UNDERSTANDING AND MITIGATING THE EFFECTS OF ARTIFICIAL LIGHT ON BATS AND NOCTURNAL ARTHROPODS IN GRAND TETON NATIONAL PARK

by

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ABSTRACT

Bat and insect populations are at risk globally, and identifying factors that may influence bat and insect populations alongside mitigation techniques for anthropogenic factors that may negatively influence these taxa will be crucial for their conservation. To identify landscape characteristics that influence bats throughout Grand Teton National Park, we placed passive acoustic monitors throughout the park in areas with different microhabitat characteristics to identify factors that influence activity. Additionally, we developed a R package, `EcoCountHelper`, to assist wildlife managers in analyzing ecological count data similar to our bat monitoring data. As a demonstration of the package, we conducted a GLMM-based analysis of this landscape-scale bat monitoring data. Following our broad-scale assessment of bat activity in Grand Teton National Park, we also installed experimental street lights capable of emitting both red and white light throughout Grand Teton National Park's Colter Bay area, and monitored bat and insect activity while altering the color of light illuminating a focal parking lot to assess red light's ability to mitigate the impacts of artificial light on bats and insects.

Through our park-wide acoustic monitoring, we found that bat habitat use varied for the seven species we fit candidate models for, with distance to water, the number of buildings suitable for roosting, and forest cover all influencing activity levels for different species of bats throughout the park. As a result of our fine-spatial-scale research surrounding light pollution mitigation, we also found that red light does not seem to be an effective method of promoting bat activity in artificially illuminated areas that is similar to that of unlit areas, but insects did exhibit more similar sample counts to unlit areas during red light treatment periods than white light treatment periods. Our findings both provide valuable information for land and wildlife managers in Grand Teton National Park to conserve bat and insect populations, and highlight the need for additional research surrounding bat-human interactions. Additionally, we hope our development of a streamlined R package for GLMM analysis using count data will facilitate and promote robust and reproducible analyses for wildlife managers and researchers alike.

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LIST OF ABBREVIATIONS

GLMM	Generalized linear mixed model
ZIP	Zero-inflated Poisson
ZINB	Zero-inflated negative binomial
AIC	Akaike information criterion
NLCD	National Land Cover Database
NHD	National Hydrological Dataset
DEM	Digital elevation model
FM	Frequency modulated
VIF	Variance inflation factor
ANOVA	Analysis of variance
LED	Light emitting diode
EMT	Electrical metallic tubing
UV	Ultraviolet

CHAPTER ONE: AN ANALYSIS FRAMEWORK AND CASE STUDY FOR UNDERSTANDING BAT HABITAT USE IN PROTECTED AREAS

Abstract

Global threats to bat conservation such as disease and deforestation have prompted extensive research to better understand bat ecology. Notwithstanding these efforts, managers operating on lands crucial to the persistence of bat populations are often equipped with too little information regarding local bat activity to make informed land-management decisions. While in-situ research often provides the strongest inference for management decisions, collecting data and employing robust statistical methods can be logistically difficult and intimidating. Here we detail the use of an R package, \`EcoCountHelper\`, and an associated analytical pipeline aimed at making GLMM-based analysis of bat passive acoustic monitoring data more accessible. To demonstrate the utility of this approach, we use our package to model acoustic bat activity data relative to multiple landscape characteristics in a protected area threatened by encroaching disease - Grand Teton National Park. We recommend a GLMM-based analysis workflow that allows the user to 1) employ selection of distributional forms (Poisson vs negative binomial) and zero-inflation (ZIP and ZINB) using AIC values and variance-mean plots, 2) examine models for goodness-of-fit using simulated residual diagnostics, 3) interpret model results via easy to understand outputs of changes in predicted responses, and 4) compare the magnitude of predictor variable effects via effects plots. Our package uses a series of easy to use functions that can accept both wide- and long-form multi-taxa count data without the need for programming experience. In our case study in the Tetons, we found that an increased prevalence of porous buildings increased activity levels of *Eptesicus fuscus* and *Myotis volans*; *Myotis lucifugus* activity decreased as distance to water increased; and *Myotis volans* activity increased with the amount of forested area. By using GLMMs in tandem with `EcoCountHelper`, managers can assess the effects of landscape characteristics on wildlife in a statistically-robust framework.

Introduction

Bats are abundant across most ecosystems on earth, they are voracious predators of nocturnal insects, and their ecological influence on arthropod communities can be greater than that of birds (Frick et al., 2017). In addition to their effects on arthropod herbivory (Kalka et al., 2008), bats also provide many additional important ecosystem services including pollination (Frick et al., 2019) and seed dispersal (Kunz et al., 2011). Yet these services are at risk (Frick et al., 2019). Recent work indicates several emerging global threats to bats. Wind turbines are causing large-scale bat mortality (Frick et al., 2017; Smallwood, 2013), a promulgating disease called white-nose syndrome is drastically reducing bat populations (Coleman, 2012; Verant et al., 2014), and deforestation has led to global decreases in foraging and roosting habitat (Mickleburgh et al., 2002). While researchers have devoted substantial effort to enhancing our understanding of bat ecology (Frick et al., 2019; Kunz et al., 2003), we still know relatively little about bat space use and habitat preferences for all but the most common bat species. As a consequence, the conservation community is equipped with too little information regarding how best to conserve bat populations.

In addition to a lack of knowledge surrounding the general habitat requirements of bats, land and wildlife managers are often tasked with forecasting the effects of specific changes in land use and landscape characteristics (e.g., predicting the impact of a new road or parking lot). In these cases, what little information is available regarding bat habitat use may be too general, and is thus insufficient to meaningfully inform the conservation of local bat populations through management actions. Managers often have the most power to influence the governance of formally protected areas, which is habitat that is particularly important to the long-term persistence of bat populations (Andelman & Willig, 2002). In fact, even common species of bat are more abundant in the Natura 2000 protected area network than in surrounding unprotected areas in Europe (Kerbiriou et al., 2018).

Perhaps one of the most flexible and powerful analyses managers can use to gauge the potential effects of management decisions on bats are GLMMs. While the process required for a statistically-sound GLMM-based analysis is well documented (Bolker, 2008; Harrison et al., 2018; Kéry & Royle, 2015; McElreath, 2020), implementing that process for a specific dataset can be tedious and difficult without guidance. Additionally, the lack of standardization in how analyses are performed can lead to variability in statistical inference (Silberzahn et al., 2018). The potential for GLMMs to be inaccessible to managers is unfortunate, as GLMM analyses can be relatively simple in execution, flexible, and allow structured (hierarchical) data to be accounted for in statistics. GLMMs are also robust to imbalanced data, are more flexible in their assumptions than many other analytical methods, and can accommodate both categorical and numeric data. These models can be particularly useful for analyses involving count data with repeated measures at multiple locations, which is often the case for data from acoustic monitoring bat activity studies, aggregated telemetry detections, avian point counts, and camera trapping studies (Bolker et al., 2009).

Grand Teton National Park, a part of the US protected area network situated at the southern end of the Greater Yellowstone Ecosystem, is dominated by high elevation coniferous forests and sage steppe plains. In March of 2016, the Washington Department of Fish and Wildlife found bats afflicted by white-nose syndrome in King County, WA (Haman et al., 2016). The arrival of the deadly *Pseudogymnoascus destructans* fungus in a Western state, 10 years after it was first introduced to North America in New York (White-nose Syndrome Response Team, 2020), increased the threat posed by white-nose syndrome to western bat populations and set a precedent to better understand habitat characteristics that may be managed to help bolster bat populations in the face of a looming epidemic. To gain a clearer picture of what habitat characteristics drive bat space use in Grand Teton National Park we undertook a passive acoustic monitoring effort throughout the park. Here, we have two aims: 1) describe our work investigating bat habitat use in Grand Teton National Park, USA, and 2) detail the function and use of an R package, `EcoCountHelper`, that we developed to aid in the analysis of multispecies count data - namely bat acoustic monitoring data.

During the summers of 2016 and 2017, we conducted acoustic monitoring surveys throughout Grand Teton National Park to assess bat activity (defined here as the number of call sequences recorded in a site-night for a given bat species) relative to habitat characteristics. In our attempts to quantify the importance of different habitat characteristics to bats in Grand Teton, we predicted that bat space use would be driven by several factors including elevation (Cryan et al., 2000), distance to water (Evelyn et al., 2004), land cover type (Evelyn et al., 2004; Russo & Ancillotto, 2015), proportion of porous buildings that could serve as day roosts (Voigt et al., 2016), lunar phase (Saldaña-Vázquez & Munguía-Rosas, 2013), ordinal date (Weller & Baldwin, 2012), and the presence of non-natural light sources (Stone et al., 2015a). While conducting this research, we recognized that assessing the effect of environmental factors on bats through rigorous statistics could be prohibitively challenging for individuals lacking programming experience. To advance future work on bat population biology and make modelling bat activity more accessible, we describe an analytical pipeline using `EcoCountHelper` to facilitate the identification of the most appropriate error distribution, assessment of zero-inflation, goodness-of-fit testing, and model interpretation processes associated with analyses incorporating GLMMs.

Materials & Methods

GLMM Workflow

We have adapted a workflow for constructing and interpreting GLMMs based on the `glmmTMB` package (Bolker, 2016; Bolker et al., 2012; Brooks et al., 2017). An outline of this adapted workflow involves the following steps for each taxonomic group of interest:

1) Deciding on predictor variables and random effects structures for a response of interest. While predictor variables can be selected via dredging with information criteria (e.g., AIC), there are many pitfalls with blindly using these methods (Bolker, 2008; Guthery et al., 2005; Link & Barker, 2006). We instead suggest

choosing predictors *a priori* based on knowledge of an ecological system and logistical constraints (Bolker, 2018; Bolker, 2008). We refer the reader to Harrison et al. (2018) for how to decide on a random effects structure; and to Bolker et al., 2012; Bolker, 2016; and Brooks et al., 2017 for details on the syntax of fitting a GLMM in `glmmTMB` (also see `EcoCountHelper` vignette; Cole & Gomes, 2021).

2) We then compare the fits of Poisson and negative binomial error distributions (as well as the potential for zero-inflation) by corroborating AIC values, mean-variance plots, and examining simulated residual test plots – the latter of which also help identify outliers and uniformity.
3) We then interpret model results through both standardized coefficient visualizations and predicted response changes given a specified increase in a predictor.

To aid researchers, and particularly land and wildlife managers, in implementing GLMM-based analyses for count data, we developed the `EcoCountHelper` R package to simplify this workflow.

