

SENSORY STRESSORS IMPACT SPECIES RESPONSES ACROSS LOCAL AND
CONTINENTAL SCALES

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 Across Local and Continental Scales

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ABSTRACT

Sensory Stressors Impact Species Responses Across Local and Continental Scales Ashley Anne Wilson

Pervasive growth in industrialization and advances in technology now exposes much of the world to anthropogenic night light and noise (ANLN), which pose a global environmental challenge in terrestrial environments. An estimated one-tenth of the planet's land area experiences artificial light at night — and that rises to 23% if skyglow is included. Moreover, anthropogenic noise is associated with urban development and transportation networks, as the ecological impact of roads alone is estimated to affect one-fifth of the total land cover of the United States and is increasing in space and intensity. Existing research involving impacts of light or noise has primarily focused on a single sensory stressor and single species; yet, little information is known about how different sources of sensory stressors impact the relationships within tightly-knit and complex systems, such as within plant-pollinator communities. Furthermore, ANLN often co-occur, yet little is known about how co-exposure to these stressors influences wildlife, nor the extent and scale of how these stressors impact ecological processes and patterns.

In Chapter 1, we had two aims: to investigate species-specific responses to artificial night light, anthropogenic noise, and the interaction between the two by using spatially-explicit models to model changes in abundance of 140 of the most prevalent overwintering bird species across North America, and to identify functional traits and contexts that explain variation in species-specific responses to ANLN stressors with phylogenetically-informed models. We found species that responded to noise exposure generally decreased in abundance, and the interaction with light resulted in negative synergistic responses that exacerbated the negative influence of noise among many species. Moreover, the interaction revealed negative emergent responses of species that only reacted when both ANLN were presented in combination. The functional trait that was the most indicative of avian response to ANLN was habitat preference. Specifically, species that occupy closed habitat were less tolerant of both sensory stressors compared to those that occupy open habitat. Species-specific responses to ANLN are context-dependent; thus, knowing the information that regulates when, where, how, and why sensory pollutants influence species will help management efforts effectively mitigate these anthropogenic stressors on the natural environment.

In Chapter 2, using field-placed light manipulations at sites exposed to a gradient of skyglow, we investigated the influence of direct and indirect light on the yucca-yucca moth mutualism by quantifying chaparral yucca (*Hesperoyucca whipplei*) fruit set and the obligate moth (*Tegeticula maculata maculata*) larval density per fruit. Although many diurnal insects are thought to exhibit minimal phototaxis, we show that direct light attracted adult moths and incited higher pollination activity, resulting in an increase in fruit set. However, larval recruitment decreased with elevated light exposure and the effect was strongest for plants exposed to light levels exceeding natural moonlit conditions (> 0.5 lux). Contrarily, increases in ambient skyglow resulted in an increase in both fruit set and larva counts. Our results suggest that plant-pollinator communities may respond in complicated ways to different sources of light, such that novel selection pressures of direct and indirect light have the potential to benefit or disrupt networks within complex diurnal plant-pollinator communities, and ultimately alter the biodiversity reliant on these systems.

By analyzing pervasive stressors across a continental-wide scale, we revealed considerable heterogeneity in avian responses to light and noise alone, as well as the interaction between them. Based on overall responses to the interaction between light

and noise, we suggest management efforts should focus on ameliorating excessive noise for overwintering bird species, which should decrease the impact from synergistic responses, as well as the negative impact from noise alone. There is still much to learn about responses to these stressors and smaller-scale studies should take our approach of systematically assessing interaction responses to ANLN. Moreover, our small-scale study revealed both local sources of direct light and skyglow impact the recruitment for both yucca moths and their reciprocal plant hosts. However, it is still unknown if or why other diurnal pollinators experience positive phototaxis, and whether direct lighting influences the physiology, behavior, or multiple factors relating to reproduction and fitness. Correspondingly, it is unknown if the novel selection pressures of direct and indirect light are disrupting complex diurnal plant-pollinator communities. Future research on artificial night light will need to investigate the intricate responses of diurnal pollinators to both direct and indirect light that will identify concrete mechanisms relating to physiological or behavioral susceptibility and inform predictions on how wide-spread communities will shift with this global driver of emerging change.

Keywords: Multi-Species Modeling, Anthropogenic Noise, Artificial Night Light, Synergistic Interaction, Functional Traits, Plant-Pollinator Communities, Recruitment

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CHAPTER 1

ARTIFICIAL NIGHT LIGHT AND NOISE INTERACT TO INFLUENCE BIRD
ABUNDANCE ACROSS A CONTINENTAL SCALE

1.1 INTRODUCTION

Pervasive growth in industrialization and transportation networks now exposes much of the world to anthropogenic night light and noise (ANLN), which pose a global environmental challenge in terrestrial environments (Swaddle et al., 2015). An estimated one-tenth of the planet's land area experiences artificial light at night (Gaston et al., 2014) — and that rises to 23% if skyglow is included (Falchi et al., 2016). Light pollution has the potential to threaten the 30% of vertebrates and 60% of invertebrates that are nocturnal and sensitive to light (Hölker et al., 2010), and responses by sensitive species could cause ecological cascades through processes such as disrupted plant-pollinator interactions (Knop et al., 2017) and food webs (Manfrin et al., 2017). Moreover, anthropogenic noise is associated with urban development and transportation networks, as the ecological impact of roads alone is estimated to affect one-fifth of the total land cover of the United States (Blickley and Patricelli, 2010) and is increasing in space and intensity (Barber et al., 2010). Studies that have isolated anthropogenic noise to understand its effects have reported decreases in species diversity (Proppe et al., 2013; Perillo et al., 2017) and changes in community structure (Francis et al., 2009). Notwithstanding the conservation relevance of impacts of light or noise alone on various taxa, they often co-occur, yet little is known about how co-exposure to noise and light influences wildlife (Swaddle et al., 2015).

Sensory stimulation from ANLN varies from synchronous exposure to asynchronous exposure, both of which can vary within a single day or across seasons (Dominoni et al., 2020b). For example, species near urban areas or traffic corridors are

exposed to excessive noise pollution during periods of high traffic density, which overlaps with dawn chorus timing and can interfere with conspecific communication, territory status, and reproductive output (Francis and Barber, 2013), especially during the pre-breeding season (Warren et al., 2006). Additionally, light exposure occurs primarily at night, which has the potential to disrupt circadian clocks, photoperiodism, melatonin production, and partitioning of activity between day and night for certain species (Gaston et al., 2013). As such, peak intensities of either stressor may occur at disparate times, but an organism may be exposed to both stressors daily and with simultaneous exposure during part of the day in some seasons. Furthermore, biotic and abiotic characteristics of the environment can affect the propagation and intensity of ANLN exposure. For instance, a study that mapped introduced sound from playbacks in three terrestrial habitats found forests had stronger sound pressure level gradients than prairie or urban habitats due to the greater potential for sound reflection and reverberation (Job et al., 2016). The relative timing of each stressor can interact with its intensity to influence the total physiological stress that an organism experiences at any one time, as well as how it responds to subsequent exposure to additional stressors (Gunderson et al., 2016). Therefore, it is important to understand whether the aggregate multisensory exposure (henceforth 'multimodal') to ANLN influences how an organism copes with these perturbations, either individually or combined.

Conventional approaches to understanding interactive effects of two or more stressors typically adopt additive effects as the null expectation (Folt et al., 1999; Crain et al., 2008). That is, if noise and light both cause a response, the expected magnitude and direction of the combined response is equal to the sum of the effect evoked by noise and the effect evoked by light. However, exposure to one stressor could potentially enhance or mitigate the effect of the other, or evoke a new emergent response only when both signals are presented in combination (Halfwerk and Slabbekoorn, 2015).

These deviations from the expected additive model are known as cumulative interactions (Partan and Marler, 1999; Piggot et al., 2015; Dominoni et al., 2020a), and we explore the different types of cumulative interactions in Table 1.1. While cumulative interactions are useful for identifying the large-scale impacts of anthropomorphic impacts on ecosystems (Brown et al., 2013), synergistic interactions are often of concern because they are a result of increased stressor intensities that overwhelm physiological compensatory mechanisms (Gunderson et al., 2016) and cause more rapid declines in ecosystems than additive or antagonistic interactions (Brown et al., 2013). While a few studies have investigated the combined influence of ANLN, they primarily focused on a specific fitness-related factor for a single species (Dorado-Correa et al., 2016; Casasole et al., 2017; Raap et al., 2017; Dominoni et al., 2020a) or a paired interspecific relationship (McMahon et al., 2017). Of these examples, only Raap et al. (2017) and Dominoni et al. (2020a) considered additive or synergistic interactions, but did not incorporate the precision of the effect of the interaction when drawing conclusions. Assuming interactions are cumulative based on whether they are more negative or positive than expected is problematic from an ecological perspective because effect direction is entirely context dependent (Piggot et al., 2015). Therefore, using a systematic approach of determining the magnitude and direction of additive and cumulative responses will provide novel insight on how ANLN influences a wide array of species-specific responses.

Several meta-analyses have quantified taxon-specific responses to either noise or light pollution (Rich and Longcore, 2013; Bennie et al., 2016; Owens and Lewis, 2018; Slabbekoorn et al., 2018; Kunc and Schmidt, 2019), yet this approach may neglect understanding why species-specific responses to ANLN diverge in magnitude and direction. Instead, knowledge of the morphological traits, habitat affiliations (henceforth “functional traits”), and ecological contexts that are relevant to how species detect and

interact with acoustic and visual stimuli could not only help explain this variation, but allow specific predictions of evolutionary responses to these anthropogenic stressors (Hopkins et al., 2018). Moreover, knowing what makes a species vulnerable and where vulnerable species are located can be very useful when land managers and conservationists need to assess the vulnerability of species for which only basic knowledge of their biology and ecology is available (Pacifi et al., 2015). If functional traits are successful in predicting responses of common species to anthropogenic stressors, then comparative studies could be utilized to predict responses of low abundance, narrowly distributed, or threatened species (Murray et al., 2002). To date, relatively few studies have sought to use trait-based analysis to understand responses to noise or light. For instance, a handful of efforts have been made to describe how changes in abundance in response to anthropogenic noise can be explained by vocal frequencies (Goodwin and Shriver, 2010; Proppe et al., 2013; Francis, 2015). However, studies comparing species-specific responses with other traits, especially those relevant to vision and light exposure, are still lacking, but urgently needed to fully understand the consequences of these stressors for conservation planning and management.

Here, we had two aims: to investigate multi-species responses when exposed to artificial night light, anthropogenic noise, and the interaction between the two, and to identify functional traits that explain variation in species-specific responses to ANLN stressors with phylogenetically-informed models. For the first aim, we used data from across the contiguous United States collected through the citizen science program Project FeederWatch, where observers report the maximum abundance of avian species seen at backyard feeders during 2-day observation periods throughout the winter season. We consolidated abundances by species across a five-year period, and we used spatially-explicit models to model changes in presence-only abundance among 140 species in response to noise, light, and the interaction between the two while also

controlling for other important natural and anthropogenic environmental variables. Several mechanisms and pathways can influence species' sensitivities to sensory stressors, yet responses to these disturbances are not always straightforward, as stressors can impact species indirectly, and depending on environmental conditions, some species may benefit from sensory pollutants. In general, most studies have reported negative effects of these stressors (Rich and Longcore, 2013; Slabbekoorn et al., 2018), and thus we expected most species would decline in abundance with exposure to ANLN. Moreover, individuals located nearby urban infrastructure are likely to experience prolonged periods of stress from the synchronous and asynchronous exposure to these stressors (Gunderson et al., 2016). As such, we predicted that the interaction between noise and light would elicit an overall decline in abundance across all 140 species, and the majority of these responses would deviate from the expected additive response as cumulative interactions (Harvey et al., 2013). In addition to the interaction between ANLN, we included an interaction between light and night length. High thermoregulatory costs and periods of nutritional stress during winter are assumed to increase energy demands (King and Murphy, 1985), yet increased illumination from artificial night light could provide adequate visual information for species to extend diurnal or crepuscular behaviors into the nighttime environment (Longcore and Rich, 2004). The prolonged perceived photoperiod could provide the opportunity for extended foraging and increased food consumption (Gaston and Bennie, 2014), and we predicted birds would increase abundance with artificial light exposure during longer nights. For our second aim to link functional traits to species-specific responses to ANLN, we expected variation in eye morphology, diet, propensity to form flocks, and habitat preferences to influence responses (Table 1.2).

1.2 METHODS

1.2.1 Project FeederWatch data

Project FeederWatch is a citizen science project run by the Cornell Lab of Ornithology, where thousands of participants report bird observations at known feeder locations across the continental United States (www.feederwatch.org). For a 21-week period from November to April participants record maximum bird counts per species in two half-day increments. Participants also record the number of observation hours into blocks of 0, 1, 4, and 8 hours per sampling event (i.e., effort hours) and geographic coordinates of the feeder. We started with all count data restricted to the contiguous United States from 2007 through 2012. We removed observations that were missing information and reported counts > 30 individuals per species to eliminate potential data entry errors and maintain observations within a more typical range. We then subset the data to only those species with > 500 observations across all years, resulting in a total of 3,458,576 observations and 140 species (Table A1).

1.2.2 Macroecological variables

1.2.2.1 Artificial night light

We estimated mean radiance values (nW) of artificial night light for 2012 using monthly averages remotely sensed by the National Aeronautics and Space Administration's Day/Night Band (DNB) sensors of the Visible Infrared Imaging Radiometer Suite (VIIRS). The spatially-explicit estimates of point-source light are measured daily and averaged to represent a lunar BRDF-corrected (bidirectional reflectance distribution function), cloud cleared mean value of light for available days of each month that excludes the influences of clouds, terrain, seasons, atmospheric

effects, snow, and stray light (Román et al., 2018). We took the log of the annual average nighttime light estimates to reduce heteroscedasticity in the predictor and created rasters with a 1 km² resolution and extracted the light value at each feeder location.

1.2.2.2 Anthropogenic noise

We obtained anthropogenic noise data for the contiguous United States (CONUS) from recent geospatial models that estimate acoustic conditions at a resolution of 270m (Mennitt and Fristrup, 2016). Sound models projected the median (i.e., L₅₀) A-weighted sound pressure levels dB re 20 µPa (L_{A50}), which represents the A-weighted sound pressure level that is exceeded half of the time and is less sensitive to infrequent, loud events (Klingbeil et al., 2020). By changing model inputs from their current values to minimize anthropogenic factors, the geospatial sound model estimated a natural sound level that includes contributions from biotic and physiographic sources only. To characterize the anthropogenic component of the acoustic environment, we used ‘exceedance’ sound levels (Buxton et al., 2017), which is calculated by the logarithmic subtraction of estimated median sound levels (L₅₀; A-weighted decibels, re 20 µPa) from natural sources from the existing median sound level estimates (L₅₀) and is expressed in A-weighted decibels (dB(A)).

1.2.2.3 Urbanization

Because sources of ANLN are related to anthropogenic activity and development, we included metrics of urbanization to control for the influence of other aspects of anthropogenic activity extraneous to the environmental pollutants we sought to study. Anthropogenic impervious surface can reflect the intensity of human use within

the landscape by quantifying artificial covers, such as roofs of buildings and roads. For this variable, we obtained 30m spatial resolution grid of percent developed imperviousness from the 2011 National Land Cover Database (Xian et al., 2011), which we scaled up to a resolution of 270m to match the resolution of our noise data prior to matching impervious surface values to feeder coordinates. To quantify human population density, we used the 2010 US Census (United States Census Bureau, 2010) block data downsampled to 1km grids (Nelson et al., 2015). The human footprint index spans 0 to 50 and reflects eight human pressures at 1 km² resolution in the years 1993 and 2009, making it the most complete and highest-resolution globally consistent terrestrial data set on cumulative human pressures on the environment (Venter et al., 2016). We extracted values from the 2009 dataset because it aligned most closely with the years of PFW observations used in this study.

1.2.2.4 Duration of night

To determine whether responses to night light depend on night length (i.e., an interaction between the two), we calculated the duration of night from the latitude and Julian date of each observation using package *geosphere* in the statistical program R (v. 3.6.1) (R Core Team, 2019) and subtracted the photoperiod length from the daily 24-hour period.

1.2.3 Species-specific response models

We used the total number of individuals per species (abundance) as the response variable and used the six previously mentioned macroecological variables as fixed effects. We also included latitude as a fixed effect in our models because it correlates strongly with variation in energy, predation risk, climatic gradients, and other

aspects of environmental variation (Hillebrand, 2004). Because the estimates for light and noise were on a log-scale, we log-transformed the remaining variables, and then centered and scaled all variables with a z-transformation, which allows direct comparison of relative effects. Additionally, we incorporated an interaction term between artificial night light and anthropogenic noise, as well as an interaction term between light and night length. To account for the potential influence of variation among observers and the length of feeder observations on counts, we used participant ID and the number of observation effort hours as random effects. We also included the winter season of observation (e.g., winter of 2007-2008) as a random effect to account for large-scale variation across winters. We log-transformed the count data and, owing to the large sample sizes, in preliminary analyses found models performed well with Gaussian error, which was used for all models.

