have increased capture success of moths under lights, not only due to increased local moth abundance, but also due to moth disorientation and altered predator avoidance behaviors. Thus, questions remain surrounding population sizes and predation rates on adult moths under ALAN. When comparing predation rates on moth larvae, i.e., caterpillars, the nuances persist. There was no effect of HPS street lighting on predation rates of tethered live waxworm larvae (Grenis et al., 2015), whereas higher abundance of arthropod predators led to higher predation rates on plasticine caterpillar models under broadband LED (Deitsch & Kaiser, 2023). These studies suggest that light type affects arthropod predation rates, with greater predation under LED lighting and lower predation under HPS lighting, as confirmed in our study.

Overall, the literature shows complex and context-dependent consequences of ALAN on insect survival. A full understanding of the relationship between ALAN and mortality requires knowledge of the traits of the specific prey and predators, environmental conditions, visual environment, time of day, and season. Previous research has shown that all of these factors can affect predation rates (Sentis et al., 2012; Mappes et al., 2014; Delhey & Peters, 2017; Roslin et al., 2017) and thus future work investigating predation under ALAN must consider them (Dominoni et al., 2020; Ditmer et al., 2021). Future comparative work could also investigate the relative impacts of prey morphology, light intensity, and light spectrum in areas with varying levels of light pollution to better understand differential insect predation rates under ALAN.

Organisms, such as the moths and avian predators examined in this study, have evolved with natural light cycles for millions of years. As municipalities switch from HPS to broad spectrum LED lighting to reduce energy consumption, organisms will experience less amber and long wavelength conditions, which more closely match the natural spectra of lunar and starlight illumination. Instead, LED lighting results in more broadband or short wavelengths conditions that match diurnal and twilight spectra (Briolat et al., 2021; McMahon et al., 2022). It is clear from our data that artificial light sources alter predator-prey interactions with possible cascading effects for food webs and community assemblages. As 50 % of Earth's terrestrial surface is estimated to be light polluted by 2050 (Sánchez de Miguel et al., 2021) and the sixth mass extinction continues with large impacts on invertebrates (Cowie et al., 2022), it is imperative that we understand the role of ALAN in insect declines.

Data availability statement

The survival and spectral data have been posted to Mendeley Data Repository entitled: "Better red than dead: plasticine moths are attacked less under HPS streetlights than LEDs". https://data.mendeley.com/datasets/v3c5xyc7mc/1.

CRediT authorship contribution statement

Brett Seymoure: Writing – review & editing, Conceptualization, Validation, Investigation, Resources, Supervision, Writing – original draft. **Tessa Parrish:** Conceptualization, Validation, Investigation, Resources, Writing – review & editing. **Kaley Egan:** Writing – review & editing, Validation, Investigation, Resources. **Malcolm Furr:** Investigation, Writing – review & editing. **Danny Irwin:** Writing – review & editing, Validation, Investigation. **Cassie Brown:** Writing – review & editing, Investigation, Resources. **Morgan Crump:** Writing – review & editing, Investigation. **Jeremy White:** Writing – review & editing, Validation, Conceptualization. **Kevin Crooks:** Resources, Supervision, Writing – review & editing, Conceptualization. **Lisa Angeloni:** Resources, Supervision, Writing – review & editing, Conceptualization.

Declaration of Competing Interest

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

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.baae.2023.11.008.

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