Package Workflow

The `EcoCountHelper` package (Cole et al., 2021a, 2021b) is meant to assist researchers for the portions of a GLMM-based analysis after the point at which candidate models have been generated. It is important that individuals using `EcoCountHelper` take care to carefully consider candidate model structures, and to appropriately implement GLMM components such as zero-inflated models (Martin et al., 2005) and random effects (Harrison et al., 2018). While there are multiple excellent resources for learning about GLMMs (Bolker, 2008), we have found that Harrison et al. (2018) is an excellent touchstone for these analyses. Once one has already generated appropriate candidate models with `glmmTMB` (Bolker, 2016; Bolker et al., 2012; Brooks et al., 2017) and prepared all data (see supplemental “EcoCountHelperExample” vignette), the workflow we suggest for GLMM analyses using the `EcoCountHelper` functions (Table 1) can be executed.

The first step in the pipeline is to select the best-fitting model for each response group under investigation, taxonomic (e.g., species, genus) or otherwise (e.g., indistinguishable grouped taxa, foraging guilds, operational taxonomic units). Two non-exclusive techniques for deciding whether to use zero-inflated models and selecting the best error-distribution family for GLMMs are: 1) examine AIC values to assess zero-inflation and determine a likely error distribution, and 2) examine the mean-variance relationship within the data and determine an error-distribution family that best mirrors the mean-variance relationship. The `EcoCountHelper` package has a function, “ModelCompare”, for simultaneously obtaining AIC values for each group’s candidate models and creating a vector of the models with the lowest AIC scores for each group. The “DistFit” family of functions aids in visual examinations of mean-variance relationships for each group in the analysis. These “DistFit” functions allow users to specify vectors by which data should be aggregated for examining the mean-variance relationship of the data. The “DistFit” functions then generate a scatterplot displaying the mean-variance relationship for the data and draw lines through the scatterplot showing three common error-distributions used for count data: Poisson, negative binomial with a linear parameterization, and negative binomial with a quadratic parameterization (Bolker et al., 2012). The functions used during the model construction process that correspond with each of these error distributions are “poisson” from the `stats` package, “nbinom1” from `glmmTMB`, and “nbinom2” from `glmmTMB`, respectively. For the sake of simplicity, we will use these function names to describe the associated distributions from this point on. After generating mean-variance plots using the “DistFit” family of functions, the user can then choose the model with the most appropriate error distribution for each group by visually examining the plots and choosing the model employing the error-distribution that best fits. By using both of these methods (AIC and mean-variance relationships) we generally arrive at the same conclusion about which distribution best fits the data. There is, however, some subjectivity in distribution choice when both Poisson and negative binomial models appear to fit similarly. In our experience with this situation, the differences in parameter estimates are usually negligible, and thus distributional choice will likely be inconsequential.

Because a model fits a dataset better than all others does not mean it is adequate for making inferences or predictions. Following the model selection process, it’s important to test the goodness-of-fit of the chosen models. There are many ways to assess goodness-of-fit, but plotting residuals (or simulated residuals) is a quick and often useful step in model criticism. EcoCountHelper’s “ResidPlot” family of functions provide a simple way to simulate residuals for models that employ a non-Gaussian error-distribution and generate plots to visually check residual uniformity, outliers, and over-/under-dispersion (important indicators of goodness of fit). These functions borrow functions from the `DHARMa` R package (Hartig, 2022). Importantly, if precise predictions are required from a model to make management decisions, the “gold-standard” for assessing the *predictive* capacity of a model is leave-one-out (a variant of k-fold) cross validation (Hawkins et al., 2003; Vehtari et al., 2017). Holding out part of a dataset to assess predictive capacity may be a computationally less intense alternative (Kim, 2009). These methods involve additional computational steps, and are outside the scope of this paper.

Assuming all selected models fit the data, the next step is interpretation of model results by visualizing model coefficients and confidence intervals. The “EffectsPlotter” function generates coefficient plots with up to three user-specified confidence intervals surrounding each coefficient value. While many managers and practitioners are most often familiar with p values (and an alpha of 0.05), any confidence interval chosen is arbitrary and we suggest thinking deeply about the consequences of type I and type II errors in your system and adjust confidence intervals accordingly. More importantly the effect size, on the scale of the original response variable, should be taken into consideration when making management decisions. Because the coefficients of fitted GLMMs (except for those using an identity link, as typically used in linear [Gaussian] models) are a product of transformed data (via the link specified during the model fitting process; with Poisson and negative binomial this is typically a log link), the coefficients cannot be used to predict the effect without back-transformation. Additionally, continuous data used during model fitting is often standardized for computational gains, increased model convergence, and comparison purposes (Gelman, 2008) which further complicates the process of making predictions with meaningful units. To simplify this process, we created the “RealEffects” family of functions in `EcoCountHelper` which allows users to rapidly assess the response to given changes in predictors using untransformed “real world” values and outputs to a readable text.

`EcoCountHelper` also has multiple accessory functions that do not directly pertain to the model fitting, model selection, and result interpretation process outlined above. One noteworthy accessory function is “scale2”. This function is identical to the base R scale function in that it standardizes a vector, but rather than subtracting the mean from each value and dividing by the standard deviation, “scale2” divides each value by *two* standard deviations as suggested by A. Gelman (2008). During the model fitting process, using the “scale2” function puts continuous values on the same scale as binary categorical variables allowing a direct comparison of standardized continuous coefficients and categorical coefficients.

Package Limitations

The `EcoCountHelper` package was designed to make GLMMs more accessible to researchers and managers who otherwise may not have sufficient programmatic skills to carry out analyses in a timely, reproducible, and statistically responsible manner. Because many of our package’s functions are designed to return specific results (e.g., plots, test statistics) while minimizing unguided data preparation, users must adhere to relatively strict object naming schemes to ensure that pattern recognizers within the functions can identify relevant objects in the global environment. This forces users to conform to a model naming scheme that provides information about the taxonomic group the model belongs to, and also creates intermediate objects that have little or no flexibility in naming conventions. While it makes some aspects of the package inflexible, this strict naming convention allows users unfamiliar with regular expressions to forgo the exercise of identifying objects in the global environment and adding them to a vector for further use either manually or through regular expressions. Because functions that generate plots require virtually no user input for plot construction, it can be difficult to make edits to resulting plots. Again, while this may be inconvenient for programmatically savvy individuals, this inflexibility in data visualization allows for programmatically inexperienced individuals to carry out GLMM-based analyses in a simple and straightforward manner.

Case Study Methods

Throughout the summers (June to September) of 2016 and 2017, we monitored bat activity throughout Grand Teton National Park, Wyoming, USA (referred to hereafter as Grand Teton) using passive acoustic monitors. Grand Teton is composed of a relatively flat, high elevation (average ~2,073 meters [National Park Service, 2019]) valley bounded by the Teton mountain range to the west, and the Gros Ventre mountain range to the east. The majority of our work occurred within the valley of the park.

To assess the potential impacts of buildings and artificial light on the bats of Grand Teton, we used Wildlife Acoustics SM2BAT and SM3BAT units to record bat echolocation at sites throughout the park with varying levels of anthropogenic infrastructure. To obtain high quality recordings, we set sampling rates for all ultrasonic recorders to 384kHz allowing us to capture frequencies up to 192 kHz. We programmed all recorders to allow ultrasonic recordings from 30 min before sunset to sunrise, and to begin recording when triggered by a 16 kHz or greater signal that was 18 dB or more above background sound levels. This triggered recording scheme generated WAV files with individual bat call sequences, allowing for rapid and automated processing using call identification software (e.g., SonoBat, Kaleidoscope).

We chose monitoring sites to capture variation in multiple landscape characteristics including elevation, distance to water, land cover, and human infrastructure that may influence habitat suitability for bats (e.g., porous buildings that could serve as day roosts [Voigt et al., 2016]), and the presence of non-natural light sources (Stone et al., 2015a). In total, we monitored bat activity at 36 sites throughout the park (see Figure 1.1), deploying acoustic monitors at 26 sites in 2016, and 27 sites in 2017 (17 of which were sites established in 2016). We deployed each acoustic monitor for 5 - 6 nights at each site during 2016 and 13 -14 nights in 2017. Our sampling effort totaled 840 site-nights, with 276 site-nights in 2016 and 564 site-nights in 2017.

To identify buildings that were suitable as bat day roosts, we examined all National Park Service-owned buildings within ~1 km of study sites. Building descriptions included construction materials (e.g., log walls, standing seam roof), any openings found in the building's exterior surfaces that would provide a sheltered area for bats to roost, and any evidence of bat inhabitation. We also photographed all building features. We then used written descriptions and photographs to classify buildings as either suitable or not for bat inhabitation. To parameterize the effect of potential roost-building presence near monitoring sites, we created a spatially-weighted potential roost-building density index using the formula

$$\sum_{i=1}^{n} \frac{1}{x_i}$$

where *n* represents the number of roost buildings classified as being suitable for bat inhabitation within 1 km of a given monitoring site, and *x* represents the distance from a building to a given monitoring site. Because bat home ranges are poorly understood, this cutoff distance of 1 km was somewhat arbitrary. Data on North American bat home range size is limited, and the literature that does exist suggests that home range sizes vary substantially based on variables including location, sex, reproductive status, and home-range estimation method. *Myotis lucifugus*, for example, have home ranges from 17.6 ha (Henry et al., 2002) to 2,739 ha (Bergeson, 2012). Our cutoff distance of 1 km would result in a ~314 ha circular area surrounding each monitoring site. While this may be an over- or under-approximation of home range size for bats in Grand Teton, the spatial-weighting we implemented offers some protection from imperfections in the cutoff distance.

To allow assessment of the potential influence of habitat characteristics on bat activity, we quantified the proportions of forested and developed areas comprising a 50-m buffer surrounding each site. We manually defined and classified polygons of forested and developed areas using high-resolution Google satellite imagery and QGIS 3.10. Using the resultant shapefile, we calculated the proportion of a 50-meter buffer comprised of forested and developed areas.

To assess the importance of proximity to water sources, we calculated the distance to the nearest persistent stream, river, lake, or pond. Shapefiles from the NHD, namely the Waterbody and Flowline shapefiles, were used as spatially referenced water features. Flowlines (streams and rivers) were truncated to Fcodes 46006 and 55800 to only include persistent and substantial flowing water features. We then calculated the minimum distance from each site to any portion of a water feature. To assess the importance of elevation, we used ⅓ arc-second USGS DEMs (Gesch et al., 2002) to sample the elevation of each monitoring site. To control for the effect of lunar illumination on bat activity (Saldaña-Vázquez & Munguía-Rosas, 2013), we used the `lunar` (Lazaridis, 2014) package in R (R Core Team, 2020a) to calculate the proportion of the moon illuminated on each night of data collection.