For each species, we compared models with and without the Matérn correlation component in the *fitme* function of package *spaMM* (Rousset and Ferdy, 2014). The Matérn correlation component is described by two correlation parameters, the scale parameter ρ , and a “smoothness” parameter ν . By fixing $\nu = 0.5$, we evaluated spatial models with the exponential spatial correlation $\exp(-\rho \cdot \text{distance})$. Best fit models were designated by having the lowest AIC value. To decrease the computation time for the spatially explicit models, we rounded latitude and longitude coordinates to 1 decimal place, providing a resolution of 11.1 km, which should still capture spatial variation in major environmental gradients that may influence abundance. Finally, due to computational demands, for species with more than 100,000 observations, we randomly subset the data to 20,000 observation pseudoreplicates and ran the models 10 times with and without the spatial correlation structure. We then averaged all the estimates for spatial and non-spatial models and used averaged AIC values to determine whether the spatial or non-spatial model received more support from the data. We report all apparent

trends with 85% confidence intervals (CI) that do not overlap zero as evidence for an influence of the predictor that warrants consideration (Arnold, 2010; Ware et al., 2015; Kleist et al., 2018). Because CI estimates require re-running linear mixed-effect models (LMMs) iteratively for each parameter estimate with the *fitme* function, and because computational demands of many of the spatial models required runtimes of several days, for practical purposes we calculated CIs as the s.e. of the parameter estimate multiplied by 1.44. To assess general trends of how species respond to ANLN, we calculated the weighted means and standard errors by summing the product of each species' estimate and sample size and dividing by the total number of observations.

To analyze the direction and magnitude of avian responses to anthropogenic stressors, we made the following assumptions, as outlined by (Halpern and Fujita, 2013): 1. Stressor parameters had roughly equal importance by eliciting relatively comparable potential impacts that contribute to the overall cumulative impact. 2. There was a uniform distribution of stressors within a pixel, which is unlikely to be typical. As such, this assumption will lead to overestimation of stressor intensity at some locations within the pixel and underestimation in others. 3. Presence only data likely underestimated responses by failing to include feeder locations that are within species' ranges and accessible, but avoided due to ANLN or other stressors.

1.2.4 Testing for multicollinearity

Anthropogenic noise and artificial night light levels are often correlated with one another and other environmental variables associated with human activities (Halfwerk and Slabbekoorn, 2015; Swaddle et al., 2015; McMahon et al., 2017), necessitating careful inspection of models for issues of multicollinearity. Because functions to check for multicollinearity in *fitme* models are not readily available, we checked for potential

collinearity and redundancy among the explanatory predictors by calculating the Variance Inflation Factor (VIF) among non-spatial models using the *lmer* function in package *lme4* (Bates et al., 2014). We obtained the maximum VIF value for each species-specific model and assessed potential issues of multicollinearity if $VIF > 10$ (Dormann et. al, 2013; Table A3). For the five species with $VIF > 10$, we removed non-ANLN parameters with the greatest VIF value in a reduced model until the maximum VIF value was < 10 (Table A4). If the reduced model did not change the interpretation of the influence of ANLN parameters (e.g., estimates in full and reduced model both had 85% CIs that did not overlap zero), then we kept the original full model. Spatially explicit and non-spatial models were used if they were the best fitting model per species as previously described.

1.2.5 Interpreting interaction direction and magnitude

For the interactions, we tested Noise:Light and Light:Night Length. We treated the additive response between interaction terms as the null model (Folt et al., 1999; Crain et al., 2008), where we would expect the interaction response to equal the sum of the effect sizes between stressor A and stressor B (henceforth denoted as 'E' for expected response). If the expected additive effect size overlapped with the 85% CI of the interaction response (henceforth denoted as 'I') for a species-specific model, then it was labeled as an additive response (Galic et al., 2018; Figure 1.1). To further describe the magnitude and response direction of deviations from the additive model prediction in absolute terms, interaction responses can be broken down into cumulative categories (Piggott et al., 2015; Table A5). A positive antagonism is less positive than predicted, and a negative antagonism is less negative than expected. Note that a negative antagonism can result in an overall positive response but the interpretation is the

interaction elicits a response that is less negative than expected; for example, if $-A + B = -E < I < B$ (Figure 1.1). A positive synergistic response is more positive than expected, and a negative synergistic response is more negative than expected. These responses can also occur if the interaction response has an opposite direction compared to the individual stressors; for example, $A + B = -I$ is a negative synergistic response. However, we also included a synergistic* response from Galic et al. (2018) for interaction responses that were more positive or negative than expected but less than the individual stressor effect sizes; for example, if $-A + B = -E > -I > -A$ (Figure 1.1). For emergent responses, if a species has no response to either stressor, where each response is equal to C, then the resulting cumulative influence would be $C + C > E$, which can either be positive or negative synergistic. We also labeled cumulative interactions as dominant, where one stressor accounted for most or all of the biological response, and was determined if a stressor effect size overlaps with the 85% CI of the actual interaction response ($A + B = A$ or B ; see Folt et al. (1999)). Since these interactions are less than what is expected and deviate from the null model, they are considered as cumulative interactions (Brown et al., 2013). However, if a species-specific model met both of the criteria for dominant and additive responses, we were not able to discriminate between the two categories and labeled it as indistinguishable. Moreover, if a species responded to at least one stressor but not the interaction between them, then the single stressor(s) response was independent from the added multimodal influence. Finally, we concluded that a species was uninfluenced by ANLN stressors if a species did not respond to single stressors or to an interaction.

1.2.6 Selection of species traits

To analyze whether predictive traits explained species-specific responses to ANLN, we gathered readily accessible trait data reflective of morphology, behavior and ecology (Table A6). We obtained diet preferences and average body mass from the EltonTraits 1.0 database (Wilman et al., 2014). To condense the number of factors for diet preference, we categorized species with the “PlantSeed” and “FruiTect” diets as herbivores, “Omnivores” remained as such, any “Invertebrate” based diet that were specifically arthropods were labeled as insectivores, and “VertFishScav” were labeled as carnivores. We obtained measurements of average wing chord and bill length for 73% of the species from Lisle et al. (2007), and the other 27% were supplemented from various sources (Table A6). We obtained body length, habitat association, and flocking behavior data from Birds of North America Online (Rodewald, 2015). We classified urban tolerance based on habitat affiliation descriptions from Birds of North America Online and following Hu and Cardoso (2009).

To obtain a variable indicative of a species’ visual sensitivity to light, we used the ratio of the corneal diameter to the transverse diameter within the eye (henceforth “light gathering ability”), which scales values to the size of the visual system and animal (Kirk, 2006; Hall and Ross, 2007). We obtained direct measurements of the corneal diameter and transverse diameter for 66 and 62 of the 140 species, respectively, from several sources (Ritland, 1983; Blackwell et al., 2009; Hall et al., 2009; Moore et al., 2013; Tyrrell and Fernández-Juricic, 2017, unpublished data). For the remaining 78 species, we imputed missing values using the *phylopars* function in package *Rphylopars* (Goolsby et al., 2017), which uses a phylogeny and an incomplete feature matrix that describes the available observations on one or more continuous features (Bruggeman et al., 2009). Estimation of missing parameters is computed by combining the known phylogenetic and phenotypic covariances with the tree topology, which is represented by

a 'Brownian motion' phylogenetic model. For imputation, we used a recent class-wide avian phylogeny (Jetz et al., 2012) and a feature matrix including body mass (g), body length (mm), and wing chord (mm), bill length (mm), the proportion of a species diet that consists of invertebrates, fruit, nectar, seeds and other plant material from the EltonTraits 1.0 database, nocturnality (one or zero), plus several measurements of eye geometry: eye corneal diameter (47% complete), eye transverse diameter (44% complete), and eye axial diameter (45% complete). Finally, we divided the complete compilation of corneal diameters by the transverse diameters to obtain the light gathering ability.

1.2.7 Trait relevance to species-specific responses

To test for relationships between responses to ANLN and traits, we used phylogenetic generalized least squares (PGLS) with the *gls* function in the R package *nlme* (Pinheiro et al., 2015). We simultaneously estimated phylogenetic signal (λ) of the model (Revell, 2011) where phylogenetic strength was evaluated on a scale between 0 and 1. In the event that PGLS estimated lambda outside of this range, we fixed lambda to the respective minimum or maximum bound. Furthermore, we accounted for the precision of estimated responses to ANLN by including a weighting function with fixed variance of one over the square root of the standard error of the response estimate (Garamszegi, 2014). Trait influence on bird responses to noise or light were assessed one at a time. Diet preference, habitat preference, urban tolerance, and flocking behavior were used for both noise and light responses. Light gathering ability was only assessed in models explaining variation in response to light. To avoid potential heteroscedasticity from phylogenetic outliers, we removed any species with a studentized residual ≥ 3.0 and reran the PGLS analyses (Jones and Purvis, 1997;

Medina and Francis, 2012). Below we report the relationships between functional traits and avian responses from models where phylogenetic outliers were removed, but also include model results with and without phylogenetic outliers in the supplement (Table A7). We considered the impact of a trait influencing responses to ANLN if the confidence interval did not overlap 0, and we report 95% CIs to reflect higher precision of estimates and 85% CIs for other apparent trends that warrant consideration for inference (Arnold, 2010).

1.3 RESULTS

1.3.1 Macroecological variables

Spatial models outperformed non-spatial models for 86 of 140 species, and there was a tendency for spatial models to outperform non-spatial models for species with more than 10,000 observations (Table A1). Parameter estimates from each approach were nearly identical for species with smaller sample sizes, but tended to diverge more for those with larger sample sizes (Table A2). Of the 140 species modeled, 69 species had a unimodal response to either artificial night light or noise. In general, species experienced a negative response when exposed to anthropogenic noise, but because of the mixed responses the overall effect across all species was not strong (overall weighted-mean $\beta = -0.014$, 85% CI: -0.045, 0.018; Figure 1.2). Importantly, variation in species-specific responses to anthropogenic noise displayed moderately strong phylogenetic structure ($\lambda = 0.65$, Figure A1). Among the 56 species (40%) that did change their abundance when exposed to anthropogenic noise, the mean apparent trend was avoidance (weighted-mean $\beta = -0.034$, 85% CI: -0.066, -0.001). Species experienced a weak positive response when exposed to artificial night light (overall weighted-mean $\beta = 0.003$, 85% CI: -0.033, 0.039; Figure 1.2), yet due to varying species

responses, the overall effect across all species was negligible. In contrast to responses to noise, we found no evidence that variation in response to light could be explained by phylogeny ($\lambda = 0$, Figure A2). Only 28 species (20%) altered their abundance with light exposure and the mean apparent trend was weak avoidance (weighted-mean $\beta = -0.008$, 85% CI: -0.044, 0.028). ANLN elicited avian responses similarly to other broad-scale urbanization factors (Figure A3), such as impervious surface (42% response, overall weighted-mean $\beta = -0.006$, 85% CI: -0.022, 0.010) and human footprint (16% response, overall weighted-mean $\beta = 0.001$, 85% CI: -0.005, 0.006). However, human population density had the strongest effect on avian abundance (37% response, overall weighted-mean $\beta = -0.033$, 85% CI: -0.063, -0.003).

1.3.2 Interaction between artificial night light and anthropogenic noise

We found evidence for an interaction between light and noise for 50 species. When exposed to both stressors, 35 species (70%) experienced a negative response to the multimodal influence, yet again because of the mixed responses the effect was weak (weighted-mean $\beta = -0.014$, 85% CI: -0.028, 0.001; Figure 1.3). Several species that responded to either light or noise were also influenced by the interaction between ANLN (31 responses, 45%). Of all interaction responses, 11 species (22%) had a non-cumulative response, where four species (8%) had an additive response where the expected response overlapped with the 85% CI of the actual response (Figure 1.3; Table A8). For example, red-breasted sapsuckers (*Sphyrapicus ruber*) had an expected response of 0.014, which overlapped with the 85% CI of the actual interaction response ($\beta_{\text{Interaction}} = 0.022$, 85% CI: 0.007, 0.034; Figure 1.4; Table A1). Thirty-nine species experienced a cumulative response that deviated from the expected additive model (Figure 1.3; Table A8). Five species (10% overall) experienced an antagonistic effect,

where the interaction ameliorated how species responded to ANLN. For example, the actual response for rufous hummingbirds (*Selasphorus rufus*) was less negative than expected but the effect was lower than the positive response to light alone ($\beta_{\text{Interaction}} = 0.021$, 85% CI: 0.001, 0.040; Figure 1.4; Table A1), resulting in a negative antagonistic response. Conversely, 20 species (40% overall) experienced a synergistic response, where the actual response was greater than what was expected. This was true for the black-chinned hummingbird (*Archilochus alexandri*), which experienced an interaction response that was more positive than expected ($\beta_{\text{Interaction}} = 0.086$, 85% CI: 0.054, 0.120). Fourteen cumulative responses (28% overall) were dominant, where 10 species had the interaction response driven by light. Interestingly, only two of these species responded to light alone, suggesting that the additional presence of noise increases the sensitivity to light for the other eight species.

Not all species that experienced a unimodal response to light or noise also responded to an interaction between the two. In this dataset, 37 species (26%) did not respond to the interaction, indicating that the addition of the second stressor did not influence how species respond to their sensory environment. However, and perhaps more importantly, the combined presence of ANLN can elicit emergent responses for species that did not react to either light or noise. Nineteen species (14%) from this dataset experienced an emergent response, with 11 synergistic, three dominant noise responses, and five indistinguishable non-cumulative responses. Eight of the 11 synergistic responses were negative (73%), indicating that these species are less tolerant to the multimodal influence than the responses to light alone, noise alone, and the expected additive effect between the two.

1.3.3 Interaction between artificial night light and night length

We found evidence for 65 responses to artificial night light when it interacted with night length (Figure 1.3; Table A8). Of the species that responded to the interaction, 47 species (72%) increased in abundance with artificial night light and longer nights (weighted-mean $\beta = 0.012$, 85% CI: 0.007, 0.019). Sixteen of the 28 species (57%) that responded to artificial night light alone were also influenced by the interaction between light and night length. Moreover, the models revealed changes in abundance for 49 additional species when the influence of night length was included. Of all interaction responses, 6 responses (9%) were non-cumulative, and only 2 responses (3%) were additive as expected. Fifty-nine species (91%) experienced a cumulative response that deviated from the expected additive model (Figure 1.3; Table A8), and these responses were roughly split between antagonistic (22 species), synergistic (21 species), and dominant responses (16 species). For antagonistic responses, most species (~80%) experienced a positive antagonism, where the actual response was less positive than expected. However, a few negative antagonistic responses resulted in a positive interaction effect size. For instance, the pygmy nuthatch (*Sitta pygmaea*) experienced a negative response to light alone ($\beta_{\text{Light}} = -0.182$, 85% CI: -0.326, -0.038), yet increased in abundance when light interacted with night length ($\beta_{\text{Interaction}} = 0.020$, 85% CI: 0.002, 0.038; Figure 1.4; Table A1). Similarly, most of the synergistic responses (~70%) resulted in a positive response. Roughly 25% of these responses were emergent, where the species only responded when light and night length interacted. For example, fox sparrows (*Passerella iliaca*) did not respond to light or night length alone, but did experience a positive response to the interaction ($\beta_{\text{Interaction}} = 0.017$, 85% CI: 0.012, 0.023). The majority of dominant responses (~70%) were driven by the response to light. For instance, the effect size of the response to light for the eastern meadowlark (*Sturnella magna*) overlapped with the 85% CI of the interaction response ($\beta_{\text{Light}} = 0.143$,

85% CI: -0.108, 0.393; $\beta_{\text{Interaction}} = 0.200$, 85% CI: 0.115, 0.286; Table A1, thus driving the response away from the expected additive response and mitigating the influence from night length (Figure 1.4).

1.3.4 Functional traits predicting avian response to ANLN

In contrast to our predictions, species that occupy closed habitats were less tolerant of both noise and light exposure than species that occupy mixed (Noise Ref: Mixed, $\beta_{\text{Closed}} = -0.031$, 95% CI: -0.061, 0.000, $\lambda = 0.27$; Light Ref: Mixed, $\beta_{\text{Closed}} = -0.037$, 95% CI: -0.067, -0.007, $\lambda = 0$) and open environments (Noise Ref: Open, $\beta_{\text{Closed}} = -0.031$, 85% CI: -0.060, -0.002; Light Ref: Open, $\beta_{\text{Closed}} = -0.052$, 95% CI: -0.090, -0.015), yet closed habitat species were also less tolerant to light compared to species in wetland (Light Ref: Wetland, $\beta_{\text{Closed}} = -0.074$, 95% CI: -0.132, -0.016) and especially disturbed environments (Light Ref: Disturbed, $\beta_{\text{Closed}} = -0.093$, 95% CI: -0.137, -0.049; Figure 1.5; Table A7). The high tolerance to light by species in disturbed habitats was further emphasized by the strong differences between species that occupy mixed (Light Ref: Mixed, $\beta_{\text{Disturbed}} = 0.056$, 95% CI: 0.014, 0.099) and open habitats (Light Ref: Open, $\beta_{\text{Disturbed}} = 0.041$, 85% CI: 0.006, 0.076). Additionally, species that occupy wetland habitat were less tolerant of noise compared to mixed (Noise Ref: Mixed, $\beta_{\text{Wetland}} = -0.049$, 85% CI: -0.094, -0.004) and open environments (Noise Ref: Open, $\beta_{\text{Wetland}} = -0.050$, 85% CI: -0.096, -0.003). A post hoc analysis of light gathering ability across habitat affiliations provides some support for a functional link for the most extreme differences in responses to light among habitats. Specifically, closed habitat species had greater light gathering ability than disturbed habitat species (Ref: Disturbed, $\beta_{\text{Closed}} = 0.029$, 85% CI: 0.003, 0.056, $\lambda = 0.19$). PGLS trait models also revealed insectivores were more tolerant

of noise exposure compared to herbivores (Noise Ref: Herbivores, $\beta_{\text{Insectivore}} = 0.041$, 95% CI: 0.006, 0.075, $\lambda = 0.42$).