We visited each monitoring site at night to document artificial light sources. For each light within ~500 m of a monitoring site, we qualitatively described the color (e.g., orange, yellow-white, blue-white) and brightness of the light, and the coordinates of the light in decimal degrees. Because some types of lights look similar but have different underlying spectra (e.g., tungsten filament and compact fluorescent bulbs), we did not attempt to extrapolate beyond the visual appearance of the light. We scored the brightness of each light on a 1-5 ordinal scale by comparing artificial light sources to two reference lights (an REI collapsible lamp and a Maglite Mini LED flashlight with the reflector and lens removed). The dimmer REI collapsible lamp represented a two on our scale, and the brighter Maglite represented a four on our scale. All artificial light sources were documented, including light sources that were likely operated by a switch (e.g., porch lights) under the assumption that a sample of lights on any given night would be representative of the lightscape in an area during the summer. Because we were unable to collect radiometric data for light sources included in this analysis, we collapsed the color of artificial lights to a binary categorical variable based on apparent color temperature (cool or warm) to ensure that our assessment of light color was accurate and as objective as possible. We then calculated the proportion of lights classified as having a cool color temperature within a 50 m buffer surrounding each site. A 50 m buffer was chosen to reflect the approximate range that our monitoring units were capable of recording low frequency bat echolocation (Agranat, 2014). Because the number of lights surrounding a site and the sum of brightness scores were highly collinear, we chose to include only the sum of brightness scores within a 50 m radius of each monitoring site because we thought it better reflected the magnitude of artificial light's impact on an area compared to a simple count of light fixtures.

We analyzed bat echolocation sequences using the SonoBat 4.3.0 software suite and checked files for FM sweeps using the SonoBat Data Wizard which moves files without FM sweeps (indicative of the absence of bat echolocation) to subdirectories that are not included in the proceeding steps of data preparation. We used Sonobat's Western Wyoming call library and set the following parameters for SonoBat to handle and identify call sequences: 10 kHz high-pass filter; acceptable call quality = 0.80; sequence decision threshold = 0.90; maximum number of calls to consider per file = 32. Following data processing with SonoBat, we aggregated output files containing file names and species identifications by site-night and species using R. After aggregating for each species, we appended spatial and temporal predictor data to each site-night of data processed by SonoBat.

Analysis

We used GLMMs to assess the effect of the predictors mentioned above on activity for each species of bat that was detected during at least 50 site-nights (*Eptesicus* *fuscus, Lasiurus cinereus, Lasionycteris noctivagans, Myotis evotis, Myotis lucifugus, Myotis volans* and *Myotis yumanensis*). We ran all models in R using the `glmmTMB` package (Brooks et al., 2017) and standardized all continuous variables using our "scale2" function. By dividing each continuous value by its respective mean then dividing by two standard deviations, scaled parameter estimates for all continuous variables are directly comparable to the "year" binary categorical variable (Gelman, 2008).

For each bat species under investigation, we generated six models (three different distribution families and a zero-inflated version of each; see below). All models shared a common conditional model structure that included year, lunar phase, ordinal date, elevation, roost-building density index, proportion of cool lights 50 m, summed brightness score of lights within 50 m, distance to the nearest water source, proportion of developed land cover within 50 m, and proportion of forested area within 50 m as fixed effects, and monitoring site as a random intercept term. Additionally, all models used a log link function. For each species, two models were generated for each error-distribution implemented in the mean-variance plots produced by the "DistFit" family of functions ("poisson", "nbinom1", and "nbinom2"): one with a zero-inflated formula, and one without. We modelled zero-inflation with ordinal date and site as predictors.

For each species, we determined the most appropriate error distribution by corroborating results from the synergistic "DistFit" family of functions and the "ModelCompare" function (see Package Workflow above). We decided *a priori* that in the case of conflicting results from the two processes above, we would rely on visual mean-variance plots for assessing a best-fit model for the proceeding analytical steps. We also used the AIC values generated by the “ModelCompare” function to assess whether a model with a zero-inflated component was necessary. The best-fitting model for each species was subsequently tested for goodness-of-fit using EcoCountHelper’s “ResidPlot” functions. We also checked VIFs of all best-fitting models in R using the function “check_collinearity” in the `performance` package (Lüdecke et al., 2020).

Model Interpretation

We first examined the scaled coefficient estimates by plotting each estimate with confidence intervals on a common scale using EcoCountHelper’s “EffectPlotter” function. These plots were used to inform understanding of the relative importance of landscape features to species-specific bat activity. While informative in terms of relative effect sizes and confidence levels surrounding those effects, these plots do not provide meaningful absolute effect sizes that can be interpreted in an ecological context. The purpose of examining effects plots of scaled and transformed coefficient estimates is to develop an understanding of the relative magnitude of effect each predictor of interest has on a bat species’ activity throughout the study area.

Rather than creating and examining effects plots, one might simply examine the p-values of coefficient estimates to assess the extent to which predictors warrant further investigation. We suggest avoiding making any decisions regarding the importance of landscape features for bat conservation using p-values alone. While there is nothing inherently wrong with this approach, relying on p-values alone is insufficient for meaningful interpretations of results (Halsey et al., 2015; Lin et al., 2013; Sullivan & Feinn, 2012; Vidgen & Yasseri, 2016). By examining scaled coefficient estimates, one can quickly assess both the relative magnitude of, and confidence in, effect sizes. It is important for `EcoCountHelper` users to select the use of confidence intervals and effect sizes that are suitable for their purposes. Many researchers have traditionally used 95% confidence intervals to conclude whether the effect of a predictor is meaningful, but any confidence interval can be used to arbitrate the validity of an effect so long as the researcher has considered the consequences of type 1 errors due to a low confidence threshold. In interpreting the results of our case analysis, we examined both 85% and 95% confidence intervals. While unable to do so as definitively as 95% confidence intervals, 85% confidence intervals still provide information regarding trends in data that, given more sampling or follow-up research, could be confirmed at a higher confidence level. Similarly, one may observe a large effect size but have insufficient data to obtain 95% confidence intervals that do not overlap zero. By tempering the interpretation of results by acknowledging the confidence surrounding those estimates, managers can act on the information available if necessary while also recognizing the need for additional research on the topic of interest. Considering the low risk posed by a type 1 error and the potential benefit of increasing our understanding of bat ecology in Grand Teton with relatively high certainty, we decided interpreting trends present at approximately the 85% confidence level was acceptable. Ultimately we suggest that researchers and managers implementing our suggested workflow do not treat it as a means of hypothesis testing, but rather as a path toward understanding a system surrounded by a level of uncertainty. Both the estimates provided by models as well as the associated uncertainty should be examined within the context of the research objectives to inform one’s conclusion about a predictor’s influence on an ecological process.

After identifying landscape features that influence activity levels, we examined more meaningful and absolute (“real-world”) effects of our predictors in unlinked and non-standardized terms by calculating the factor by which bat activity changes relative to a percentage change in each predictor and associated confidence intervals. In the case of models implementing a (natural) log-link, this entails back-transforming the coefficient estimate by first unscaling and then exponentiating Euler’s number (*e*) by that quotient/value. Then the resulting term is exponentiated by the difference of interest in the values of the predictor. For example, if one is interested in the relative change across 50 m of elevation change, this difference (δx) would be 50 (since the rest of the term has already been back-transformed to the original units and represents 1 unit change; in this example 1 meter). Because we scaled continuous variables using two standard deviations, we used the formula

$$\left(e^{\frac{\beta}{2\sigma}}\right)^{\delta \mathrm{x}}$$

where β represents the model coefficient of interest, σ represents the standard deviation of the unstandardized predictor, *e* represents Euler’s number, and δx is the difference of interest in predictor x. To facilitate these calculations, the \`EcoCountHelper\` package contains a “RealEffect” group of functions that back-transform estimates and return unscaled response for specified changes in predictors.

Results

For the seven species of bats for which we constructed models (see Table 1.2), all exhibited model convergence for at least one candidate model. Corroboration of mean-variance plots and AIC values indicated that data were not zero-inflated and the "nbinom2" error-distribution family best fit the data for all species modelled. There were no conflicting results regarding mean-variance plots and AIC values. All models exhibited adequate goodness-of-fit as assessed by examining diagnostic plots, and no model parameters exhibited excessive VIF values (James et al., 2013, pp. 101–102), though the parameter capturing a site's summed light brightness scores showed moderate collinearity (VIFs between 5.04 and 5.76) in models for *E. fuscus, M. volans,* and *M. yumanensis*.

Model results are shown in Table 1.2. Results presented in this format can be difficult to interpret. The "EffectsPlotter" function in the `EcoCountHelper` package allows users to quickly visualize model results as shown in Figure 1.2. As mentioned in the Methods section, it is difficult to interpret meaningful effects from scaled predictor coefficients. We used multiple approaches to assess more ecologically-meaningful model results. Utilizing the `EcoCountHelper` "RealEffect" functions, we examined the change in model-predicted change in nightly recorded bat call sequences (as a percent) by specified changes in predictors. This can be done using the "RealEffectText" function which prints a sentence describing the predicted change in nightly bat call sequences for a given change in a single predictor. Using the "RealEffectText" function to interpret the effect of a 10-day increase in ordinal day on *M. lucifugus* activity results in the sentence: the response variable increases 22.81% (± 5.91%) for every 10 day increase in the predictor. In this output, the parenthetical value indicates the 95% confidence interval, but the "RealEffectText" function allows users to specify any confidence level for errors surrounding the predicted change in the response variable. Because our analysis included a total of seven parameters of interest for each of the seven species-level models, we chose to use the “RealEffectTab” functions instead of the “RealEffectText” function. The “RealEffectTab” functions accept vectors of models, predictors, and specified changes in each predictor, and then generates a table similar to Table 3.

We also produced plots that fall outside of the scope of our package due to the necessary specificity of their construction relative to model structure for visually-appealing plots (see associated GitHub repository for the code used to produce these plots). These plots are essentially visualizations of the sentences produced by the “RealEffectText” function, but across the continuum of observed values of each predictor and with predicted nightly call sequences as an absolute metric of bat activity rather than percent change (Figure 1.3). Additionally, all other predictors are held constant at their median values in Figure 1.3. Both the table generated with the “RealEffectTab” functions and the plots in Figure 1.3 were used to gauge the ecological significance of the relationship between predictors and bat activity.

Discussion

While the scientific community’s understanding of bat ecology has grown substantially in recent years (Weller et al., 2009), our knowledge of demographics and spatial ecology is often over-generalized such that it may not provide adequate information for managers to effectively assess the potential consequences of management decisions. The `EcoCountHelper` package presented here is structured with the intent of making model interpretation and visualization more accessible for wildlife managers. Using the `EcoCountHelper` package and an associated analytical workflow, we examined the effects of multiple landscape characteristics on bat activity throughout Grand Teton National Park.

In our case study example, we examined the potential impact of several landscape features on bats in Grand Teton National Park and found that the presence of porous buildings suitable for roosting had a positive effect on both *E. fuscus* and *M. volans* activity. While bat activity and abundance should not be treated as synonymous metrics, a large body of literature exists documenting a multitude of bat species occupying buildings in high numbers (Geluso et al., 2004; Johnson et al., 2019; Voigt et al., 2016) which is consistent with these findings. Increased bat activity near buildings may be a result of increased bat roosting and foraging near buildings due to decreased predation risk, energetically efficient shelter, or conspecific attraction (Voigt et al., 2016). We also found that distance to water had a negative effect on *M. lucifugus* activity which is consistent with other findings regarding myotid distribution and roost locations (Evelyn et al., 2004; Womack et al., 2013). The propensity of *M. lucifugus* to roost near water may be due to increased insect densities above water (Barclay, 1991) and the use of waterways as travel corridors. Additionally, we found that the proportion of forest in an area had a significant positive impact on *M. volans* which is consistent with the frequent use of largely forested areas by this species (Baker & Lacki, 2006; Johnson et al., 2007; Lacki et al., 2013).

While research from Europe suggests that both the presence of artificial light as well as the color of that light may influence bat space use (Spoelstra Kamiel et al., 2017; Stone et al., 2012a), we were unable to detect a relationship between bat activity and artificial light color. It is possible that these North American bats are not substantially affected by artificial lights, yet we caution that we had a low number of artificially lit sites (n = 6) which may increase the probability of a type II error.

Our findings suggest that land managers in Grand Teton National Park that are hoping to maximize general bat activity should pay special attention to actions that may affect bat habitat nearby water and continue to prioritize the presence of uninhabited historic structures on the landscape. Conversely, if managers aim to minimize bat-human conflict, sealing human-inhabited, porous buildings to reduce bat access should be prioritized, especially in areas nearby perennial water sources. Grand Teton has a rich history of human settlement, ranching, and interactions between humans and natural water features (National Park Service, 2015a, 2015b, 2015c). The intertwinement of buildings, water and forested areas that was once a product of agriculture and resource provisioning has now become an integral part of bat ecology and natural history in the region. Preserving the porous nature of these historic buildings to provide bats with artificial roosts may allow bats to maintain more robust population sizes that may provide greater resilience to white nose syndrome via genetic diversity or disease-free refuges. However, this approach may also lead to increased wildlife-human conflicts when bats and humans cohabitate these buildings. We recommend that porous structures unoccupied by humans near water and forest patches (e.g., Menor's Ferry, the Lucas-Fabian homestead) be maintained in order to provide bats with ample roosting habitat. We also recommend that perennially human-occupied historic buildings (e.g., Colter Bay Village guest cabins, UW-NPS Research Station housing) be properly sealed to minimize human-wildlife conflict.

The framework outlined in this paper is meant to serve as a guide for land and wildlife managers to conduct similar research with locally-relevant parameters in mind. There are many analytical solutions for researchers to assess the effect that habitat features and environmental variables have on bats and other wildlife such as spatial autoregressive models (Li & Wilkins, 2014; Ver Hoef et al., 2018), ANOVA (Kalcounis et al., 1999), and models that can account for detectability at the species (i.e., occupancy modelling) (Mendes et al., 2017), site/population (i.e., N-mixture), or individual levels (i.e., mark-recapture) (Kéry & Royle, 2015). We think, however, that the GLMM-based workflow outlined in this paper paired with the `EcoCountHelper` package provides a balance of accessibility, statistical robustness, and research flexibility for analyzing ecological count data. While it was initially written with bat conservation in mind, this package and framework can also be used in tandem for any type of count data (e.g., avian point counts, insect samples, camera trap data).

Figures

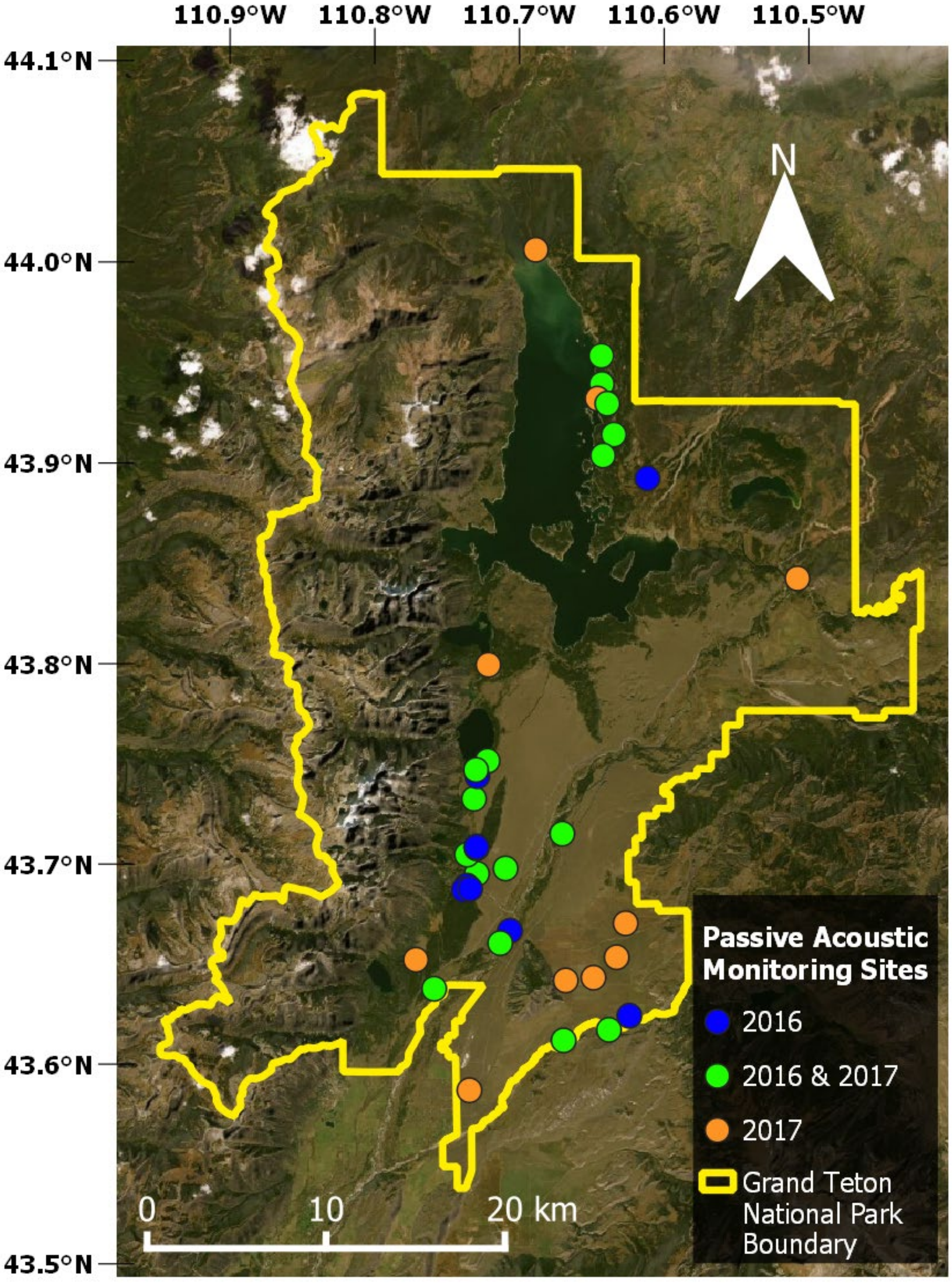

Figure 1.1. Map of the study area. Our research was conducted throughout the valley of Grand Teton National Park. The data included in our analyses are from the 36 sites shown in this map, with the color of each site indicating the year(s) that data were collected. Map data ©2015 Google.

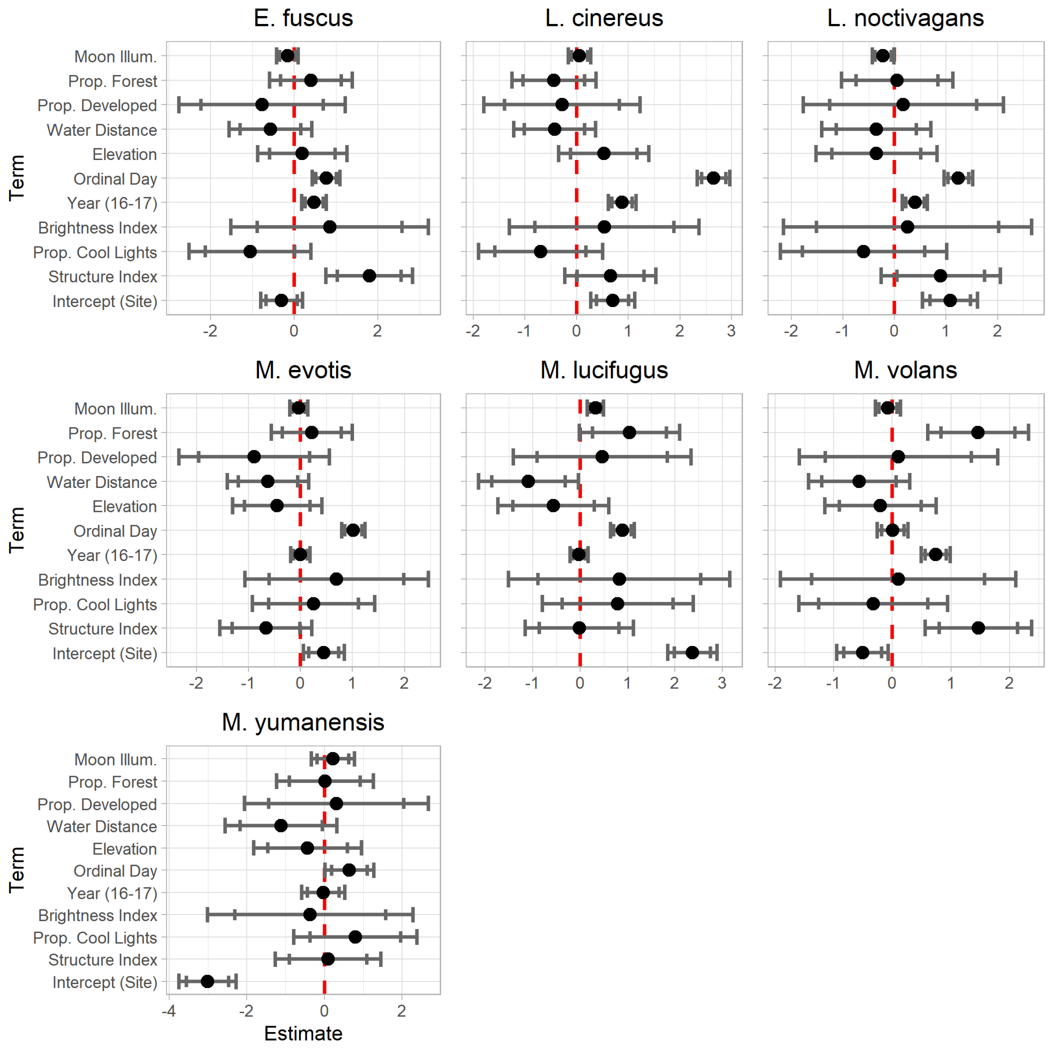

Figure 1.2. EffectsPlotter function output. Following the model construction and selection process, we used EcoCountHelper's "EffectsPlotter" function to visualize scaled parameter estimates with 85% and 95% confidence intervals (inner and outer error bars, respectively). Each plot represents a species-level model, with the associated species indicated by the four-letter code above each plot (see Table 1.2 for species code definitions).