1.4 DISCUSSION

Despite calls to enact studies to analyze the multimodal influence of anthropogenic noise and artificial night light on natural populations (Halfwerk and Slabbekoorn, 2015; Swaddle et al., 2015), there is still a dearth of research investigating the potential of cumulative responses to these stressors for a wide array of taxa. Moreover, the few multimodal studies that exist are all small-scale (e.g., McMahon et al., 2017, Ferraro et al., 2020), which do not consider the gradients of exposure to these anthropogenic stressors that occur at landscape, regional, and global scales. Our continental-wide study is the first, to our knowledge, to systematically evaluate the impact of the interaction between these stressors in terms of non-cumulative and cumulative responses on changes in abundance, and we did so for 140 of the most prevalent residential bird species in North America. Not only did most species decline in abundance when exposed to both stressors, but these responses were primarily cumulative, where the actual response deviated from the expected additive response. Moreover, the interaction revealed negative emergent responses of species that only reacted to the multimodal influence of ANLN. Additionally, the interaction between light and night length revealed an increase in abundance with light exposure during longer nights for most species, emphasizing that environmental context is equally important

when assessing the impacts of these stressors. Below we discuss potential mechanisms, as well as functional traits, for explaining avian responses to ANLN.

1.4.1 Species response to artificial night light and anthropogenic noise

We found 40% of species in this dataset responded to noise exposure, and the majority of species (70%) generally decreased in abundance. Birds may avoid anthropogenic noise due to masking, under which they are unable to detect biologically relevant cues such as conspecific communication or sounds made by predators (Barber et al., 2010; Zhou et al., 2019). Individuals that can still detect cues but fail to appropriately process and respond may be experiencing distraction or misleading mechanisms (Grade and Sieving, 2016; Dominoni et al., 2020b). The noise-induced impaired ability to detect or discriminate predation cues may elicit a continual state of perceived unpredictability and reduced security (Kleist et al., 2018), which could cause individuals to avoid noisy areas. Alternatively, species might compensate for increases in perceived risk by aggregating in flocks with the tradeoffs of longer flight initiation distance (Morelli et al., 2019) and increased competition, disease transmission, and increased conspicuousness to predators (Rubenstein, 1978). These and other anti-predator strategies might be related to the lack of responses to noise (62 species, 44%) or even increased abundance (17 species, 12%) for some species. However, increases in abundance or no change in abundance may not reflect the ultimate fitness consequences of noise. For example, migrating birds exposed to noise from a 'phantom road' had lower body condition than those that were in adjacent quiet locations, which would likely impact survival (Ware et al., 2015). In a breeding context, Western bluebirds (*Sialia mexicana*) appear not to avoid noise in nest site selection (Kleist et al., 2017), yet incur reproductive costs of increased hatch failure and altered chick development with

noise exposure (Kleist et al., 2018). Additionally, accumulated stress from exposure to sensory stressors could establish long-term adverse effects by dysregulating development, metabolism, immune responses (Langgartner et al., 2015), and impeding reproductive success during the breeding season (Ouyang et al., 2011).

Artificial night light did not elicit strong species-specific responses to the same extent as noise, as only 28% of species altered abundances when exposed to this stressor. However, context seems to matter, as nearly half of the species in this study altered abundance in response to the interaction between light and night length (see below). Still, that fewer species responded to light than noise could be due to other local-scale variables that we could not include here, such as habitat composition and fragmentation (Ciach and Fröhlich, 2017) and the spectral composition of light (Ulgezen et al., 2019). Additionally, when we accounted for the multimodal influence of the interaction between noise and light, models revealed most species (70%) decreased in abundance, which matched our predictions. An organism's tolerance of one stressor tends to be lower when other stressors are in operation (Myers, 1996), and in this case the inclusion of light often exacerbated the negative influence of noise. When organisms are exposed to constant lighting, the alteration of the circadian timing results in the disruption of the rhythmicity of hormones such as glucocorticoids and melatonin, which can induce a cascade of effects such as disrupted sleep patterns, inefficient metabolic processes, and immunological modulation (Navara and Nelson, 2007). While these changes may not elicit changes in abundance, they could alter an organism's physiological state and decrease tolerance to heterotypic pervasive stressors (Gunderson et al., 2016), such as anthropogenic noise. Moreover, 40% of interaction responses were synergistic, such that changes in abundance were stronger than the simple addition of effects from each stressor. Importantly, our results should be considered relatively conservative because the nature of presence-only data limits our

inference about whether species completely avoid some sensory environments. As such, future local-scale research with true absence data would nicely extend the insights from our study.

The extent of the number of species that respond to ANLN can be further demonstrated by the discovery of emergent interactions, as several species-specific responses were identified by the multimodal influence of both stressors. Emergent properties present more information than isolated parameters in an ecological system (Nielson and Müller, 2000), and therefore provide additional context of how species are responding to light and noise when they overlap spatially and/or temporally. Specifically, the majority of emergent responses (73%) resulted in species avoiding polluted areas, which increases the necessity and urgency of effective management strategies mitigating the influence of anthropogenic stressors.

1.4.2 Species response to artificial night light and night length

In general, the majority of species (72% of responses) increased in abundance when exposed to artificial night light and longer nights. The presence of artificial night light has the potential to expand the temporal niche and elongate the perceived photoperiod. Yet, there have been relatively few studies that have formally examined the effect of artificial light on altering behavior or restructuring temporal niche partitioning (Gaston et al., 2013). Northern mockingbirds (*Mimus polyglottos*) and common blackbirds (*Turdus merula*) expand foraging times when artificial light is present (Stracey et al., 2014; Russ et al., 2015). However, these studies recorded behavior during the breeding season when birds have a different seasonal foraging pattern and life history requirements. Research regarding the influence of light at night for wintering bird activity near urban feeders pre- and post-twilight have reported conflicting results. For example,

a winter-long observational study of 24 common feeder species in a residential area in Norway found only three species were regularly active at night, yet this activity could be beneficial if individuals partition their time between defending territories at night and efficiently foraging during the day (Byrkjedal et al., 2012). Other studies suggest that there is weak evidence to support birds are altering the timing of foraging with the presence of light pollution (Da Silva et al., 2017), and birds tend to arrive later in the morning to feeders rather than earlier when artificial light is present (Clewley et al., 2016).

Temperature could also be a contributing factor for whether a species utilizes light to extend foraging time. For example, the three species that increased activity at night described by Byrkjedal et al. (2012) advanced foraging when temperatures were colder than normal, most likely because they suffered higher mass loss on colder nights. Depending on a species' thermal tolerance, increased light levels from anthropogenic sources might not be beneficial enough to justify prolonged foraging activity, or they could interact with temperature to allow adaptive responses to exploit the extended photoperiod. In addition to modifying behavior with optimal temperature and potential foraging opportunities, birds might be innately attracted to sources of artificial light. For example, a study that compared roosting preferences of male great tits (*Parus major*) in a laboratory setting under lit and dark conditions found males preferred to roost under lit conditions (Ulgezen et al., 2019). While selecting these sites might provide birds an advantage by increasing food availability, as well as extra-pair paternity gains during the breeding season, the additional exposure to light could have negative consequences on individual physiology and fitness. These can include, but are not limited to, altered gene expression (Dominoni et al., 2018), immune function (Cissé et al., 2017), oxidative stress (Navara and Nelson, 2007), and disrupted sleep patterns (Aulsebrook et al., 2020). Further research is needed to assess whether the benefits of light-polluted areas

outweigh the costs of exposure to light at night in the context of night length and ambient temperature, perhaps by taking advantage of a latitudinal gradient.

1.4.3 Functional traits predicting avian response to ANLN

The trait that was the most indicative of avian response to anthropogenic noise and artificial light was habitat preference. Specifically, species that occupy closed habitats were less tolerant of both sensory stressors compared to those that occupy open habitat. Avian responses to these stressors can be explained by the physical properties of the stressors and how they operate in different environments.

Communication among birds is often adjusted to local acoustic conditions such that birds in forested environments have low-frequency signals (Boncoraglio and Saino, 2007; Tobias et al., 2010). However, low-frequency calls of forest-dwelling birds are prone to masking by anthropogenic noise (Nemeth and Brumm, 2009) and previous research suggests that breeding birds with low-frequency vocalizations are more sensitive to noise exposure than those with higher-frequency signals (Goodwin and Shriver, 2011; Francis 2015). Although we did not explicitly evaluate call frequency here given the high number of functionally different calls within and among species (Marler, 2004), it is possible that lower-frequency signals among forest birds could explain their decline in abundance with noise exposure relative to birds affiliated with other habitats. Light intensity, spectral composition, and timing vary drastically between closed and open habitats. In a forest habitat, canopy architecture and leaf phenology represent spatial and temporal strategies for light interception, respectively (Ishii and Asano, 2010). The light microclimate produced by canopy structure could contribute to species sensitivity, as variability in light levels limits dispersal capabilities (Pollock et al., 2015) as well as orientation and activity levels (Wood and Lustick, 1989). Moreover, birds that occupy

disturbed habitat are exposed to light even when they avoid light-polluted areas such as streets and business districts, which could contribute to acclimation and increased tolerance (Dominoni et al., 2014). The differences in light sensitivity among habitat affiliations were supported by closed-habitat species possessing greater light gathering ability, which is a pattern confirmed by a similar trait-based study among breeding birds (Senzaki et al., In press). In addition to differences in habitat preference and sensory sensitivity, PGLS models also revealed insectivores were more tolerant of noise than herbivores. This finding contrasts with comparable research on diet preferences explaining avian sensitivity to noise (Francis, 2015; Senzaki et al., In press), which alludes to sensitivities by diet are season-dependent.

Although we did not find many functional traits that predicted avian response to ANLN, we did measure the phylogenetic strength of general avian response to these stressors. Specifically, we found changes in abundance in response to noise are moderately conserved among residential overwintering birds. To further investigate how birds perceive and respond to noise, future research should test the relationship between intrinsic traits that represent anatomical and physiological sensitivities to sound. In a survey that ranked the degree of traits impacting the survival, persistence, performance, and regeneration of a species, experts identified the ability to discriminate in noisy environments, auditory spectral resolution, and auditory bandwidth as the most plausible traits to predict vertebrate sensitivity to noise (Ditmer et al., In review).

Conversely, we found no evidence that variation in response to light could be explained by phylogeny, suggesting avian responses to light could be more indicative of environmental contexts than evolutionary conserved intrinsic characteristics. This contradicts our expectations, as the natural day / night cycle is a fundamental organizing force in biology that regulates the timing of many behaviors and physiological processes across all forms of life (Gaston et al., 2013). Despite using the light gathering ability trait

that directly relates to light sensitivity and showed a strong phylogenetic signal, we were unable to link a light-specific intrinsic trait to changes in abundance with respect to artificial night light. As such, rather than using anatomical traits, overwintering bird response could be predicted by traits representing ecological sensitivities, such as activity patterns, trophic level, vagility, and habitat specializations (Ditmer et al., In review). If more functional traits are identified, synergistic effects between traits should also be considered for assessing avian response to ANLN, as the combination of traits could increase extinction risk (Davies et al., 2004). Combinations of traits could increase sensitivities to light or noise, or sensory-specific traits could interact to overwhelm a species, which in turn could explain avian responses to the interaction between light and noise.

1.5 CONCLUSION

By analyzing pervasive stressors across a continental-wide scale, we revealed considerable heterogeneity in avian responses to light and noise alone, as well as the interaction between them. Based on overall responses to the interaction between light and noise, we suggest management efforts should focus on ameliorating excessive noise for overwintering bird species, which should decrease the impact from synergistic responses, as well as the negative impact from noise alone. There is still much to learn about responses to these stressors and smaller-scale studies should take our approach of assessing responses to ANLN. Local-scale studies will allow for adequately replicated field manipulations to investigate potentially non-linear responses to overlapping stressors for well-described communities (Brown et al., 2013). Furthermore, higher temporal resolution of stressor characteristics can determine whether stressors occur in quick succession and induce a synergistic response or if the timing between stressor

occurrences allows an organism to prime itself for additional perturbations, resulting in an overall response to the stressors that is smaller than the sum of their isolated effects (i.e., an antagonistic interaction; Gunderson et al., 2016). Careful temporal sampling of stressor intensities will also allow management to clearly define 'sensory danger zones' as specific temporal windows or spatial areas in which light and noise overlap and impact potentially vulnerable species (Dominoni et al., 2020b). Pairing these sensory danger zones with functional traits and contexts that predict responses of targeted species to these co-occurring stressors can encourage management efforts to enact regulation that prevents the spread and limits the intensity of these stressors from reaching protected areas (Buxton et al., 2017). In closing, knowing when (seasonal and diurnal patterns), where (locations of anthropogenic disturbance), how (sensory mechanisms), and why (functional traits) sensory pollutants influence species will help management efforts effectively mitigate impacts from these globally pervasive anthropogenic stressors.

Table 1.1: Definitions and examples of cumulative interaction responses between two environmental stressors.

Interaction Response	Definition	Example
Antagonistic	The addition of a second stressor ameliorates the influence of the existing stressor, indicating a diminished response to a composite stimulus compared with either unimodal component in isolation (Munoz and Blumstein, 2012).	The three-way interaction between nitrate, high temperature, and scarring interacted antagonistically to produce less community distance or distinctness on the microbiome of the coral <i>Pocillopora meandrina</i> than scarring or high temperature alone (Maher et al., 2019).
Dominant	One stressor accounts for most or all of the biological response (Folt et al., 1999).	Herbicide reduces the growth of populations of the model microalga <i>Chlamydomonas reinhardtii</i> , yet growth remains unaltered when microalga are exposed to additional stressors, such as nutrient depletion (Brennan and Collins, 2015).
Emergent	A response emerges only when both signals are presented in combination (Halfwerk and Slabbekoorn, 2015).	Chickens (<i>Gallus gallus domesticus</i>) ignored chemical and visual warning signals and did not discriminate between palatable and unpalatable formulas when presented in isolation, but were shown to avoid food items when both signals were presented together in an emergent interaction (Rowe and Guilford, 1996).
Synergistic	The combined effect of multiple stressors that exceeds the sum of individual stressor effects. The heightened perception of the environment may help the animal capitalize on the multimodal cues and enhance fitness-related factors, or the animal may become more sensitive to the increased stressor severity (Bartlett et al., 2016).	The interactions between acid rain and low pH soils and between acid rain and habitat fragmentation elicited stronger negative influences on the breeding success of wood thrushes (<i>Hylocichla mustelina</i>) than the expected sums between each stressor combination (Hames et al., 2002).

Table 1.2: Predictions of functional trait relationships with overwintering avian abundance when exposed to ANLN.

Functional Trait	Explanation	Hypotheses	Stressor Predicted Effect on Abundance
Light gathering ability	The ratio between the corneal and transverse diameters within the eye, which provides a measure of light sensitivity	Birds with large eyes detect lower intensities of light, and are therefore more sensitive and will respond more strongly to artificial night light (Hall and Ross, 2007).	Light -
Diet preference	1) Herbivore (Plants, seeds, fruit, nectar) 2) Omnivore (equal proportion of plant and animal diet) 3) Insectivore (invertebrates) 4) Carnivore (vertebrates, scavenger)	Anthropogenic noise can conceal biologically relevant cues and interfere with prey detection (Francis, 2015). As such, omnivorous species and those with animal-based diets will be more sensitive to noise. Conversely, the altered perceived photoperiod can extend foraging opportunities for diurnal species (Titulaer et al., 2012), which will propagate an increase in abundance for all diet types.	Noise - Light +
Flocking behavior	1) Aggregate in winter flocks, either with conspecifics or mixed species flock 2) Does not flock	Gregarious species are deceived to perceive anthropogenic noise as a threat (Bowles, 1995) and are more likely to participate in anti-predator strategies, such as increasing flock size (Morelli et al., 2019). Birds vocalize more frequently when they become disoriented by artificial night light, which attracts additional members of their flocks (Winger et al., 2019).	Noise & Light +
Habitat preference	1) Closed (Dense tree cover) 2) Mixed (Partial tree cover) 3) Wetlands (ponds, lakes, marsh) 4) Open (No tree cover) 5) Disturbed (Fragmented, developed lands)	Species in open and developed areas are less protected from light and noise, as foliage from canopies shield birds from light (Canham et al., 1990) and acoustic cues degrade with decreasing vegetation cover (Nemeth and Brumm, 2009). Therefore, higher exposures to sensory stressors will result in decreased abundances.	Noise & Light -

Urban tolerance	1) Habitat depends on human-made structure 2) Habitat is natural and not human dependent	Urban species that tolerate urbanization will acclimate to anthropogenic stressors such as light and noise, and will be more equipped to survive in polluted areas (Hu and Cardoso, 2009; McCabe et al., 2018) than non-tolerant species.	Noise & Light +
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Table 1.3: Summary statistics of untransformed predictor variables used in analyses. All variables were centered and scaled in analyses to facilitate model convergence and direct comparison of predictor effects.