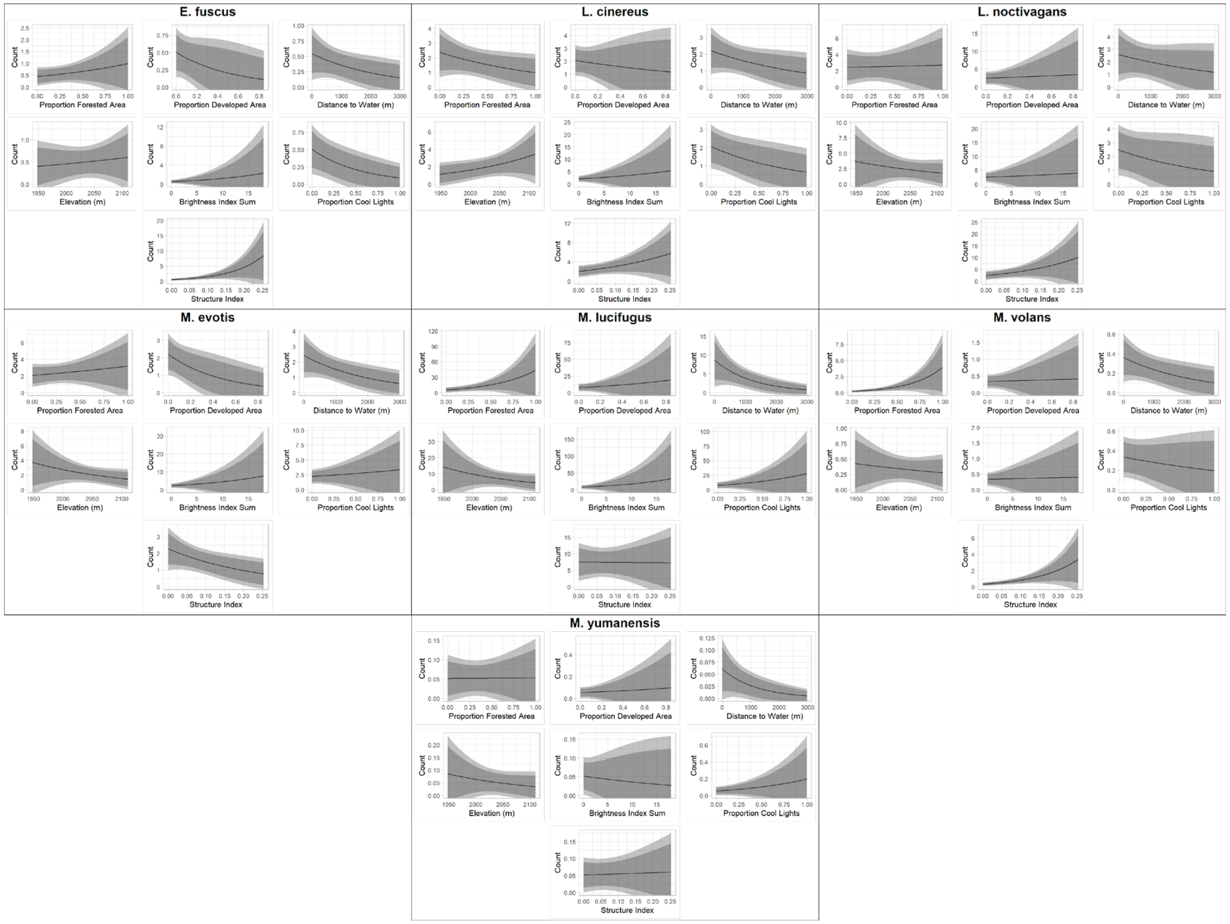

Figure 1.3. Continuous model predictions for each parameter by individual species. Plot titles indicate the four-letter code of the bat species with which each plot is associated (see Table 1.2 for species code definitions). The most appropriate model for each species was identified and validated using functions from EcoCountHelper. All parameters of each model were held at their median observed value except the parameter to be plotted, which was equally distributed throughout its range of observed values. Dark and light shaded areas indicate 85% and 95% confidence intervals, respectively.

Tables

Table 1.1. EcoCountHelper function purposes. Each step in the analytical framework we outline in this document can be facilitated by one or more EcoCountHelper functions.

Analytical Framework Component	Associated Function(s)
Choose an error distribution family Are data zero-inflated?	ModelCompare, DistFitLong, & DistFitWide
Goodness-of-fit Diagnostic Plots/Tests	ResidPlotLong & ResidPlotWide
Examining Relative Effect Sizes	EffectsPlotter
Interpreting Scaled Estimates	RealEffectText, RealEffectTabLong, & RealEffectTabWide

Table 1.2. **Species-level model results. For each species-level model (7 models total), we have listed the model estimate, standard error (SE) and p-value for all predictors included in the fixed-effects model structure. Species to which values correspond are identified in the first column. All models were constructed using the glmmTMB package in R, and interpreted using functions from EcoCountHelper. Models for all species utilized a negative-binomial quadratic error-distribution. Values in the column labelled "Intercept (Site)" correspond with the random-intercept term that incorporates a site-dependence of observations in the models.**

Species	Value	Brightness Index	Prop. Cool Lights	Prop. Developed	Structure Index	Elevation	Moon Illum.	Ordinal Day	Prop. Forest	Water Distance	Year (16-17)
E. fuscus	Estimate	0.811	-1.004	-0.734	1.880	0.507	-0.160	0.888	0.435	-0.718	0.477
	SE	1.151	0.708	0.971	0.555	1.421	0.132	0.197	0.546	0.633	0.150
	p	0.481	0.156	0.450	<0.001	0.721	0.227	<0.001	0.426	0.257	0.002
L. cinereus	Estimate	0.513	-0.664	-0.272	0.685	1.373	0.056	3.077	-0.475	-0.537	0.878
	SE	0.895	0.582	0.739	0.470	1.160	0.109	0.187	0.448	0.508	0.137
	p	0.567	0.254	0.713	0.145	0.237	0.606	<0.001	0.290	0.290	<0.001
L. noctivagans	Estimate	0.245	-0.571	0.163	0.939	-0.911	-0.221	1.439	0.056	-0.443	0.395
	SE	1.174	0.784	0.948	0.617	1.562	0.108	0.162	0.597	0.679	0.125
	p	0.835	0.467	0.864	0.128	0.56	0.041	<0.001	0.925	0.513	0.002
M. evotis	Estimate	0.663	0.239	-0.854	-0.698	-1.175	-0.036	1.179	0.235	-0.787	-0.005
	SE	0.863	0.572	0.708	0.473	1.146	0.088	0.134	0.430	0.500	0.094
	p	0.442	0.676	0.228	0.140	0.305	0.681	<0.001	0.585	0.115	0.955
M. lucifugus	Estimate	0.789	0.755	0.447	-0.020	-1.468	0.325	1.037	1.127	-1.369	-0.026
	SE	1.141	0.772	0.915	0.611	1.556	0.088	0.148	0.587	0.676	0.097
	p	0.489	0.328	0.625	0.974	0.346	<0.001	<0.001	0.055	0.043	0.787
M. volans	Estimate	0.094	-0.312	0.098	1.538	-0.533	-0.075	0.008	1.587	-0.712	0.741
	SE	0.982	0.616	0.827	0.487	1.263	0.109	0.156	0.475	0.553	0.127
	p	0.924	0.612	0.905	0.002	0.673	0.492	0.957	<0.001	0.198	<0.001
M. yumanensis	Estimate	-0.352	0.762	0.296	0.100	-1.125	0.218	0.748	0.016	-1.399	-0.025
	SE	1.293	0.770	1.158	0.730	1.852	0.284	0.374	0.688	0.924	0.283
	p	0.785	0.322	0.798	0.891	0.544	0.442	0.045	0.981	0.130	0.929

Table 1.3. **Model-predicted responses to changes in predictors of interest. Using EcoCountHelper's RealEffectTab functions, we predicted responses of each modelled species to a specified increase in unscaled (i.e., in the original units) predictors (specified in the "Unit Increase" column), then formatted the table in R. The seven right-most columns each contain the change in species-level activity (represented as a percentage value) as well as the 95% confidence interval range listed parenthetically as "x / y", where x is the lower boundary of the confidence interval, and y is the upper boundary of the confidence interval. Species are identified by their respective four-letter code (see Table 1.2 for species code definitions).**

Predictor Classification	Predictor	Unit Increase	*E. fuscus*	*L. cinereus*	*L. noctivagans*	*M. evotis*	*M. lucifugus*	*M. volans*	*M. yumanensis*
Anthropogenic	Structure Index	0.05	+82.29 (40.79 / 123.79)	+24.46 (-9.73 / 58.64)	+34.97 (-12.21 / 82.15)	-19.97 (-54.43 / 14.48)	-0.63 (-47.22 / 45.95)	+63.43 (27.83 / 99.03)	+3.24 (-54.63 / 61.12)
	Proportion Cool Lights	0.2	-28.30 (-86.68 / 30.08)	-19.74 (-65.73 / 26.24)	-17.24 (-83.68 / 49.20)	+8.25 (-36.73 / 53.23)	+28.41 (-36.70 / 93.53)	-9.83 (-59.02 / 39.36)	+28.74 (-36.16 / 93.64)
	Brightness Index	5	+50.02 (-158.81 / 258.85)	+29.22 (-111.16 / 169.60)	+13.04 (-202.89 / 228.98)	+39.28 (-93.62 / 172.18)	+48.34 (-157.43 / 254.11)	+4.82 (-156.97 / 166.61)	-16.15 (-271.2 / 238.89)
	Proportion Developed	0.2	-29.44 (-176.37 / 117.49)	-12.11 (-111.07 / 86.84)	+8.04 (-133.60 / 149.67)	-33.34 (-126.69 / 60.01)	+23.65 (-110.64 / 157.95)	+4.78 (-111.13 / 120.70)	+15.09 (-178.78 / 208.96)
Natural	Elevation (m)	50	+39.45 (-482.12 / 561.02)	+146.15 (-198.61 / 490.90)	-45.01 (-690.08 / 600.07)	-53.73 (-390.18 / 282.72)	-61.84 (-701.87 / 578.19)	-29.53 (-437.02 / 377.95)	-52.19 (-1033.85 / 929.48)
	Water Distance (m)	250	-12.54 (-38.62 / 13.53)	-9.54 (-29.96 / 10.88)	-7.95 (-36.15 / 20.25)	-13.66 (-33.73 / 6.41)	-22.56 (-50.62 / 5.50)	-12.45 (-34.91 / 10.00)	-22.99 (-63.25 / 17.27)
	Proportion Forested	0.2	+19.08 (-34.58 / 72.74)	-17.35 (-59.64 / 24.94)	+2.29 (-57.63 / 62.21)	+9.88 (-30.35 / 50.10)	+57.22 (-1.45 / 115.89)	+89.11 (43.80 / 134.41)	+0.65 (-71.18 / 72.49)