Predictor	Mean	Standard Deviation	Minimum	Maximum
Noise (exceedance, dB(A))	10.87	4.19	0.91	32.08
Light (radiance, nW (logarithmic))	0.56	0.71	-1.28	2.28
Human population density (per km ²)	656.73	918.7	0	41463
Percent anthropogenic impervious surface (per 0.27 km ²)	16.36	18.05	0	100
Human footprint (index from 0 to 50)	27.92	11.92	0	50
Latitude (degrees)	39.83	4.00	25.08	48.95
Night length (hours)	13.6	1.1	10.62	15.77

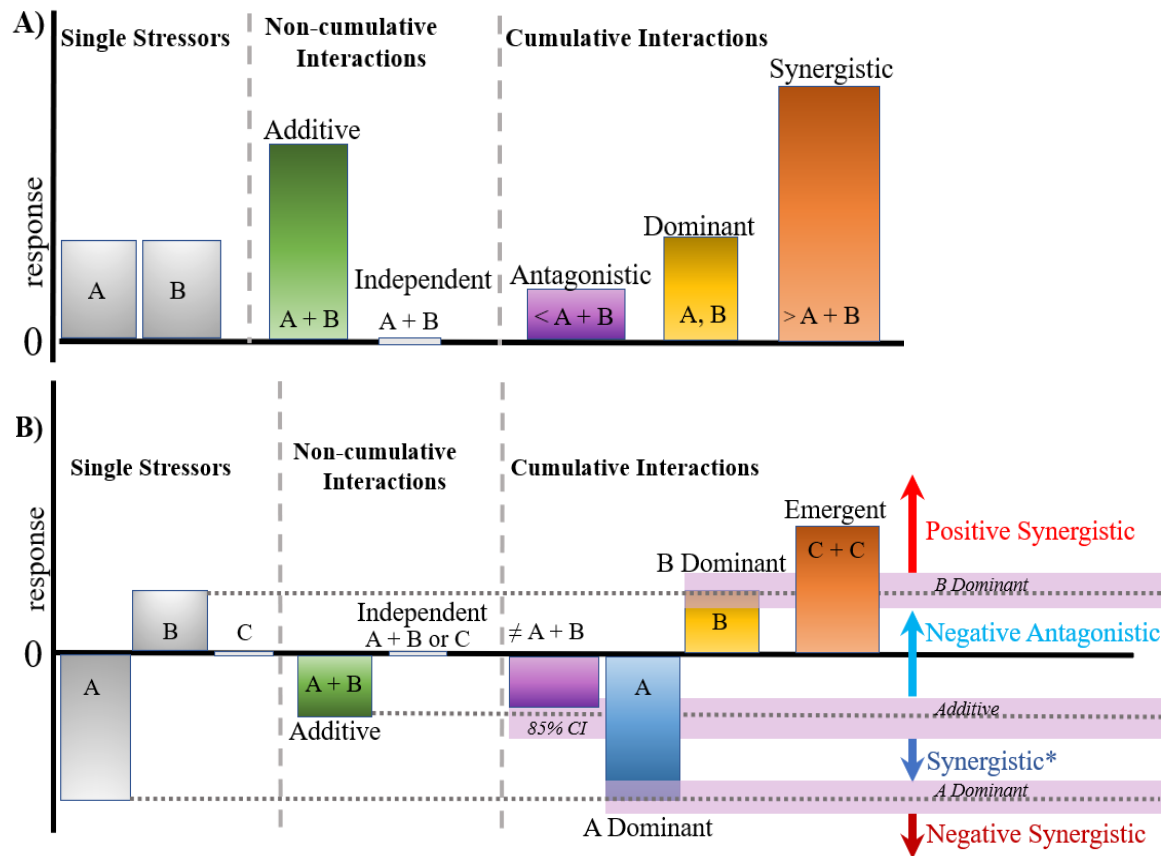


Figure 1.1: Conceptual approach to interpreting interaction types determined from the magnitude and direction of the interaction effect in absolute terms, as adapted from Côté et al. (2016) and Galic et al. (2018). (A) Non-cumulative interactions occur when the effect size is equal to the summation between two stressors ($A + B$) or is independent with no response. Deviations from the expected null model result in cumulative interactions, where the response is less than (antagonistic or dominant) or more than (synergistic) expected. (B) The interaction type and direction from opposing stressors is evaluated by whether the effect size of the interaction response overlaps with the 85% confidence interval (85% CI, purple bands) of additive and dominant responses, and whether the magnitude is greater or less than the expected null model. Emergent interaction responses can arise when species only respond to the combined efforts of both sensory stressors ($C + C$; Halfwerk and Slabbekoorn, 2015).

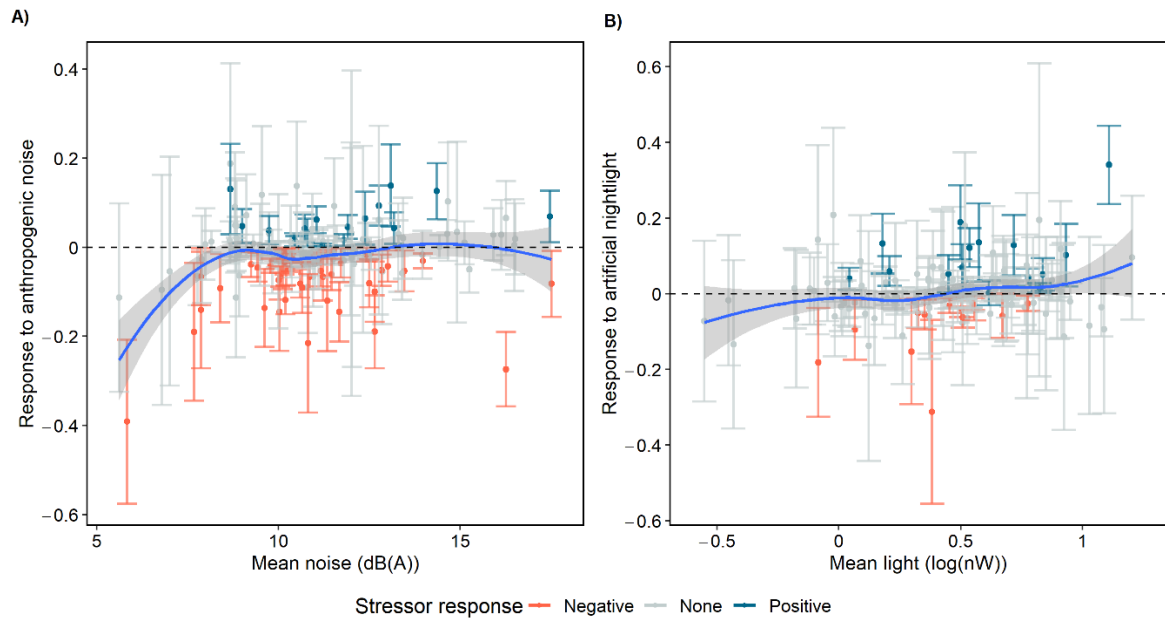


Figure 1.2: Avian responses to (A) anthropogenic noise and (B) artificial night light when exposed to increasing stressor intensity. The locally weighted smoothing line represents general avian responses to either noise or light across all 140 species. Effect sizes of species-specific responses are plotted against mean values of noise and light exposure, with error bars representing 85% confidence intervals.

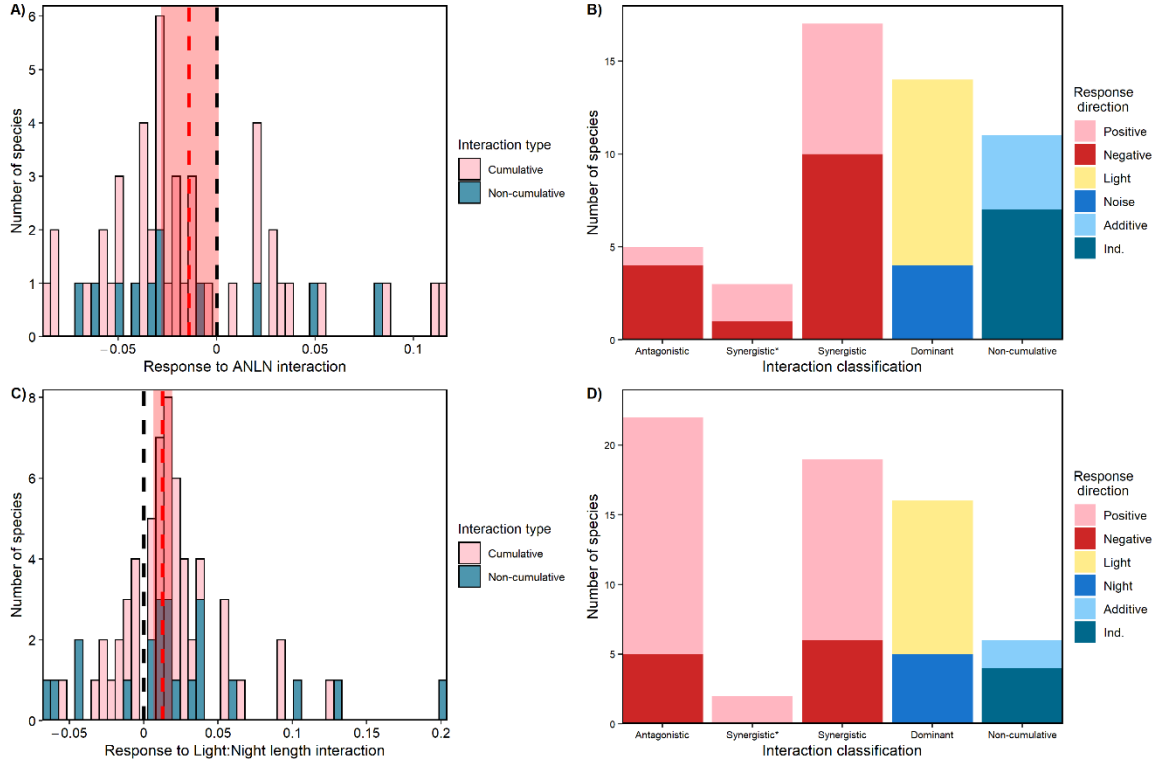


Figure 1.3: Species responses to the interaction between noise and light (A and B) and between light and night length (C and D). Histograms show the distribution of the number of species that responded to the ANLN interaction (A) and the light:night length interaction (C) for cumulative and non-cumulative interactions. The weighted-mean of all species responses is indicated by the dotted red line with an 85% confidence interval band. Stacked bar plots show the number of interaction classifications and associated directions for species responses to the ANLN interaction (B) and the light:night length interaction (D). Responses were either cumulative (antagonistic, synergistic*, synergistic, or dominant) or non-cumulative (additive or indistinguishable (ind.)).

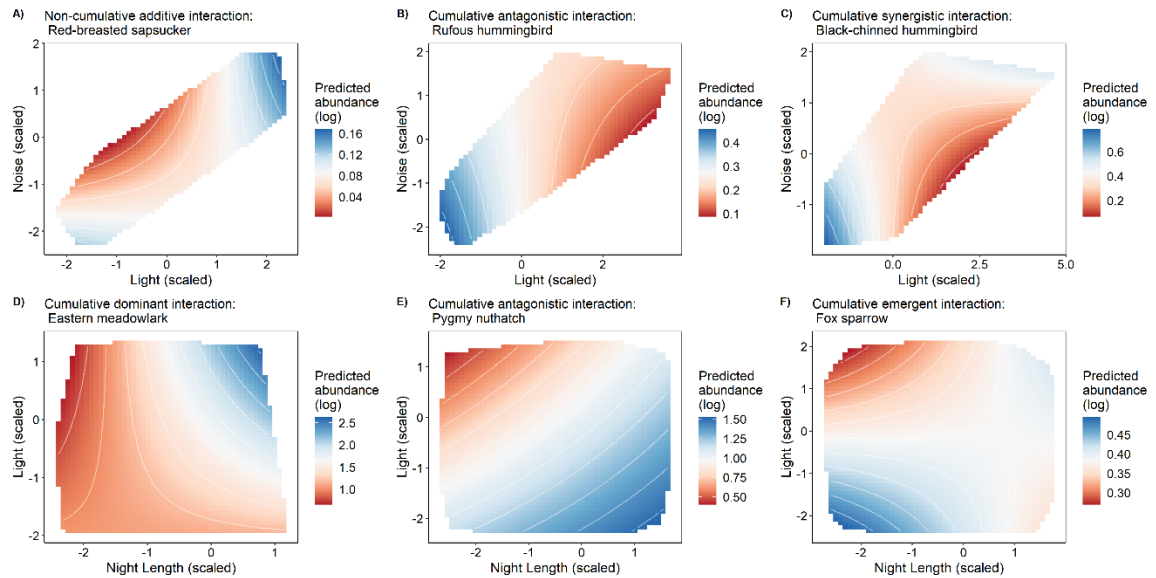


Figure 1.4: Partial dependency plots for non-cumulative and cumulative interactions between noise and light (A-C) and light and night length (D-F) for six representative species. The color scale represents the intensity of how the interaction variables influence the predicted response, with the region of values representing the species-specific area the predictor space model was trained on. Non-cumulative interactions arise when the interaction effect size does not deviate from the expected additive response (A). Cumulative interactions arise when the interaction response deviates from the expected response. Both B) and E) show the antagonistic interaction response that is less negative than what was expected but with a magnitude smaller than the response to light. Dominant responses occur when the effect size of a stressor drives the biological response, such as the effect size of light in the interaction with night length for eastern meadowlarks (D). Synergistic responses result in an interaction effect size that is greater than expected. For example, black-chinned hummingbirds (C) have an interaction that is more positive than expected, but is smaller than the response to light, resulting in a diminished positive region when both noise and light intensity increase. However, fox sparrows (F) experience an emergent synergistic response and only respond to light and night length when those factors interact.

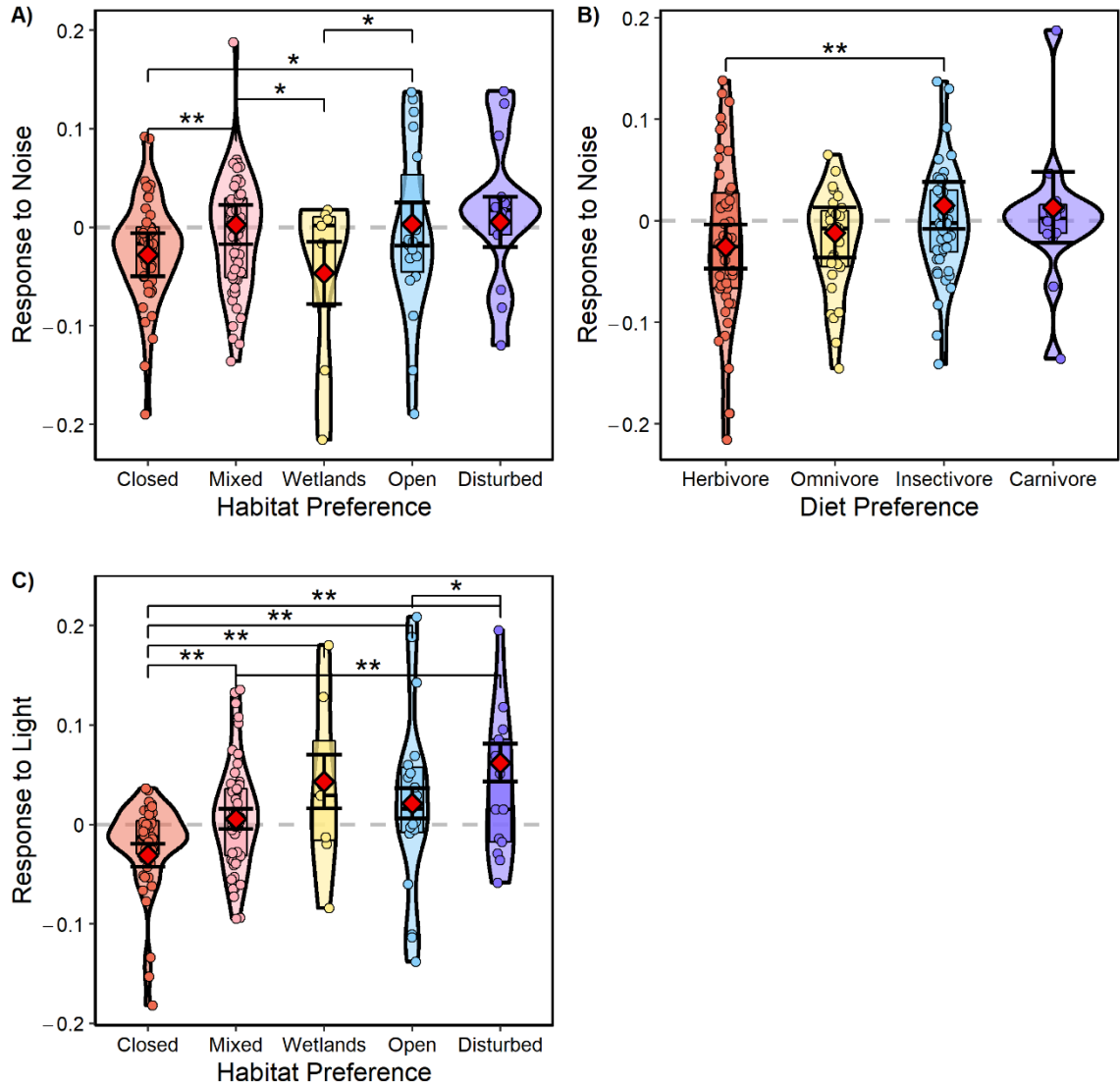


Figure 1.5: Violin plots representing functional trait relationships with avian response to anthropogenic noise (A and B) and artificial night light (C) with the predicted mean, symbolized by the red diamond, and standard error bars. The influence of a trait on the response was determined if the confidence interval did not overlap zero, where a single asterisk denotes an 85% CI and a double asterisk denotes an 95% CI.

CHAPTER 2. DIRECT AND AMBIENT LIGHT POLLUTION ALTERS RECRUITMENT FOR A PLANT-POLLINATOR SYSTEM

2.1 INTRODUCTION

The coevolutionary arms race between flowering plants and pollinators have shaped angiosperms to become the most speciose group of land plants on the planet (Ollerton, 1996). Flowering plants have developed specialized features to balance the need to attract pollinators selecting for floral traits and mating systems, as well as constructing defense mechanisms to prevent herbivores, including pollinator larvae, from decimating plant reproductive output (Ramos and Schiestl, 2019). Simultaneously, pollinators underwent behavioral and structural adaptations, such as altering the quantity and quality of flower visitation, features that increased efficiency of gathering and transferring pollen, or traits that increased the success of capitalizing on nutritious and / or reproductive benefits (Mitchell et al., 2009a). As such, the reciprocal advances in both plants and pollinators were a major promoter of evolutionary radiation and biodiversity. While pollination systems have persisted for millions of years, there is growing recognition that plant-pollinator interactions can be drastically influenced by anthropogenic changes to ecosystems, such as climate change, habitat fragmentation, and species' invasions (Mitchell et al., 2009b). The alteration of pollinator communities is likely to have cascading effects on plant population persistence, as pollinator decline intensifies pollen limitation, reduces plant reproductive success, and threatens the loss of genetic diversity (Thomann et al., 2013). One aspect of anthropogenic disturbances on plant-pollinator communities that is not yet fully understood is the impact of artificial light at night (ALAN).

Within the last few decades, advances in lighting technology have caused the cost per unit brightness to fall and the intensity and quantity of light installations increase

exponentially, resulting in 2% annual growth in total light radiance globally (Kyba et al., 2017). This rate of growth exceeds the human population growth rate of 1.05% and is often ascribed to two primary factors: more light emitted per capita and a greater percentage of uplight from light fixtures (National Park Service, 2017). Moreover, modern ALAN is no longer confined to urban centers; it radiates outwards along road networks that run through or around otherwise pristine areas (Owens et al., 2020), and emanates as skyglow, which occurs from atmospheric scattering of light (Kyba et al., 2015). Consequently, many natural systems experience considerable light pollution.

Natural light regimes are a fundamental organizing force in biology and regulate the timing of foraging, migration, circadian rhythms, and reproduction (Gaston et al., 2013; Seymoure et al., 2019a). However, ALAN dysregulates the amount, spectral conditions, and timing of light exposure (Gaston et al., 2017; Seymoure et al. 2019a). The consequence is that ALAN creates evolutionarily novel lighting conditions that differ strongly from those in which organisms have evolved (Seymoure et al., 2019b), resulting in changes to temporal use of habitat and increasing competition for crepuscular and nocturnal species, as well as interfering with circadian cycles, among other effects (Gaston et al., 2013). Among plant pollinators, species that rely on visual cues may become disoriented, decrease vigilance for predators, decrease flowering-visiting activity, or suppress oviposition, resulting in an overall decrease in recruitment (Gaston et al., 2013; Macgregor et al., 2015; Owens et al., 2020). Furthermore, many nocturnal pollinators are naturally attracted to light sources and may experience increased predation from species that forage under longer periods of nocturnal illumination (Macgregor et al., 2015, Owens and Lewis, 2018). Altered nocturnal pollinator behavior or declines in pollinator abundance could have reciprocal changes for the plants they pollinate (Macgregor et al., 2015). For example, an experimental study in Switzerland showed rural fields exposed to streetlights experienced a 29% decrease in nocturnal

pollinator species composition, resulting in fewer pollinator visits by 62%, and subsequently a 13% reduction in fruit set (Knop et al., 2017). Furthermore, this reduction in plant reproductive output could indirectly affect diurnal pollinators by depleting a potential food source, decreasing network connectivity, and even altering the plant community (Fontaine et al., 2005). Yet, how responses to ALAN among diurnal pollinators directly influence the plants with which they interact is unknown.

Moths may be especially vulnerable to ALAN, as this stimulus can guide moths towards an incorrect target, often leading to a maladaptive response, or even increased mortality, in a process known as misleading (Dominoni et al., 2020a). Examples of misleading include interpreting artificial light sources as the moon (Baker and Sadovy, 1978) or perceiving dark bands around sources of light as places of refuge, leading to non-stop flight patterns circling the light (Hsiao, 1973). However, despite a recent meta-analysis regarding diurnal Lepidoptera species' attraction to sources of ALAN (van Langevelde, 2018), the mechanisms of attraction towards artificial light and potential consequences on fitness for diurnal pollinators is still largely unclear. To understand how the presence of ALAN influences the relationship between diurnal moths and their plant hosts, we investigated the effects of an artificial direct light treatment (henceforth "direct light") and artificial indirect light from ambient skyglow (henceforth "skyglow") on an obligate mutualism.

Flowers from yucca plants (*Yucca* and *Hesperoyucca* spp.) are only pollinated by their unique mutualist moths (*Tegeticula* and *Parategeticula* spp.), and likewise moths will only oviposit in yucca flower ovaries, which become a secure food source for the larvae (Baker, 1986). As such, outside influences, such as other pollinator species or competing inflorescence plants, are eliminated in this closed plant-pollinator system. However, given the tight one-to-one relationship, the interaction is especially susceptible to destabilizing forces (Buchmann and Nabhan, 2012), such as ALAN and other human-

induced environmental conditions. Furthermore, while all other yucca moths are nocturnal, *T. maculata* is a diurnal pollinator (Powell and Mackie, 1966). Therefore, by introducing two external variables to the closed interaction between *T. maculata* and its mutualist yucca plant, we were able to directly measure the influence of direct light and skyglow on the behavioral response of a diurnal pollinator and the reciprocal effects on its host.

Using field-placed light manipulations at sites exposed to a gradient of skyglow, we investigated the influence of direct and indirect light on the yucca-yucca moth mutualism by quantifying chaparral yucca (*Hesperoyucca whipplei*) fruit set and the obligate moth (*Tegeticula maculata maculata*) larval density per fruit. Exposure to ALAN is known to influence a variety of behaviors among insects (Macgregor et al., 2015; Owens and Lewis, 2018) and could result in disrupted melatonin synthesis, and subsequently a cascade of adverse effects, such as decreased sex pheromone production, sterility, and ultimately inhibiting reproductive output (Desouhant et al., 2019). Therefore, we predicted that the presence of direct artificial light would disrupt pollination and oviposition activity (Macgregor et al., 2015), resulting in a decrease in mature fruit per plant and fewer moth larvae per fruit. Conversely, because skyglow is diffusely spread in the night sky and contributes minimally to scene luminance when compared to direct light sources, skyglow is likely to influence moth reproductive output through other mechanisms. The presence of skyglow in a naturally dark environment may mislead diurnal moths by altering their perception of photoperiod, positively masking the nocturnal environment, and thereby increasing nocturnal activity and opportunities to reproduce (Macgregor et al., 2015; Desouhant et al., 2019). Therefore, we predicted yucca fruit set and moth larvae per fruit will increase with the intensity of indirect light from skyglow.

2.2 METHODS

2.2.1 Study species

We studied chaparral yucca plants (*Hesperoyucca whipplei*) and yucca moths (*Tegeticula maculata maculata*) in natural areas surrounding San Luis Obispo, California. Individual plants grow as rosettes for several years and then bloom in the spring, sending up a single, large, paniculate inflorescence that reaches 1.4-4 meters in height. Each flower remains open for several days, and an individual plant may continue to open flowers for as long as ten weeks (Aker and Udovic, 1981). Yucca moths tend to be abundant wherever their obligate host plant is found. As moth adults only live for a few days and do not feed as adults, they have evolved unique tentacles on their maxillary palps to actively collect and compact pollen from the flowers of their yucca hosts (Aker and Udovic, 1981). This direct fertilization ensures the flower will mature into a fruit pod and produce seeds, ensuring the future recruitment of the plant, while providing a viable food source for moth larvae. Once the eggs are secured inside the flower's ovary, the larvae hatch inside the developing fruit and consume seeds within their immediate vicinity. As the pods begin to harden and are ready to dehisce, full-grown larvae bore out of the pods and descend to the ground, form cocoons under the soil, and wait for an environmental cue to pupate and emerge as adults (Baker, 1986).

2.2.2 Experimental design

We selected five sites with abundant yucca at the start of the flowering season in April 2019 (Figure A4). Sites were selected based on the presence of serpentine soil, coastal sage—chaparral scrub habitat, which are both environmental indicators of *H. whipplei* habitat (Gucker, 2012), and if the blooming inflorescence density was high enough to provide plants along a 30 m transect. Each site included three 30 m transects

that were randomly assigned either a treatment of exposure to a gradient of direct artificial night lighting (“light-treated”) or no exposure (“control”). In total, we designated eight light-treated transects and seven control transects. Light towers marked the beginning of each transect and consisted of two solar powered spotlights (DINHAND, 54 led 400 lumen) attached to a 3-meter pole (Figure 2.1). Direct light-treated transects provided artificial light from dusk until dawn every night of the experiment. The direction of each light-treated transect was designed to ensure emitted light did not shine towards nearby transects and all transects per site were situated along the same elevation to minimize variation in abiotic conditions. Additionally, transects were located at least 100 meters from each other to maintain independence, as the range of adult yucca moths do not typically exceed 50 meters (Marr et al., 2000).

On each transect we selected yucca plants at four distances from the light towers: 1 m, 3 m, 9 m, and 30 m (Figure 2.1). Distances were chosen to represent the inverse square law of light attenuation, resulting in 4 orders of magnitude difference in light levels along the transects. Because flowering yucca plants did not always occur at our predetermined distances, we selected the closest flowering plant to each point and measured actual distances to the light source for each. Yucca plants were monitored once a month to assess the progress of blooming yucca stalks until the fruit were fully developed, which lasted from April through August 2019. Ideally, this design would have resulted in four plants per transect for a total of 60 plants; however, two of the selected plants at the 1-meter mark did not produce inflorescence due to herbivory. Consequently, these plants were dropped from the final analysis, resulting in a total of 58 plants for our analysis of fruit set.

2.2.3 Adult moth phototaxis

We deployed a separate set of light towers during the peak of yucca flowering to assess whether adult moths responded to the direct light treatment with phototaxis. Four light towers were installed at a sixth site (Table A4) independently located from the towers used in the fruit set and larva recruitment experiment. These towers were deployed for seven days (May 10-17) with two control towers and two light treatment towers that were at least 100 meters apart. At approximately an hour before sunset (17:00- 18:00) we attached two dual-sided 15.24 cm x 20.32 cm yellow adhesive sticky traps (GIDEAL, Inc.) to the poles to collect flying invertebrates, specifically moths. At approximately an hour after sunrise the next morning (7:00-8:00) we collected the sticky traps, quantified the number of yucca moths and other arthropods trapped, and switched the treatment for each tower (i.e. control became treatment and vice versa). This process repeated each night for seven nights. Additionally, the density of blooming yucca and dead stalks were counted within a 15-meter radius (706.9 m²) to account for site variation and potential deviations in the density of emerging adult yucca moths.

2.2.4 Light measurements

We used separate instruments to measure direct ALAN and skyglow. Light intensity from the towers was measured with a handheld light meter (Minolta-T10a, Konica Minolta Sensing Americas, Inc), where direct light brightness was measured in units of lux, which is an illuminance value relative to human vision (Seymoure et al., 2019b). At each sample plant three separate measurements were taken by orienting the light meter directly towards the light tower. We used the mean of the three measurements for subsequent analyses.

We measured indirect artificial light from skyglow using a Sky Quality Meter-Lens (SQM-L) device (Unihendron). The SQM-L is a hand-held device that incorporates a lens for collecting light from a narrow field of view that is approximately 20 degrees wide, specifically for city use where surrounding lights or buildings may affect the reading. Skyglow values were recorded as magnitudes/ arcsecond² (mpsas), which report brightness in magnitudes spread out over a square arcsecond of the sky. Measurements were taken on nights of similar conditions between May 23rd to June 14th. All light measurements were taken after astronomical twilight had started, when the sun was at least 12-18° below the horizon. To only capture light conditions produced by ALAN, measurements were taken when the moon was positioned below the horizon. Ideally, measurements should be taken under cloudless conditions to ensure the SQM-L is accurately measuring light at the zenith. However, the marine fog layer was almost always present during measurements, so these values report conditions yucca plants and moths typically experience during the flowering season.

We measured skyglow at each sampled plant along the transects by holding the SQM-L directly towards the zenith and recorded six measurements. We discarded the first measurement to calibrate the device, and we averaged the remaining five measurements for subsequent analyses. Furthermore, because skyglow would not systematically vary within each transect, we averaged the measurements at the 3 m, 9 m, and 30 m plants per transect, but excluded those at the 1 m plants because the angle from the SQM-L at that location would have detected light emitted by the treatment lights. Because the mpsas scale is logarithmic, relative, and reversed, we converted skyglow values to candelas (cd/m²) using $10.8 \times 10^4 \times 10^{(-0.4 \times (\text{mpsas}))}$. Finally, we confirmed measurements did not systematically differ between light-treated and control transects (two-sample t-test, $t = 0.214$, 95% CI: -0.003, 0.003) or between astronomical and true night measurements (two-sample t-test, $t = -1.861$, 95% CI: -0.006, 0.0003).

2.2.5 Environmental variables

To control for biotic variation among sites, we used circular plots within a radius of 7.5 m (176.6 m² area) of each selected yucca plant and counted the total number of yucca rosettes, number of plants that were blooming, and the number of dead inflorescence stalks. For plants at the 1- and 3-meter locations, densities were calculated from areas that overlapped with the arc of emitted light and distance from the treatment towers (sampled areas of 100.1 m² and 123.7 m², respectively). These variables are indicative of potential moth recruitment, as moth larvae from previous years will emerge from underneath plants with senesced stalks and will travel to nearby blooming plants to lay their eggs (Aker and Udovic, 1981). Therefore, the density of flowering yucca from previous seasons, as well as the number of blooms in near proximity, are important covariates that could influence the number of adult moths interacting with plants in our transects. Finally, using the geographic coordinates of each plant, we measured elevation (meters), slope (percent) and aspect (degrees) in ArcGIS (ESRI 2011).

2.2.6 Yucca plant and yucca moth recruitment

Once yucca plants aborted excess flowers and the pollinated fruits matured, we counted the total number of fruit for each plant as a metric of recruitment (henceforth “fruit set”). Previous studies have shown that the number of yucca fruits produced is an excellent predictor of seed set and therefore plant recruitment (Aker and Udovic, 1981). For moth recruitment, we collected fruit from sampled plants (which ranged from 1 to no more than 5), dissected the fruit within 24 hours of collection, and counted the number of moth larvae per fruit as a metric of moth recruitment. If a selected plant did not produce fruit, we sampled fruit from a different plant within 5 meters of the original plant. Of the

58 plants we measured, 17 plants did not have fruit, and 8 of these were replaced with alternative plants with fruit for analyses of moth recruitment. Plants without replacements were dropped from the larval analyses, resulting in a total of 49 plants and 234 fruit. For the direct light measurements, half of the alternative plants were in the control transects, and modifications to the distance from the treatment tower did not change the amount of light exposure. For the other four alternative plants in the light transects, replacements were selected 2-3 meters behind the original plant. As such, the direct light intensity measurements used in the subsequent models were a slight overestimate of the true value.

2.2.7 Analyses

We used program R (R Core Team, 2019) for all analyses. We used generalized linear mixed models (GLMMs) with Poisson error for all models with packages *lme4* (Bates et al., 2014) and *MASS* (Venables and Ripley, 2002). Because preliminary analysis revealed a slight overdispersion for models explaining fruit set and adult moth abundance, we included an observation-level random effect (OLRE) for these models to provide each data point a unique level of a random effect (Harrison, 2014). In the moth larval models, we included plant ID as a random effect to account for variation among individual plants. Transect ID was also included as a random effect in all models. All fixed effects were centered and scaled to facilitate direct comparison of their effects.

To avoid overfitting models, we first used two sets of candidate models to assess the influence of abiotic or biotic environmental variables on mature fruit set and larva counts before including light measurements. Abiotic variables include elevation, slope, and aspect. Biotic variables include yucca rosette density, blooming inflorescence density, dead stalk density, and mature fruit set counts for the larval models. We ranked

all combinations of the abiotic or biotic environmental variables using AIC with the package *MuMIn* (Barton and Barton, 2019). For each set, variables whose effect sizes were within a model with $\Delta AIC \leq 2$ and with 85% confidence intervals (CI) that did not overlap zero were included in subsequent light models that addressed our hypotheses (Tables A9, A11, A13, A15 for ranked models of biotic fruit, abiotic fruit, biotic larval, and abiotic larval variables).