CHAPTER TWO: MITIGATING THE COSTS OF LIGHT POLLUTION FOR BATS AND INSECTS

Abstract

Light pollution has become a major ecological problem for a suite of taxa in recent decades. Bats and nocturnal insects are among the wildlife that have been shown to change their habitat use and behavior in response to artificial light. Red light sources (e.g., street lights) have been effectively used in Europe to promote bat and insect activity and habitat use similar to those found in unlit areas, however the efficacy of red light as a light pollution mitigation technique has not yet been proven in North America. To test red light's ability to promote natural bat and insect activity, we monitored bats and insects in and around an experimentally lit parking lot in Grand Teton National Park while periodically changing the color of lights illuminating the parking lot between red and white. Using a GLMM-based analysis, we found that red light was an ineffective means of promoting bat activity in lit areas similar to that found in adjacent dark areas, however multiple orders of insects exhibited more natural activity under red light compared to white light. The relatively short treatment periods we implemented alongside differences in analytical frameworks may contribute to why our findings surrounding bats are not in agreeance with other research testing red light as a light pollution mitigation technique. Additional research surrounding red light's efficacy as a mitigation technique for bats and insects should implement longer color treatment periods to ensure local wildlife have ample time to habituate to changes in lightscape suitability.

Introduction

Dramatic increases in light at night have altered nocturnal light levels across the planet (Falchi et al., 2016). Light pollution has changed the natural light regimes of ecosystems (Longcore & Rich, 2004) and influences bird behavior (Russ et al., 2015), habitat use (McLaren et al., 2018), and physiology (Dominoni Davide et al., 2013); sea turtle hatchling orientation (Truscott et al., 2017) and nest abundance (Brei et al., 2016); mammal reproductive timing (Le Tallec et al., 2016; Robert et al., 2015); and nighttime pollinator activity (Knop et al., 2017), among other effects (Gaston et al., 2017). However few studies have assessed potential mitigation techniques to ameliorate the impacts for wildlife habitat chronically exposed to artificial light. As the human footprint continues to grow, it is imperative that we fully understand the effects of light pollution and how these costs can be alleviated, especially in relation to the conservation of at-risk taxa (Dominoni & Nelson, 2018).

Insects provide valuable ecological services (i.e., pollination, crop pest removal, supporting terrestrial trophic webs; (Losey & Vaughan, 2006; Scudder, 2017), many insects are strongly attracted to lights (Desouhant et al., 2019), and insects may suffer population declines from this attraction (Owens et al., 2019). Several factors are likely driving insect declines (habitat loss, climate change, and pesticides; Wagner, 2020) and recent evidence indicates that light pollution is among the likely causes (Owens et al., 2019). For example, nocturnal moths, attracted to artificial light, appear to be declining much more quickly than diurnal moths and butterflies, at the same locations (van Langevelde et al., 2018). The spectral characteristics of the light to which insects are exposed influences the magnitude of their response, which presents a potential avenue for mitigation. Blue, short-wavelength light attracts more insects than lights with longer wavelengths (yellow or red; [van Langevelde et al., 2011; Wakefield et al., 2016]). When green, red, and white streetlights were placed in previously dark areas in the Netherlands, fewer insects were captured under red lights than other light colors, effectively showing that red light can mitigate artificial light's impact on insects (Spoelstra et al., 2017).

Bats are inextricably linked to insects. Some species of insectivorous bats, particularly in Europe, respond strongly to artificial light sources (Rowse et al., 2016; Stone et al., 2012b, 2015b), either avoiding lit areas or opportunistically exploiting insects at lights (Rowse et al., 2016). Some bats, just as insects, exhibit activity levels closer to those seen at unlit sites when exposed to red streetlights compared to white or green (Spoelstra et al., 2017). Understanding light's effects on bats may prove to be crucial for bat conservation, as bat numbers across North America have fallen dramatically due to the white-nose syndrome epidemic sweeping across the continent. In 2012, an estimated 5.7 million to 6.7 million bats had died from white-nose syndrome since its discovery in 2006 (Coleman, 2012). The disease has since been confirmed in 33 US States and 7 Canadian provinces (White-nose Syndrome Response Team, 2020). Our knowledge of bat responses to artificial light, and mitigation techniques to encourage natural bat habitat use may be key to recovering bat populations across the continent.

Here we test the efficacy of two key mitigation strategies to promote insects and bat activity more similar to what may be observed without artificial light present: altering the light color and light intensity of artificial lights. Over two summer field seasons we turned 32 proprietary LED luminaires containing both red and white LEDs from red to white in either 3-night blocks (2019) or 7-night blocks (2020). We asked if red light or dimmer intensities reduced attraction of insects to artificial lights, or if red lights and dimmer light sources produced beneficial effects for bats and insects. To do so we tracked bats using both passive acoustic monitoring and telemetry while simultaneously monitoring nocturnal insect abundance.

Methods

Study Area

We conducted this work in the parking lot of Grand Teton National Park's largest visitor center, Colter Bay. This T-shaped parking lot is surrounded by dense coniferous forest and multiple buildings including the visitor center, the general store, and the marina office. While these buildings have some light sources including small high-pressure sodium, incandescent, and LED bulbs, the primary light source in the parking lot is an array of 32 pole-mounted streetlights. At three lit sites and four adjacent unlit (dark) sites throughout the Colter Bay area (Figure 2.1), we monitored bats and insects. We selected dark sites with similar habitat characteristics to lit sites - dense forest surrounding clearings of both paved and natural substrates.

An Experimental Lightscape

In 2019, we replaced the existing 32 streetlights in the Colter Bay parking lot (previously a mixture of high-pressure sodium vapor lamps and ~4000 K white LEDs) with proprietary LED luminaires. These luminaires project a nearly pure red light (Signify Fortimo ClearField™) in addition to a ~3400 K white light, and have wireless controls (Nedap Luxon™) that enable dimming or switching between the two light sources. Throughout the summers of 2019 and 2020, we experimentally manipulated the Colter Bay lightscape from red to white in either 3-night blocks (2019) or 7-night blocks (2020) while altering the brightness of the lights every six nights during the 2019 field season. After examining preliminary results from 2019, we concluded that there may be a carryover effect constituted by latency in bat responses to treatment changes (i.e., bats may continue to exhibit behavior associated with the previous treatment into the next treatment period), and that light brightness within the range of treatments we presented had no to little effect on bat or insect activity. Thus, we extended the treatment periods in 2020 to 7 days and maintained a constant luminaire brightness (95% of maximum wattage).

Bat Monitoring

We monitored bat activity (defined here as the number of bat call sequences recorded each site-night for a given species) at our 7 sites using ultrasonic acoustic recording units (Wildlife Acoustics SM4BAT) that we mounted on 3 m lengths of 1.27 cm EMT conduit, placed in the center of natural clearings or parking lots, and oriented microphones toward the center of the open space. We programmed units to record bat echolocation from 30 minutes before sunset until sunrise. In 2019, we also monitored bat habitat use with radio telemetry. We used mist nets to capture bats between August 5 and August 19, and fitted males and non-pregnant/non-lactating females (15 *Myotis lucifugus* in total) with radiotags (Lotek® coded Nanotags; signaling interval: 5 sec). At each of our seven monitoring sites we deployed a Lotek SRX-800 paired with a four-element

Yagi antenna. Any time a tagged bat passed close enough to a telemetry logger and antenna, its presence was logged with an associated date, time and identity code.

Insect Monitoring

In 2019, we deployed a flight-intercept trap (~60 cm plastic veins; collection container with dry poison, No-pest® Strip2) at each site, nightly (Figure 2.2). At lit sites, we suspended traps directly below streetlights using a pulley and cord, and at dark sites we suspended traps between trees (10+ m apart) using cord. As this approach collected few insects (with the exception of Diptera), perhaps because traps tended to rotate in the wind, we used UV bucket traps (BioQuip) in 2020. We deployed UV bucket traps with dry poison for 3 consecutive nights (nights 4-6 of each block) at each site. Each trap was paired with a timer switch that turned the UV light on for 2 hours, starting 30 minutes after sunset.

Data Preparation

We processed all acoustic recordings with SonoBat 4.3.0 using the SonoBat Western Wyoming call library. We used an acceptable call quality value of 0.80, a sequence decision threshold of 0.90, and a maximum of 32 calls to consider per call sequence. We aggregated the resultant tabulations of call sequence detection count by site-night for each species. Passive acoustic monitoring site-nights that overlapped with UV bucket trap insect sampling were excluded from this analysis to ensure any bat activity changes resulting from the presence of UV light and consequent changes in insect habitat use did not confound effects of lighting treatment. Similarly, we aggregated all telemetry detections by site-night and tag ID. All insects composing insect samples were identified to Order.

Analysis

The entirety of our analytical process was carried out using the statistical program R (R Core Team, 2020b). Our analytical framework followed the protocol outlined in the EcoCountHelper R package (Cole et al. *in prep*). This framework (outlined below) was executed for each species of bat detected during at least 100 site-nights using acoustic monitoring, aggregated telemetry detections, and each insect Order present in insect samples.