We constructed three light models to explicitly test our predictions for the influence of light exposure on fruit set and larva count. The first model tested for a treatment effect (light-treated vs control) to identify if the presence of direct artificial light elicited changes in recruitment for these species (henceforth “treatment” models). The second model tested for a relationship between the light intensity emitted by the treatment towers and fruit set or larva count (henceforth “illuminance” models). Finally, to put a biological perspective on illuminance levels, the third model separated direct light intensity into three categories relative to natural nocturnal light levels (henceforth “exceedance” models). These categories include ‘natural dark’, where light levels represented minimally lit conditions (0.0001 to 0.001 lux), light levels within the range experienced under naturally lit conditions (0.01 to 0.5 lux, denoted as ‘natural moonlight’), and light levels exceeding illuminance produced by a full moon (>0.5 lux, denoted as ‘exceeding’ light; Gaston et al., 2013; Seymoure et al., 2019a). The treatment, illuminance, and exceedance models also included an interaction term with skyglow. Variables in the light models were assessed by ranking models by AIC and we report the compiled list of top performing models. We concluded that variables within models in the competitive set ($\Delta AIC \leq 2$) had an influence on the response if the confidence interval did not overlap zero, which is a common use for evaluating effects in information theoretics (Arnold, 2010). Specifically, we report 95% CIs to reflect higher precision of estimates and 85% CIs for others that warrant consideration for inference.

Finally, because the modeling effort and data inspection suggested that nonlinear functions may also explain the relationships between direct light or skyglow and fruit set and larva count, we considered second order polynomial functions of logarithmically scaled light values in a post hoc analysis. We compared these models and assessed the influence of parameter estimates as described above to determine whether the polynomial function improved model fit over the linear relationships in strongly supported models.

2.3 RESULTS

2.3.1 *Adult moth phototaxis*

The presence of direct artificial light strongly increased the mean counts of arthropods ($\beta = 0.887$; 85% CI: 0.240, 1.515) and yucca moths ($\beta = 3.183$; 95% CI: 1.553, 6.091) caught on traps relative to control conditions (Figure 2.2).

2.3.2 *Light and yucca fruit*

All light models pertaining to mature fruit set were assessed with skyglow and a variable representing direct light because no additional abiotic or biotic environmental parameter had an influence on fruit set (Tables A10 and A12). While treatment appeared in a competing model, it did not have a strong influence on fruit set. Illuminance models revealed a positive relationship between light exposure and mature fruit set ($\beta = 0.326$; 85% CI: 0.019, 0.657; Table 2.1; Figure 2.3). However, exceedance models did not reveal any strong differences in fruit set among the three light intensity categories. Across all light models, skyglow consistently appeared in the top ranked model and resulted in an increase in mature fruit set ($\beta = 1.033$; 95% CI: 0.186, 2.038). Strongly supported intensity models also included an interaction between direct light and skyglow;

however, confidence in the effect size was low. Comparisons between the top competing models for skyglow (Tables A17, A18, and Figure A5) and illuminance (Figure A6) both show an inclusion of a second order polynomial term did not improve model performance for predicting fruit set ($\Delta AIC = 0.36$ and 0.78 , respectively).

2.3.3 *Light and the yucca moth*

All larval light models were assessed with yucca rosette density, dead stalk density, and aspect (Tables A14 and A16, respectively). For all models, larva count was strongly influenced by increased yucca rosette density ($\beta = 0.242$; 95% CI: $0.054, 0.437$; Table 2.2). Aspect appeared in competing models ($\beta = -0.173$; 85% CI: $-0.350, -0.008$), as conditions favored plants on hills facing North and East. Additionally, a portion of competing models included density of dead stalks, but this variable did not have a strong influence on larva count.

In contrast to the increase in fruit set with direct light exposure, moth larva counts were lower on light-exposed treatments than control sites ($\beta = -0.407$; 85% CI: $-0.789, 0.001$; Table 2.2; Figure 2.4). While illuminance levels appeared in a competing model, it did not have a strong effect, suggesting larva counts did not vary across the gradient of direct light. However, larva counts were lower among plants exposed to exceeding light levels than those in naturally dark conditions ($\beta_{\text{Ref: Natural dark}} = -0.674$; 85% CI: $-1.230, -0.082$). Matching the positive association between mature fruit set and skyglow, an increase in skyglow was associated with an increase in larva counts ($\beta = 0.216$; 85% CI: $0.024, 0.419$; Table 2.2; Figure 2.5). Despite direct light and ambient skyglow affecting larval count independently, the interaction between the two did not strongly influence moth recruitment. Inclusion of a second order polynomial term for skyglow did not

improve model performance over the top ranked model with skyglow as a linear effect for larva counts ($\Delta AIC = 1.47$; Tables A17, A18, and Figure A7).

2.4 DISCUSSION

Light pollution created by ALAN is increasingly recognized as a major driver of nocturnal insect declines (Knop et al., 2017; Owens et al., 2020), yet little research has investigated the effects or mechanisms behind diurnal pollinator response to this anthropogenic stimulus. Here, we provide evidence that a diurnal yucca moth exhibits positive phototaxis to artificial night lighting. Moreover, we only caught one moth across all trials under dark conditions, and all trap locations received both light and dark conditions, thus serving as their own controls, which provided additional confidence in this observed response. Plants exposed to direct artificial light produced higher fruit set; however, this increase in plant recruitment did not have a reciprocal benefit for moth recruitment, as larva counts decreased with exposure to artificial light, especially under light levels exceeding natural moonlight intensity. Because *H. whipplei* is self-incompatible (Powell and Mackie, 1966), an increase in fruit set alludes to an increase in pollination, which purportedly occurs after oviposition (Aker and Udovic, 1981). Despite resulting in increased plant fruit set, direct light elicited a decrease in larva counts, suggesting there are other mechanisms influencing moth reproduction and recruitment, such as physiological damage or misdirected behaviors. Furthermore, both plants and moths experienced an increase in recruitment under brighter light polluted areas, suggesting the ambient artificial light provides more opportunities for moths to pollinate and oviposit. The presence of ALAN most likely influences adult moth behavior and other factors that contribute to reproductive output, for unlike other moth species, yucca larvae develop inside an enclosed fruit pod (Baker, 1986) and are thus shielded from

ALAN. Therefore, we discuss possibilities for how direct light and ambient skyglow influence adult moth reproductive activities.

2.4.1 Direct light

Fruit counts increased not only within the light treatment compared to the control, but with increasing light intensity as well. This suggests moth behavior follows the concentration hypothesis (Macgregor et al., 2015), such that moths are attracted and disperse towards plants closer to light sources and end up pollinating a greater number of flowers for these individuals. Because moths are not seen to oviposit on the same inflorescence after pollination (Aker and Udovic, 1981), a higher yield of pollinated flowers would suggest there is a higher number of moths interacting with these plants. The presence of direct lighting acts as a misleading cue, as incorrectly drawing moths towards the anthropogenic stimulus. For example, Heitzman (1965) suggested diurnal Lepidoptera species become startled from their resting places and become attracted to the source of artificial light. Beshkov (1998) experienced a similar phenomenon by catching diurnal butterflies and releasing them near a light at night, and noted most, but not all, individuals traveled towards the light similarly as nocturnal Lepidopterans. If moths expend a large amount of energy traveling to plants nearby the source of light, then it would be most beneficial for females to oviposit at these plants with their remaining energy reserves. This is the first experimental study that directly measured the influence of ALAN on positive phototaxis for a diurnal moth, yet the reasoning behind this dispersal is still unclear.

Although the described sequence of pollination following oviposition would suggest that larva recruitment should match the pattern of increased fruit set with direct light exposure, we found larva recruitment to be lower among light treated plants and

those that were exposed to light intensities that exceed values similar to maximum moonlight illuminance. There are no clear explanations for the mismatch in the effect of direct light on yucca fruit set and yucca moth larva counts. One possibility is artificial lighting that exceeds natural nighttime conditions could elicit adverse physiological consequences or misdirected behaviors. Indeed, several aspects of moth reproduction have been recorded to change when exposed to ALAN, such as inhibiting female sex pheromone release, inducing male sterility, and disrupting female oviposition (Owens and Lewis, 2018). However, the yucca moth in our study is diurnal and thus regularly experiences light intensities many orders of magnitude greater than those in our treatments. Still, evidence from other diurnal insects, such as *Drosophila melanogaster*, suggests that even exposure to dim ALAN levels (i.e. ~1 lux) can disrupt oviposition and lead to fewer eggs laid (McLay et al., 2017), suggesting that the mere presence of ALAN can alter fitness-relevant behaviors. If moths experience positive phototaxis and are dispersing to plants closer to direct sources of light, then perhaps the exposure to light during their resting period is eliciting physiological damage (Gaston et al., 2013; Desouhant et al., 2019). This could explain why pollination is successful and oviposition is not, as moths are able to carry out reproductive activities during the day with full visual capabilities, yet they are unable to produce viable offspring. However, the presence of ALAN might mislead moth activity to extend their temporal niche into the night (Macgregor et al., 2015; Desouhant et al., 2019), and the nocturnal behavior could interfere with the moth's visual system. Moths flying away from the light may be functionally blinded as the pigment within the eye expands in response to the stimulus (Hamdorf and Höglund, 1981). If moths are engaging in nocturnal oviposition activity, there is the possibility that they are no longer able to discriminate between the stamen and pistil and are misdirected when they deposit eggs. Another example of misdirected activity was observed by Aker and Udovic (1981), as they described a behavior where

female moths drew their tentacles across the stigma, searching for pollen, but made no attempt to oviposit. Misdirected behaviors could be amplified by the presence of ALAN, yet further research is needed to decipher whether the decrease in moth recruitment is altered by mechanisms influencing physiology, behavior, or a combination of these factors. If decreased diurnal pollinator recruitment due to direct ALAN exposure is widespread, then the gradual decline in population size could lead to decreased genetic diversity and increased vulnerability to climatic stressors, which could change community structure to the point where pollination function is compromised (Vanbergen, 2014).

Moreover, the lack of response along the gradient of light intensity alludes to a strong sensitivity to a small amount of light, which escalates when the light intensity surpasses naturally lit conditions. To accurately model moth response to light levels, future research should monitor the degree of oviposition activity along a range of light exposure to reveal the shape of the response curve. This information will not only provide the lower and upper limits of moth response to ALAN but will also improve estimates of species 'indicator values' for environmental assessment, as well as improving simulation models for predicting ALAN impacts on other diurnal pollinators.

2.4.2 Ambient skyglow

Skyglow increased both yucca fruit set and larva counts, suggesting that skyglow increases nocturnal pollination and oviposition activity. Skyglow increases background brightness up to three orders of magnitude above natural nighttime conditions (Seymoure et al., 2019a) and can result in ambient lighting of up to 0.15 lux in wilderness areas near cities (Gaston et al., 2013; Seymoure et al., 2019a). This intensity could be bright enough to alter the perceived photoperiod (Macgregor et al., 2015;

Desouhant et al., 2019). The probability of moth activity extending into the night will depend on peak flight activity, as diel activity is not strictly confined to daylight hours and varies by species (Lamarre et al., 2015). Presumably, species that naturally fly around dusk will be more likely to extend their temporal activity with the presence of ALAN. While diurnal insect sensitivity to wavelengths have been described for several species (see Donners et al., 2018), sensitivities to light intensity is relatively unknown, such as the threshold of artificial light that misleads diurnal insects into extending their temporal activities into the night and potentially inciting phototaxis. Even without knowing the specificities of moth visual sensitivity, the degree to which ALAN influences nocturnal oviposition can be determined by the yucca moth's natural photoperiodic entrainment. For example, when exposed to varying daylight hours, the ovipositional rhythm of the diurnal *Culex tarsalis* was reciprocally altered to oviposit bimodally during the first few hours of the photophase and again at the beginning of the scotophase, alluding to ovipositional behavior controlled by entrainment to light intensity changes (Beck, 1980). If yucca moths entrain to oviposit with variation in light levels in a similar way, extension of light duration could alter their ability to properly entrain for oviposition. Furthermore, increased exposure to ALAN might alter metabolic processes. Melatonin is not only responsible for endogenous patterns such as enhanced cell maintenance and mitochondrial activity, but it also is a major driver of biological rhythm and daily activities (Jones et al., 2015). While *T. maculata maculata* only survives as an adult for a few days, the extended temporal activity could have dire consequences on longer lived species, as long-term exposure to stress can lead to compromised immune responses, regulation of metabolism, and decreased reproductive output (Desouhant et al., 2019). Conversely, female yucca moths have finite energy reserves, and the combination between increased metabolic work when exposed to artificial nightlight and allocating energy to dispersal and egg production could contribute to decreased moth recruitment.

While both the yucca plant and moth experienced an increase in recruitment, the influence of skyglow could implicate a cascade of rippling effects. Ambient skyglow is detectable tens to hundreds of kilometers from urban centers, particularly under overcast conditions (Kyba et al., 2015), which could influence diurnal pollinators at the population and community levels (Sanders and Gaston, 2018) or fill an empty niche (Gaston and Bennie, 2014) if nocturnal species experience negative phototaxis (Owens and Lewis, 2018). The variation in community structure will depend on the extent to which species avoid or reduce competition or predation (Sanders and Gaston, 2018). Alterations in species composition due to ALAN have already been shown to affect network structure and trait distributions with consequences for ecosystem functioning (Sanders and Gaston, 2018), yet this extent has not been revealed for diurnal communities.

2.4.3 Plant response to ALAN

Changes in moth behavior are the most likely explanation for changes in plant and moth recruitment; however, the possibility exists that plants respond directly to variation in direct and indirect light. Plants interact with light via photosynthesis mechanisms, yet the light produced by skyglow is unlikely to be adequate to elicit a sufficient response on carbon fixation, and ultimately should not alter the physiology or resource allocation to fruit set (Bennie et al., 2016). Moreover, reproductive output for yuccas is resource- and not pollinator-limited. For example, a study on *Yucca elata* mature fruit set showed that regardless of yucca moth abundance or hand-pollination of flowers on inflorescences, plants did not alter mature fruit set and aborted ninety percent of moth-pollinated flowers (James et al., 1994). *H. whipplei* relies most heavily on rainfall pattern for plant flowering and resource allocation (Baker, 1986); however, the presence of artificial light could alter the timing of blooms. Timing of yucca blooms is crucial for

yucca moths because their activity is limited by ambient temperatures sufficient for flight activity. Several studies have reported plant blooms occur earlier seasonally with the presence of light pollution (French-Constant et al., 2016; Singhal et al., 2019), and early blooms with colder temperatures could decrease pollination attempts and dispersal distances of moths. Conversely, later blooming events in response to light exposure (as summarized in Bennie et al. (2016)) may not have sufficient water for flowering or fruiting, as well as causing desiccation for adult moths that cannot withstand higher temperatures (Addicott et al., 1990). Future studies should compare the timing of yucca blooms under the presence of varying levels of skyglow to see if ambient light pollution advances or delays flowering, and consequently if moth emergence and pollination activity follow suit. Modification of plant mating systems by anthropogenic changes has the potential to drive changes in the densities or dispersion of conspecific plants that change pollinator-mediated connectivity within a plant population, which can lead to altered pollen flow and consequently elevate the risk of inbreeding depression and negatively affecting plant fitness (Venbergen, 2014). Whether these changes occur with the presence of ambient skyglow remains to be determined.

2.5 CONCLUSION

Depending on the source of ALAN, the abundance, behavior, and physiological response of the yucca moth may result in fewer successful pollination attempts (Aizen and Feinsinger, 2003), and over time this positive feedback loop could contribute to a decrease for both plant and pollinator reproductive output. We report a decline in moth larva recruitment when exposed to direct artificial lighting, yet if a threshold-type response exists for intensities that exceed natural moonlight conditions, then this response could be more drastic with respect to the light source intensity and scale.

Moreover, we report an increase in both plant and moth recruitment when exposed to ambient skyglow. While studies have investigated the potential outcomes of exposure to ALAN for nocturnal populations (Wilson et al., 2018; Desouhant et al., 2019; Owens et al., 2020), we are the first study to provide evidence that both direct and indirect ALAN influences recruitment for a diurnal pollinator. However, it is still unknown if or why other diurnal pollinators experience positive phototaxis, and whether direct lighting influences the physiology, behavior, or multiple factors relating to reproduction and fitness. Correspondingly, it is unknown if the novel selection pressures of direct and indirect ALAN are disrupting complex diurnal plant-pollinator communities. Evolution of reinforced interactions with pollinators could eventually be an evolutionary trap if pollinators are declining from exposure to direct ALAN (Thomann et al., 2013), as a reduction in pollinators could result in decreased visitation to less-rewarding flowering species, resulting in a decline in biodiversity (Mitchell et al., 2009a). Furthermore, changes in blooming phenology due to indirect ALAN could alter synchrony with different pollinator species, thus excluding seasonal pollinators that no longer overlap in flowering time (Memmott et al., 2007). Future research on ALAN will need to investigate the intricate responses of diurnal pollinators to both direct and indirect ALAN that will identify concrete mechanisms relating to physiological or behavioral susceptibility and inform predictions on how wide-spread communities will shift with this global driver of emerging change.