We first developed a general conditional model structure that would be used to build models for a given data set (acoustic recordings, telemetry, or insect sampling). We also constructed a general zero-inflated formula to be used in the model selection process. We then constructed multiple models for each taxonomic group using all combinations of frequently used count-data error-distribution families (negative-binomial with a linear parameterization, negative-binomial with a quadratic parameterization, and Poisson) and zero-inflation formula presence (zero-inflated formula included or not). AIC values were generated for each of the resultant models, and mean-variance plots were generated for each group-level and error-distribution family combination. AIC values and mean-variance plots were corroborated to assess the most appropriate error distribution for each taxonomic group. *A priori*, we decided that in the event of any conflicts between AIC values and mean-variance plots, the model using the best error-distribution family as suggested by the mean-variance plots would be selected. Following taxonomic-group-level model selection, we examined residual diagnostic plots to check for goodness-of-fit via residual dispersion, outliers, and uniformity. At this point we also checked VIF values for each model to ensure that there were no instances of multicollinearity. In total, we constructed models for four data sets: acoustic monitoring data, telemetry data, flight-intercept trap data, and UV-bucket trap data. The general conditional model structure for all candidate models is shown below:

Acoustic Monitoring

Calls/Night = Ordinal Date + Year + Moon Illumination + Site Classification +
Light Color +
Light Brightness + Latency Days + Site Classification:Light Color + Light
Brightness:Light Color + Site Classification:Light Color:Latency Days + (1|Site)

Telemetry

Detections/Night = Ordinal Date + Moon Illumination + Site Classification +
Light Color + Latency Days
+ Site Classification:Light Color + Site Classification:Light Color:Latency Days
+ (1|Site) + (1|Tag ID)

Flight-Intercept Traps

Arthropods/Night = Ordinal Date + Year + Moon Illumination + Site
Classification + Light Color +
Light Brightness + Latency Days + Site Classification:Light Color + Light
Brightness:Light Color + Site Classification:Light Color:Latency Days + (1|Site)

UV-Bucket Traps

Arthropods/Night = Ordinal Date + Moon Illumination + Site Classification + Light Color + Site Classification:Light Color + (1|Site)

Models including zero-inflated formulas had the same general structure as shown below.

Acoustic Monitoring

Calls/Night = Ordinal Date + Site

Telemetry

Detections/Night = Ordinal Date + Bat ID + Site

Flight Intercept Traps & UV Bucket Traps

Arthropods/Night = Ordinal Date + Site

Following model fitting, best-fit model identification and goodness-of-fit testing, we used the “predict.glmmTMB” prediction method from the `glmmTMB` package to predict changes in response variables between different light color treatments at both dark and lit sites for all best-fitting models while holding all other predictors constant at their median value. These predictions provide metrics of response change that integrate both site classification and lighting treatment. This final analytical exercise not only isolates the combined effects of lighting color and site classification, but also provides metrics of change in unstandardized and untransformed metrics, effectively allowing for assessment of statistical significance (p-values <0.05) *and* ecological significance.

Results

In 2019, we monitored bats via passive acoustic monitoring continuously from June 25 – September 20 barring equipment malfunctions for a total of 562 site-nights. Flight intercept traps were used to monitor insects from June 25 – August 21 barring equipment malfunctions for a total of 355 site-nights. *Myotis lucifugus* were radio tagged throughout the summer, but due to telemetry receiver issues before August 19 and battery limitations after that point, only telemetry monitoring data from August 19 – September 8 were included in this analysis. From June 25 – September 20, each light color treatment was implemented for 15 three-day periods.

In 2020, we monitored bats via passive acoustic monitoring from June 26 – August 14 excluding nights UV bucket traps were active for a total of 171 site-nights. We also monitored insects via UV bucket traps on the fourth, fifth, and sixth nights of each treatment period from July 14 – August 14 for a total of 106 site-nights. Because our study site must be lit regardless of research activities, we had red light illuminating the parking lot from May 1 – July 4, 2020. From July 4 – August 29, each color treatment was implemented for 5 seven-day periods. The first three days of a white light treatment were also carried out until the morning of September 1 at which point all passive acoustic monitors had exhausted their power supply while researchers were away.

Bat Acoustic Monitoring

Throughout passive acoustic monitoring efforts in 2019 and 2020, SonoBat attributed call sequences to *Antrozous pallidus* (71 in 55 site-nights), *Eptesicus fuscus* (4,414 in 577 site-nights), *Euderma maculatum* (1 in 1 site-night), *Lasiurus cinereus* (56,264 in 951 site-nights), *Lasionycteris noctivagans* (82,042 in 872 site-nights), *Myotis californicus* (12 in 12 site-nights), *Myotis ciliolabrum* (20 in 18 site-nights), *Myotis evotis* (418 in 268 site-nights), *Myotis lucifugus* (26,149 in 959 site-nights), *Myotis thysanodes* (2 in 2 site-nights), *Myotis volans* (526 in 301 site-nights) and *Myotis yumanensis* (73 in 64 site-nights). For the 6 species of bats we created candidate models for that were detected during 100 or more site-nights (*Eptesicus fuscus*, *Lasiurus cinereus*, *Lasionycteris noctivagans*, *Myotis evotis*, *Myotis lucifugus*, and *Myotis volans*), there were no conflicts between AIC values and error-distribution plots. All top models were zero-inflated and implemented a quadratic error distribution excluding the top *M. volans* model which implemented linear error distribution. Residual diagnostic plots showed exceptional model fit with regards to dispersion, outliers, and uniformity. All models had low VIF values, with the highest VIF being 3.97. Model results are in Figure 2.3 and Table 2.1.

Of the species included in this analysis, all but *E. fuscus* exhibited significantly different activity levels between dark and lit sites with light color held constant, with *L. cinereus, L. noctivagans*, and *M. lucifugus* showing increased activity in lit areas, and *M. evotis* and *M. volans* showing decreased activity in lit areas (Figure 2.3 and Table 2.1). Additionally, 95% confidence intervals for predicted activity in both dark and lit areas during red light treatments overlapped for both *L. cinereus* and *L. noctivagans* (Figure

2.4). For both *E. fuscus* and *M. lucifugus* there was a significant and negative interaction between site classification and light color treatment, which indicates a decreased difference in activity levels between dark and lit areas during white lighting, but not red lighting, for these species. Only *L. cinereus* exhibited a significant response to light intensity, with species-level activity increasing with light intensity irrespective of site classification.

Bat Telemetry

When corroborating the AIC values and error-distribution plots for radio tagged *M. lucifugus*, there were conflicting results and selected the model implementing a quadratic negative-binomial error distribution and a zero-inflated formula as suggested by AIC values. Residual diagnostic plots indicated good model fit with regards to dispersion, outliers, and uniformity. All model parameters exhibited low VIFs, with the highest VIF being 4.09. Model results can be seen in Figure 2.5 and Table 2.2. In contrast to the *M. lucifugus* echolocation, radio tagged *M. lucifugus* individuals showed similar habitat use patterns in lit areas compared to dark areas irrespective of light color (Figures 2.5 and 2.6). Radio tagged bats exhibited no significant response to color treatment in either dark or lit areas (Figures 2.5 and 2.6). Individual bat detection metrics by color treatment can be found in Table 2.3

Insects: Flight-Intercept Traps

There were no conflicts between AIC values and the error distribution plots for any of the four arthropod Orders we constructed candidate models for, with both model selection methods suggesting that a Poisson error distribution best fit Araneae and Coleoptera data, and a quadratic error distribution best fit Diptera and Hemiptera data. Additionally, AIC results suggested that zero inflated models best fit the Coleoptera data. All residual diagnostic plots suggested adequate goodness of fit. Two terms in the Hemiptera model, light color and the interaction between site classification and color, had moderate VIFs (>5), while all other models had no VIFs greater than 4.41. Model results can be seen in Figure 2.7 and Table 2.4.

Dipterans and Hemipterans were more active in lit areas compared to dark areas irrespective of lighting treatment (Figure 2.7 and Table 2.4). Additionally, for Diptera, there was a positive and significant interaction between site classification and light color, indicating that disparities in activity between dark and lit areas are exacerbated under white light conditions compared to red light conditions (Figure 2.7 and Table 2.4). Based on predictions with varying lighting conditions and site classifications, Dipterans used dark and lit areas equally during red light treatment periods, but favored lit areas during white light treatment periods (Figure 2.8) which indicates that Dipterans exhibit more natural behavior under red lighting conditions.

Insects: UV-Bucket Traps

There were no conflicts between AIC values and the error distribution plots for any of the eight arthropod Orders for which we constructed models (Acari, Coleoptera, Diptera, Ephemeroptera, Hemiptera, Hymenoptera, Lepidoptera, and Tricoptera). All top models implemented glmmTMB’s quadratic error distribution aside from the top Hymenoptera model which used a linear error distribution. Additionally, AIC values suggested that zero-inflated negative-binomial models best fit the Acari and Ephemeroptera data. All residual diagnostic plots suggested adequate goodness of fit. No model terms had a VIF greater than 4.54. Model results can be seen in Figure 2.9 and Table 2.5.

For all Orders modelled, white light led to higher nightly counts than red lighting conditions (Figure 2.9 and Table 2.5). Coleoptera and Trichoptera also showed higher counts in lit areas irrespective of lighting treatment (Figure 2.9 and Table 2.5). Only for Diptera and Hemiptera was there a significant interaction between site classification and light color treatment with Diptera showing a smaller difference between dark and lit site counts under white light conditions in comparison to red light, and Hemiptera showing a larger difference between dark and lit site counts under white light conditions in comparison to red light (Figure 2.9 and Table 2.5). Based on model predictions holding all predictor values constant at their medians and varying both lighting treatment and site classification, Hemipterans, Hymenopterans, Lepidopterans, and Trichopterans were less active at lit sites during red lighting treatments compared to white lighting treatments (Figure 2.10). These predictions also showed that Acari, Colepterans, Dipterans, Ephemeropterans, Hemipterans, Hymenopterans, and Lepidopterans were equally active at lit and unlit sites during red light treatment periods (Figure 2.10).

Discussion

Our findings show strong evidence for red light being an effective mitigation technique for reducing artificial light's effects on nocturnal arthropods, but little evidence for red light's efficacy as a mitigation technique for bats. Our results for UV bucket traps indicate that red lights not only provide reduced arthropod attraction to light fixtures, but also that red lit areas have similar activity levels to dark areas. The flight intercept trap results are less supportive of red light's efficacy as a mitigation technique, however there are multiple caveats pertaining to these results that inform the implications of our findings. While deploying flight intercept traps, we observed a strong effect of wind on trap movement. Even slight breezes caused the traps to spin at a high speed, which likely increased the trap's detectability to aerial arthropods, perhaps contributing to the cause of problematically low sample resolutions (individuals per site-night) for all Orders but Diptera included in this analysis.