Table 2.1: Model selection table of all models for the treatment, illuminance, and exceedance effects on mature fruit set, in addition to the null model (intercept only). All models include transect ID and the OLRE as random effects. *K* indicates the total number of parameters in the model and weight corresponds to competing models within 2.00 ΔAIC . Model parameters included in the global model are Skyglow, Treatment (light-treated or control), direct light intensity emitted from the treatment towers (Illuminance), Exceedance (natural dark, natural moonlight, and exceeding light levels), the interaction between skyglow and treatment (Skyglow*Treatment), the interaction between skyglow and illuminance levels (Skyglow*Illuminance), and the interaction between skyglow and exceeding light levels (Skyglow*Exceedance). Bolded variable names indicate predictors with 85% confidence intervals that do not overlap zero.

<i>Model</i>	<i>K</i>	<i>AIC</i>	<i>ΔAIC</i>	<i>weight</i>
Skyglow	4	401.34	0.00	0.38
Skyglow + Illuminance	5	402.06	0.72	0.27
Skyglow + Treatment	5	402.79	1.45	0.19
Skyglow + Illuminance + Skyglow*Illuminance	6	403.00	1.65	0.17
Null	3	404.8	3.46	--

Table 2.2: Model selection table of all models for the treatment, illuminance, and exceedance effects on moth larva counts, in addition to the null model (intercept only). All models include transect ID and plant ID as random effects. K indicates the total number of parameters in the model and weight corresponds to competing models within 2.00 Δ AIC. Light model parameters included in the global model are Skyglow, Treatment (light-treated or control), direct light intensity emitted from the treatment towers (Illuminance), Exceedance (natural dark, natural moonlight, and exceeding light levels), the interaction between skyglow and treatment (Skyglow*Treatment), the interaction between skyglow and illuminance (Skyglow*Illuminance), and the interaction between skyglow and exceeding light levels (Skyglow*Exceedance). Environmental variables tested are yucca rosette density (Density), dead stalk density (Dead stalks), and Aspect. Bolded variable names indicate predictors with 85% confidence intervals that do not overlap zero.

<i>Model</i>	<i>K</i>	<i>AIC</i>	<i>ΔAIC</i>	<i>weight</i>
Density + Skyglow + Aspect	6	798.38	0.00	0.13
Density + Skyglow + Treatment	6	798.57	0.20	0.12
Density + Skyglow	5	798.66	0.28	0.12
Density + Aspect	5	798.95	0.58	0.10
Density + Skyglow + Dead stalks	6	799.24	0.87	0.09
Density + Skyglow + Aspect + Dead stalks	7	799.40	1.02	0.08
Density + Skyglow + Treatment + Aspect	7	799.50	1.12	0.08
Density + Skyglow + Exceedance	7	799.80	1.42	0.07
Density + Aspect + Dead stalks	6	799.92	1.54	0.06
Density + Skyglow + Treatment + Dead stalks	7	800.03	1.65	0.06
Density + Skyglow + Illuminance+ Aspect	7	800.18	1.80	0.05
Density + Skyglow + Exceedance + Aspect	8	800.38	2.00	0.05
Null	3	804.5	6.12	--

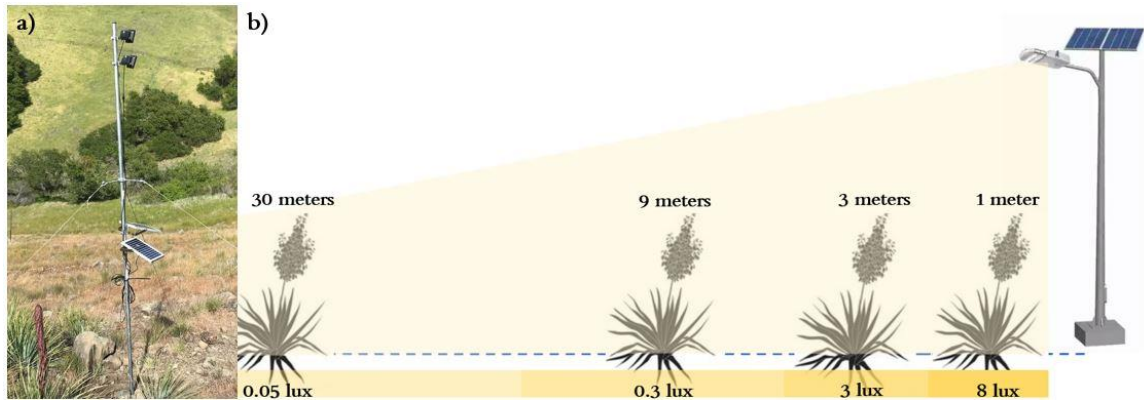


Figure 2.1: Treatment tower set up for each of the fifteen transects at our study sites (a). Experimental design of transects and yucca placement from the treatment towers (b). Yucca plants are selected at approximately 1 m, 3 m, 9 m, and 30 m from the light towers, and plants are exposed to direct artificial light in the designated light-treated transects, as shown with approximate illuminance values (lux).

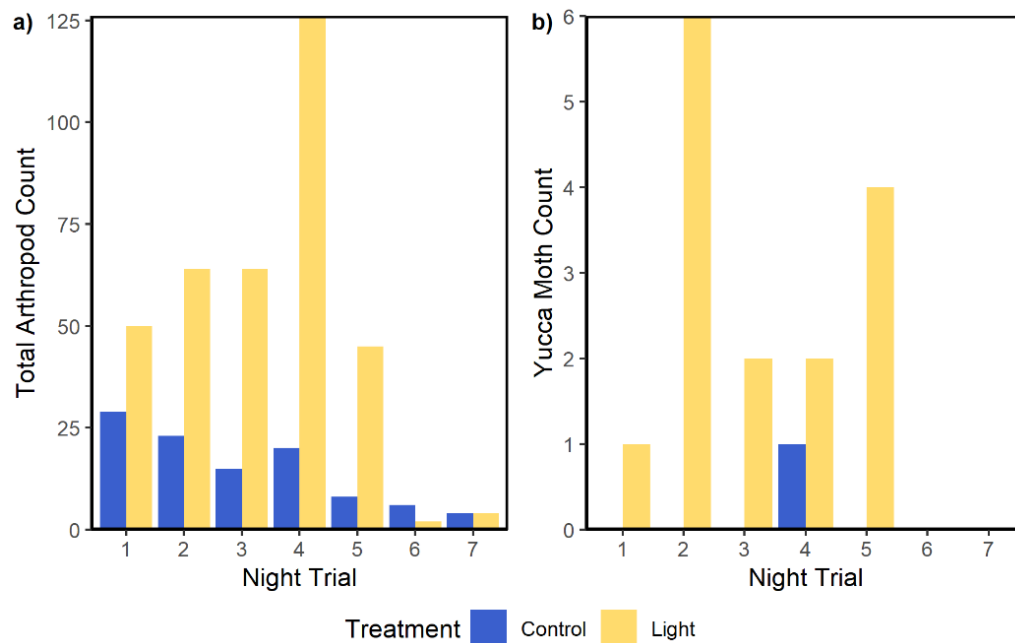


Figure 2.2: Bar plots represent (a) the distribution of total arthropods (control $n = 165$, light $n = 551$) and (b) adult yucca moths (control $n = 1$, light $n = 22$) caught on insect traps per trial.

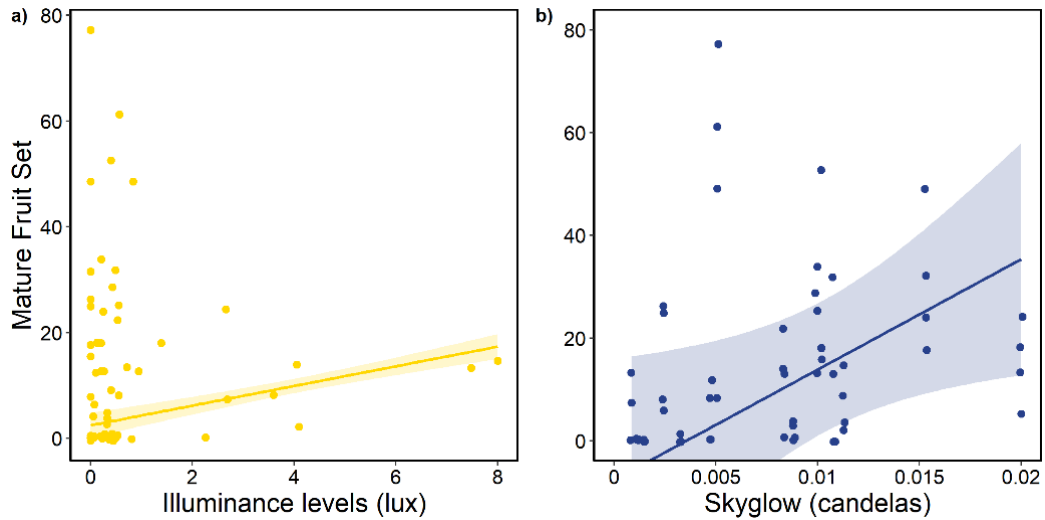


Figure 2.3: Estimated effect sizes of fruit set counts when exposed to increasing (a) illuminance levels (lux) and (b) skyglow (candelas) with points representing empirical counts and bands representing the 85% and 95% confidence level interval, respectively, around the estimated effect size. Independently, both direct light and skyglow cause plants to increase mature fruit set production.

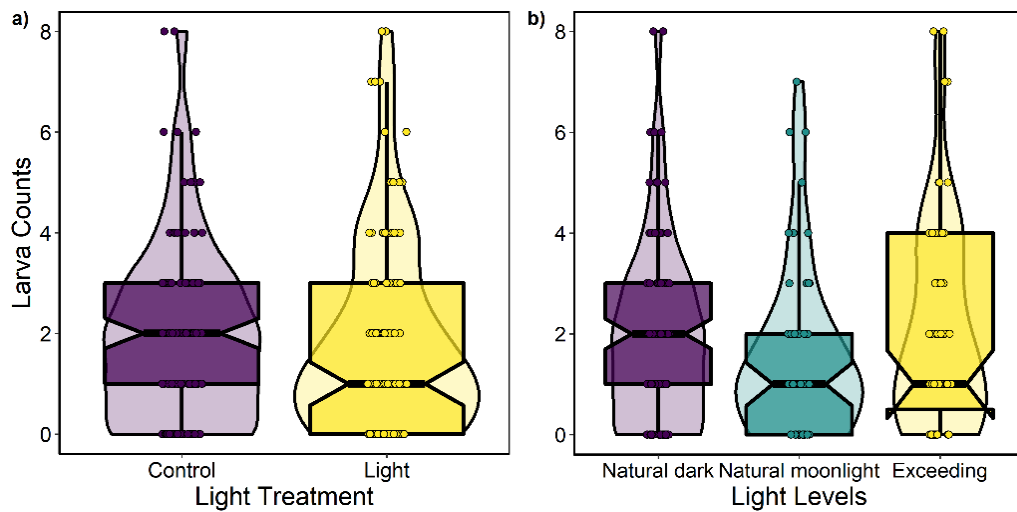


Figure 2.4: Violin plots of empirical larva counts between the control and light treatments (a), which is further dissected in the exceedance light level blocks (b). Black bars represent the 1st quartile, median, and 3rd quartile of the empirical data. The presence of the light treatment caused a strong decrease in larva counts, which is further emphasized when the intensity of direct light exceeds 0.5 lux.

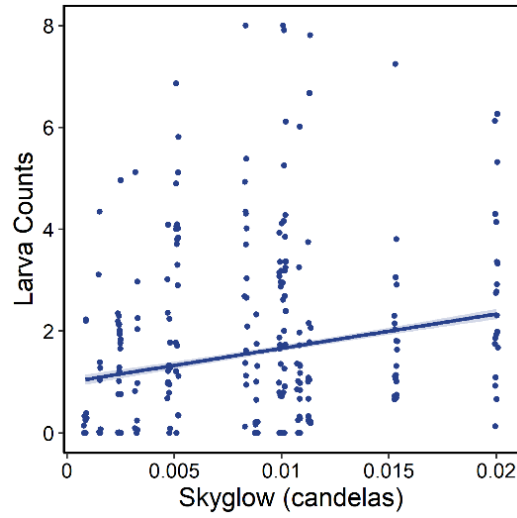


Figure 2.5: Estimated skyglow effect on larval count per fruit across all sites. Points represent empirical counts, and bands represent the 85% confidence level interval around the estimated effect size. High levels of skyglow saw an increase in larva counts across all sites.

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APPENDICES

Supplementary Tables and Figures

Table A1: Best fit model results for 140 species-specific analyses

See supplementary file: Appendix_A.xlsx

Table A2: Comparison of spatial and non-spatial model results for 140 species-specific analyses

See supplementary file: Appendix_B.xlsx

Table A3: Summary of the maximum Variance Inflation Factor (VIF) for species-specific models

See supplementary file: Appendix_C.xlsx

Table A4: Full and reduced model results of species-specific models when $VIF > 10$

See supplementary file: Appendix_D.xlsx

Table A5: All possible outcomes of cumulative responses for the interaction between multimodal stimuli. Interaction direction is dictated by the direction of the expected effect size (E) of the sum between stressor A + stressor B and whether it exceeds the effect sizes of either A or B.

Stressor A	Stressor B	Expected Response (E)	Actual Interaction Response (I)	Interaction Direction
+A	+B	+E	$0 < +I < +E$	Positive Antagonistic
+A	-B	+E	$+E > \pm I > -B$	Positive Antagonistic
+A	-B	+E	$+E < +I < +A$	Synergistic*
+A	-B	-E	$-E > -I > -B$	Synergistic*
+A	-B	-E	$-E < \pm I < +A$	Negative Antagonistic
-A	-B	-E	$-E < -I < 0$	Negative Antagonistic
-A	+B	+E	$+E > \pm I > -A$	Positive Antagonistic
-A	+B	+E	$+E < +I < +B$	Synergistic*
-A	+B	-E	$-E > -I > -A$	Synergistic*
-A	+B	-E	$-E < \pm I < +B$	Negative Antagonistic
+A	+B	+E	$+I > +E$	Positive Synergistic
-A	-B	-E	$+I > 0 > -E$	Positive Synergistic
-A	+B	+E	$+I > +B$	Positive Synergistic
-A	-B	-E	$-I < -E$	Negative Synergistic
+A	+B	+E	$-I < 0 < +E$	Negative Synergistic
-A	+B	-E	$-I < -A$	Negative Synergistic

Table A6: Functional traits of the 140 species in the Project FeederWatch dataset
See supplemental file: Appendix_F.xlsx

Table A7: PGLS model results evaluating the relationship between responses to noise or light exposure and functional traits among 140 species
See supplemental file: Appendix_G.xlsx

Table A8: Interaction classification and direction for the Noise:Light and Light:Night length interactions
See supplemental file: Appendix_H.xlsx

Table A9: Ranked model selection for mature fruit set biotic variables. All models include transect ID and the OLRE as random effects. Biotic variables tested in the model selection were yucca rosette density (Yucca density), blooming inflorescence density (Blooms), and dead stalk density (Dead stalks). Null represents the model with random effects only. *K* indicates the number of parameters in the model and weight corresponds to competing models within 2.00 Δ AIC.

<i>Model</i>	<i>K</i>	<i>AIC</i>	<i>ΔAIC</i>	<i>weight</i>
Null	3	404.78	0.00	0.42
Yucca density	4	405.81	1.03	0.25
Blooms	4	406.50	1.72	0.18
Dead stalks	4	406.77	1.98	0.16

Table A10: Biotic variable 85% and 95% confidence intervals for mature fruit set. Biotic variables that were supported in the ranked models for mature fruit set included yucca rosette density (Yucca density), blooming inflorescence density (Blooms), and dead stalk density (Dead stalks). Parameter strength was evaluated if the confidence intervals did not overlap zero. None of these variables had a strong relationship with mature fruit set and were omitted from the light models.

Variable	<i>85% Confidence Interval</i>		<i>95% Confidence Interval</i>	
	Low CI	High CI	Low CI	High CI
(Intercept)	0.72	2.10	0.38	2.37
Yucca density	-0.24	0.97	-0.48	1.19
Blooms	-0.36	0.38	-0.49	0.52
Dead Stalks	-0.53	0.32	-0.69	0.47

Table A11: Ranked model selection for mature fruit set abiotic variables. All models include transect ID and the OLRE as random effects. Abiotic variables tested in the model selection were Elevation, Aspect, and Slope. Null represents the model with random effects only. *K* indicates the number of parameters in the model and weight corresponds to competing models within 2.00 ΔAIC .

<i>Model</i>	<i>K</i>	<i>AIC</i>	<i>ΔAIC</i>	<i>weight</i>
Null	3	404.8	0.00	0.423
Elevation	4	406.0	1.27	0.225
Slope	4	406.3	1.55	0.195
Aspect	4	406.8	1.98	0.157

Table A12: Abiotic variable 85% and 95% confidence intervals for mature fruit set. Variables that were supported in the ranked models for mature fruit set included Elevation, Aspect, and Slope. Parameter strength was evaluated if the confidence intervals did not overlap zero. None of these variables had a strong relationship with mature fruit set and were omitted from the light models.

<i>Variable</i>	<i>85% Confidence Interval</i>		<i>95% Confidence Interval</i>	
	<i>Low CI</i>	<i>High CI</i>	<i>Low CI</i>	<i>High CI</i>
(Intercept)	0.70	2.1	0.36	2.4
Elevation	-1.1	0.42	-1.5	0.71
Aspect	-0.41	0.35	-0.56	0.49
Slope	-0.42	0.71	-0.64	0.93

Table A13: Ranked model selection for moth larvae biotic variables. All models include transect ID and the plant ID as random effects. Biotic variables tested in the model selection were yucca rosette density (Yucca density), blooming inflorescence density (Blooms), dead stalk density (Dead stalks), and mature fruit set (Fruit set). Null represents the model with random effects only. *K* indicates the number of parameters in the model and weight corresponds to competing models within 2.00 Δ AIC.

<i>Model</i>	<i>K</i>	<i>AIC</i>	<i>ΔAIC</i>	<i>weight</i>
Yucca density	4	800.45	0.00	0.18
Yucca density + Dead stalks	5	800.90	0.46	0.14
Yucca density + Fruit set	5	801.07	0.62	0.13
Yucca density + Dead stalks + Fruit set	6	801.34	0.89	0.12
Dead stalks	4	801.68	1.23	0.10
Yucca density + Dead stalks + Blooms	6	801.88	1.43	0.09
Yucca density + Blooms	5	801.90	1.45	0.09
Yucca density + Dead stalks + Fruit set + Blooms	7	802.01	1.56	0.08
Yucca density + Fruit set + Blooms	6	802.39	1.94	0.07
Null	3	804.5	4.07	--

Table A14: Biotic variable 85% and 95% confidence intervals for larvae counts. Variables that were supported in the ranked models for mature fruit set included mature fruit set (Fruit set), blooming inflorescence density (Blooms), dead stalk density (Dead stalks), and yucca rosette density (Yucca density). Parameter strength was evaluated if the confidence intervals did not overlap zero, where bold face represents a strong relationship, and therefore these variables were included in the light models.

Variable	85% Confidence Interval		95% Confidence Interval	
	Low CI	High CI	Low CI	High CI
(Intercept)	0.23	0.59	0.14	0.66
Fruit set	-0.0075	0.28	-0.063	0.33
Blooms	-0.30	0.032	-0.36	0.091
Yucca density	0.091	0.44	0.027	0.51
Dead stalks	0.012	0.34	-0.049	0.40

Table A15: Ranked model selection for moth larvae abiotic variables. All models include transect ID and the plant ID as random effects. Abiotic variables tested in the model selection were Elevation, Aspect, and Slope. Null represents the model with random effects only. *K* indicates the number of parameters in the model and weight corresponds to competing models within 2.00 ΔAIC .

<i>Model</i>	<i>K</i>	<i>AIC</i>	<i>ΔAIC</i>	<i>weight</i>
Aspect	4	802.9	0.00	0.439
Null	3	804.5	1.63	0.195
Aspect + Slope	5	804.6	1.73	0.185
Aspect + Elevation	5	804.7	1.77	0.181

Table A16: Abiotic variable 85% and 95% confidence intervals for larvae counts. Variables that were supported in the ranked models for moth larvae included elevation, slope, and aspect. Parameter strength was evaluated if the confidence intervals did not overlap zero, where bold face represents a strong relationship, and therefore were included in the light models.

<i>Variable</i>	<i>85% Confidence Interval</i>		<i>95% Confidence Interval</i>	
	<i>Low CI</i>	<i>High CI</i>	<i>Low CI</i>	<i>High CI</i>
(Intercept)	0.17	0.60	0.07	0.68
Elevation	-0.30	0.20	-0.41	0.30
Slope	-0.22	0.31	-0.33	0.40
Aspect	-0.44	-0.050	-0.52	0.018

Table A17: Model selection table of linear and second order polynomial models for direct light illuminance and skyglow. Mature fruit set models include transect ID and the OLRE as random effects, and larva count models include transect ID and plant ID as random effects. *K* indicates the number of parameters in the model and weight corresponds to competing models within 2.00 Δ AIC. Each set of models compare either skyglow or direct light illuminance (bolded) with corresponding parameters that appear in the best fit model as described by the Methods section. Illuminance was not included in the top competing models for larva count, so we did not assess model fitness here.

Model	K	AIC	ΔAIC	weight
<u>Mature Fruit Set: Skyglow</u>				
Linear	4	401.35	0.00	0.54
2 nd Order Polynomial	5	401.71	0.36	0.46
<u>Mature Fruit Set: Illuminance + Skyglow</u>				
Linear	5	402.07	0.00	0.60
2 nd Order Polynomial	6	402.85	0.78	0.40
<u>Larva Count: Skyglow + Density + Aspect</u>				
Linear	6	798.38	0.00	0.68
2 nd Order Polynomial	7	799.84	1.47	0.32

Table A18: Model estimates of linear and second order polynomial terms for direct light illuminance and skyglow. Mature fruit set models include transect ID and the OLRE as random effects, and larva count models include transect ID and plant ID as random effects. Each set of models compare either skyglow or direct light illuminance (bolded) with corresponding parameters that appear in the best fit model as described by the Methods section. The estimate and lower and upper bounds of the 85% Confidence Interval (CI) are reported for the bolded light parameter.

Model	Estimate	Std. Error	Lower CI	Upper CI
<u>Mature Fruit Set: Skyglow</u>				
Linear Term	1.0	0.43	0.42	1.7
1 st Polynomial Term, 2 nd Order	7.8	3.1	3.4	12.9
2 nd Polynomial Term, 2 nd Order	-3.9	3.1	-8.8	0.50
<u>Mature Fruit Set: Illuminance + Skyglow</u>				
Linear Term	0.19	0.17	-0.052	0.44
1 st Polynomial Term, 2 nd Order	1.2	1.2	-0.58	3.0
2 nd Polynomial Term, 2 nd Order	1.3	1.2	-0.43	3.1
<u>Larva Count: Skyglow + Density + Aspect</u>				
Linear Term	0.22	0.13	0.024	0.42
1 st Polynomial Term, 2 nd Order	3.3	2.0	0.35	6.3
2 nd Polynomial Term, 2 nd Order	-1.4	2.0	-4.5	1.5

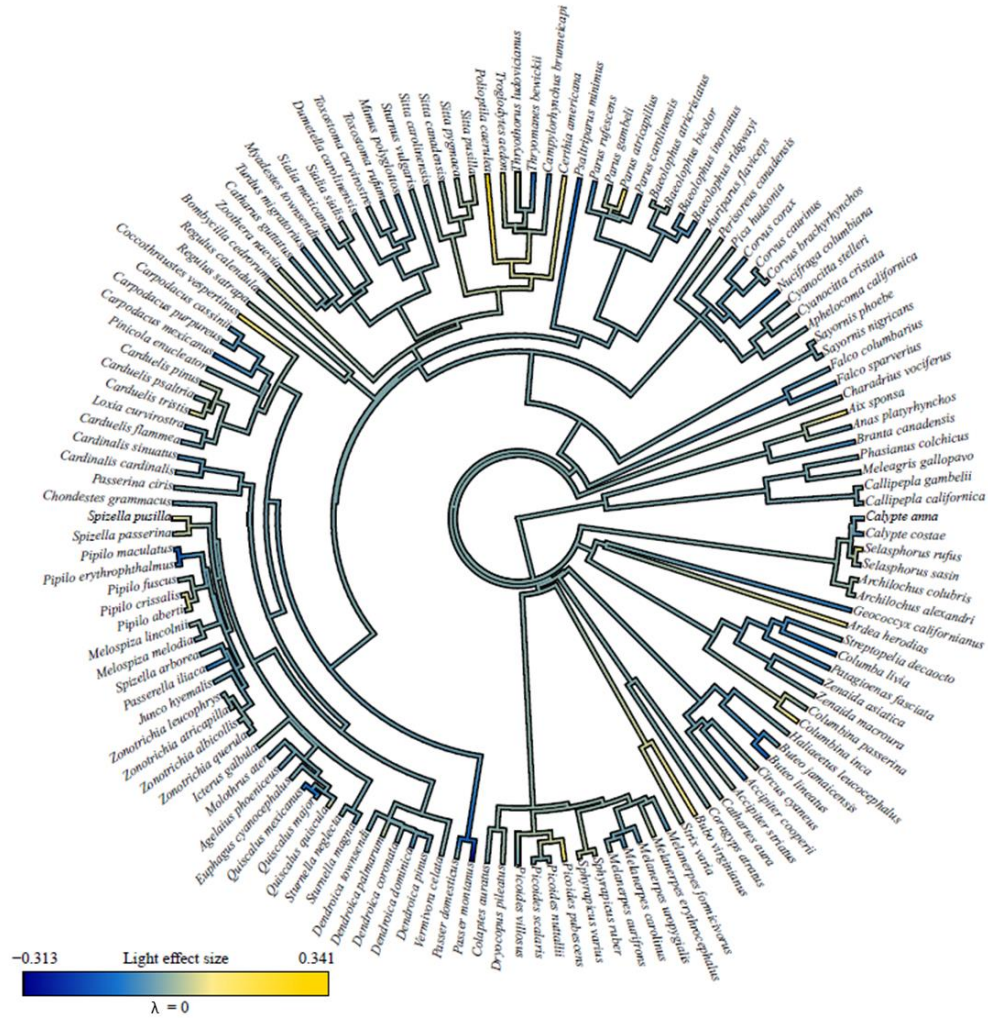


Figure A2: Association with artificial light pollution mapped as a continuous character on a single posterior phylogeny of 140 North American breeding bird species from Jetz et al. (2012) as implemented by the function *contMap* in the R package *phytools* (Revell, 2012). Pagel's lambda (λ) represents the phylogenetic signal of the relationship between mean light radiance exposure (nW) and species response, which was estimated using the *fitContinuous* function in the *geiger* package (Harmon et al., 2008).

Figure A3: A phylogenetic tree representing the 140 species relatedness and a matrix of species responses to macroecological variables. Colors represent parameter strength, where the 95% Confidence Interval (95CI) or the 85% Confidence Interval (85CI) do not overlap 0. Blue designates a positive response, where species increased abundance when exposed to a macroecological variable, and red designates a negative response, where species decrease abundance. Beige denotes a negligible effect on avian response.

See supplemental file: Appendix_J.pdf

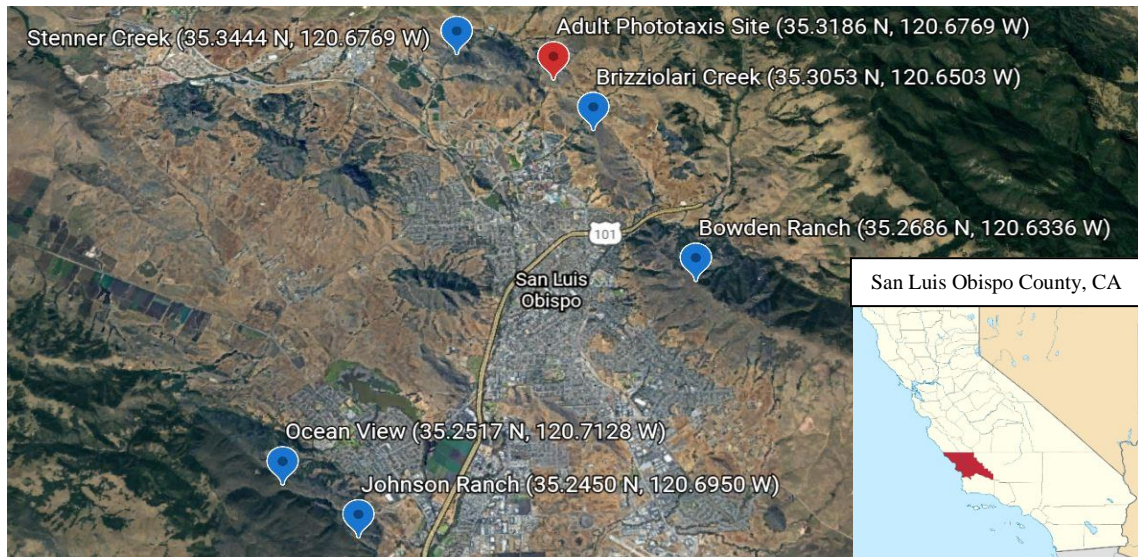


Figure A4: Geographic coordinates of field sites. The locations of all field sites in San Luis Obispo County, CA, as shown in the inset map. The plant and moth recruitment study involved five sites, each containing three 30m transects and are denoted with blue markers. Additionally, a sixth site was set up independently of the recruitment sites to observe adult phototaxis behavior, denoted in red.

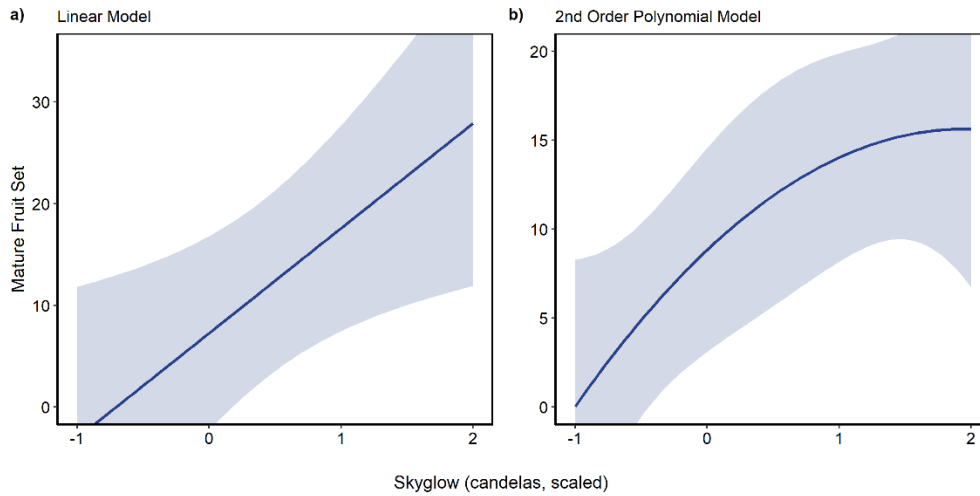


Figure A5: Skyglow effects on mature fruit set with a linear (a) and second order polynomial relationship (b).

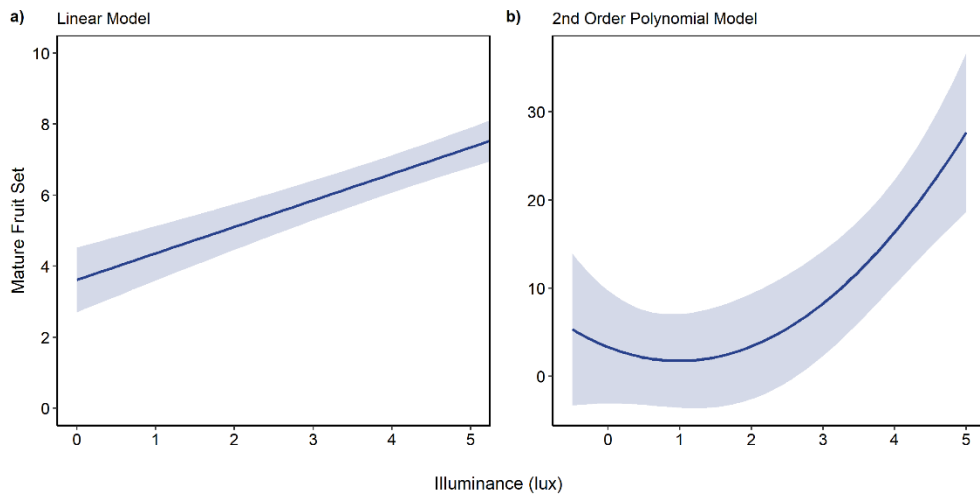


Figure A6: Direct light intensity ("Illuminance") effects on mature fruit set with a linear (a) and second order polynomial relationship (b).

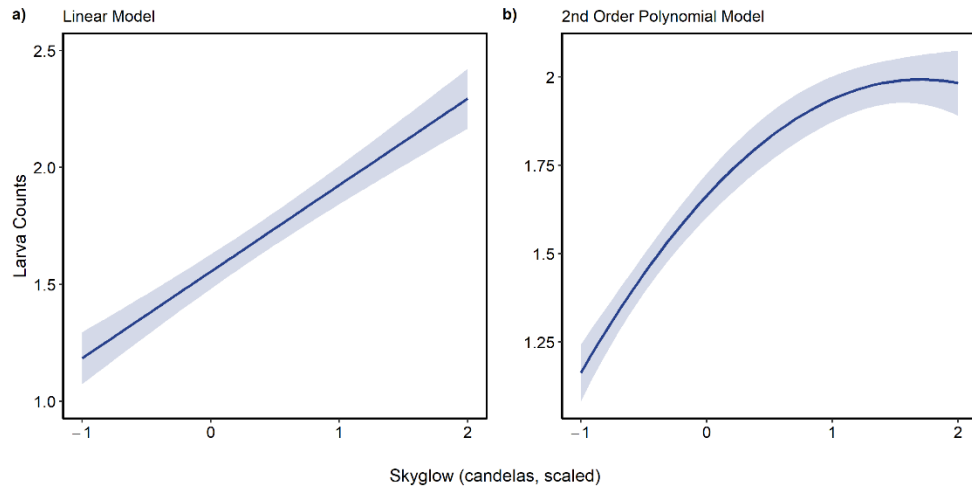


Figure A7: Skyglow effects on larva counts with a linear (a) and a second order polynomial relationship (b).