Additionally, while flight intercept trap results suggest that red light may be an effective mitigation technique for decreasing the propensity of artificially attracting Diptera, UV bucket trap results do not show strong evidence for red light reducing the impacts of artificial light on this order. This difference in results may be driven by a discrepancy in the spatial scale of response measurement in combination with potential implications of Dipteran physiology. While flight intercept traps were hung from light fixtures, effectively sampling insects that were in the immediate vicinity of a single light, bucket traps were placed in the median of the parking lot and sampled individuals that were within the entirety of the lit area.

Recent research indicated that *Drosophila* photoreceptors are more sensitive to long-wavelength light than previously assumed (Sharkey et al., 2020). Both the modest positive effect of red light on Dipteran counts we found as well as the potential for Dipterans to perceive, and be attracted to, both red and white light suggest that some Dipterans at our lit sites may have approached the street lights surrounding the bucket traps rather than the UV bucket traps. If some Dipterans were, in fact, more attracted to the surrounding street lights than to the UV lights on our bucket traps, our effect sizes for both red and white light in lit areas may be artificially low.

Our UV bucket trap results suggest that, for many Orders, the use of red lights in lieu of more traditionally used light colors may be an effective means of mitigating potential negative effects of insect attraction to artificial light (Owens & Lewis, 2018). Given trends of declining arthropod populations globally (Sánchez-Bayo & Wyckhuys, 2019) and their importance to socioecological systems (Losey & Vaughan, 2006), taking action to reduce artificial light's impacts on arthropod populations through implementation of red lights in lieu of traditional white lights may be prudent.

In contrast to our finding surrounding arthropods, we found little evidence of red light being an effective means of mitigating artificial light's influence on the bats of Grand Teton, with only one species (*L. cinereus*) showing similar activity at both dark and lit sites during red light treatments. While our results deviate from those of Spoelstra et al. (2017), the contradictory results we obtained may be attributed to different analytical techniques. While Spoelstra et al. aggregated all species-level detections by year and lighting treatment (effectively making a treatment-year the experimental unit), we elected to aggregate by site and sampling date to maintain representation of variation between sampling nights, as well as to allow us to determine how time since the beginning of a treatment influences the biological responses — an experimental artifact that was not present in Spoelstra et al.'s 2017 research. Our decision to aggregate by site-night and the associated changes to our model structures may contribute to the contradictory, though not antagonistic, results we obtained from this project.

Additionally, Spoelstra et al. (2017) used a fundamentally different experimental design to assess red light's impact on bat and insect activity. Rather than changing the light treatment at each site, Spoelstra et. al. used permanently fixed color treatments at each of their sites. While our experimental design allowed us to eliminate latent variables stemming from the characteristics of sites to influence our results as well as anomalous events (e.g., arthropod erruptions), the short-term treatment periods (three and seven days in 2019 and 2020, respectively) we implemented may not have provided adequate time for local wildlife to exhibit behavior that may manifest after acclimation to a long-term light installation.

Reducing light intensity also appeared to be an ineffective means of mitigating artificial light's impacts on bats, with only *L. cinereus* showing a significantly positive relationship with light intensity. Despite our largely negative findings surrounding decreased light intensity as a light pollution mitigation technique for bats, the presence of any artificial light within the range of intensities that we implemented significantly impacted activity for five of the six bat species we constructed models for. Although the mitigation techniques we implemented had little meaningful effect on local bat activity, our findings highlight the idea that the presence of artificial light does influence ecological systems, and further research is necessary to identify lighting practices that reduce light pollution's impacts on bats.

While impactful, our results should be expanded upon in future research to better our understanding of the long term effects of artificial light mitigation efforts. Our treatment periods were only three days in 2019, and seven days in 2020. While seven days appeared to be a sufficient period of time for individuals already inhabiting our study area to acclimate to a change in lighting treatment, it likely does not give bat and arthropod populations sufficient time to respond, and therefore our research cannot address the long-term effects of a permanent change from white streetlights to red streetlights. Future work surrounding red light as a mitigation technique can aim to quantify not only the immediate responses of bats to red light, but also the long term changes associated with a change in light color.

Figures

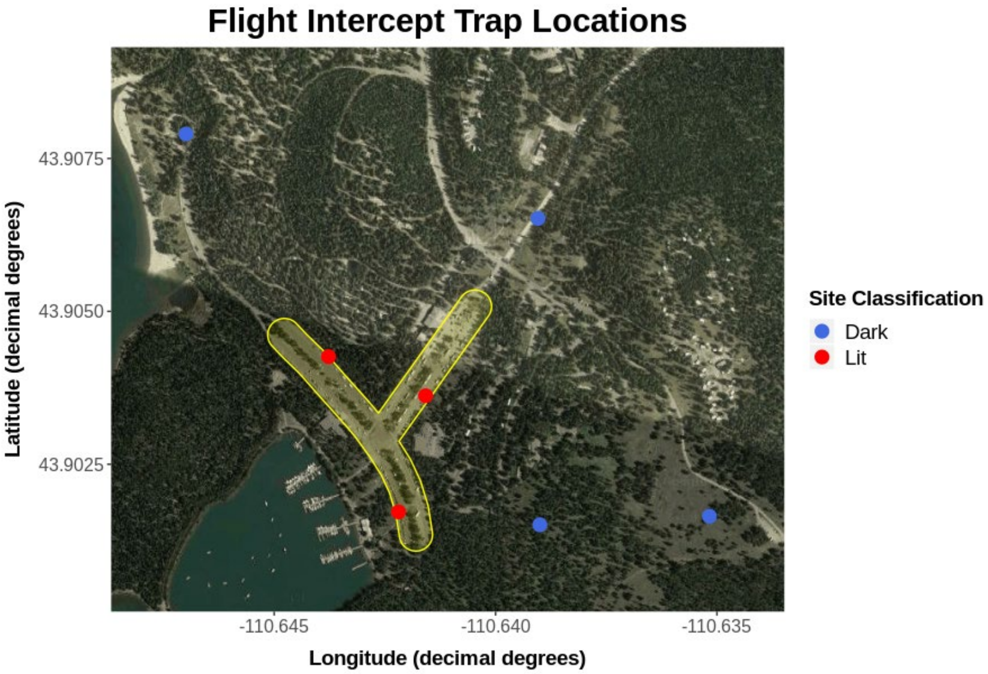

Figure 2.1. Bat and insect monitoring site locations in Colter Bay, Grand Teton National Park, WY.

Figure 2.2. Insect trap designs. Flight intercept traps (left) consisted of two 24”x18” acrylic sheets cut half way up their longitudinal axis and slid together, a wooden top support, and a tarp funnel below with a collection container. Collection containers were filled with cut pieces of No-pest® Strip2. UV bucket traps (right) use a UV bulb to attract insects toward intersecting acrylic sheets that stand above a collection container with No-pest® Strip2.

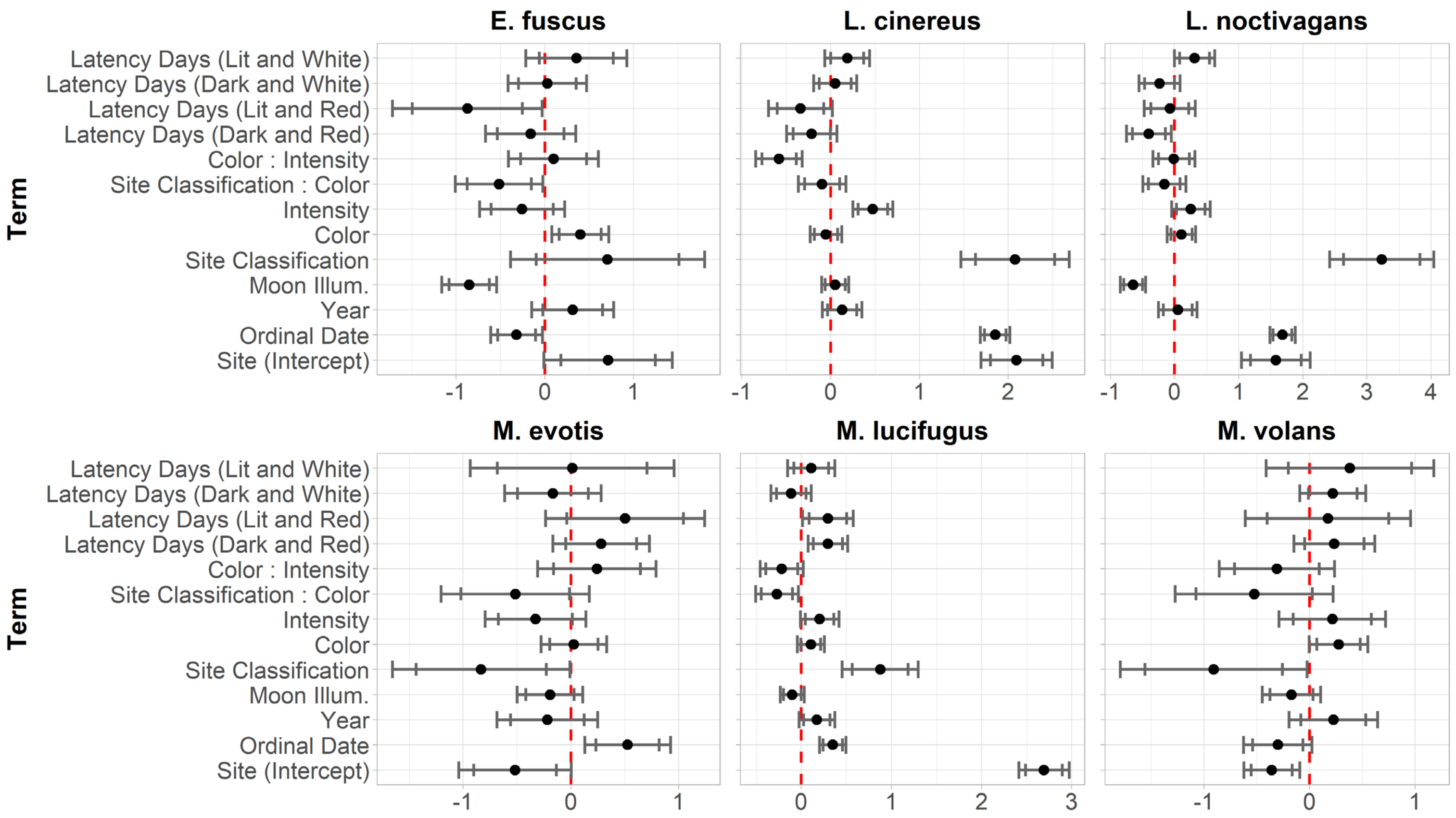

Figure 2.3 **Model coefficients for species-specific bat activity measured with passive acoustic monitoring. Following the model construction and selection process, we used EcoCountHelper's "EffectsPlotter" function to visualize scaled parameter estimates with 85% and 95% confidence intervals. Each plot represents a species-level model, with the associated species indicated by subplot titles.**

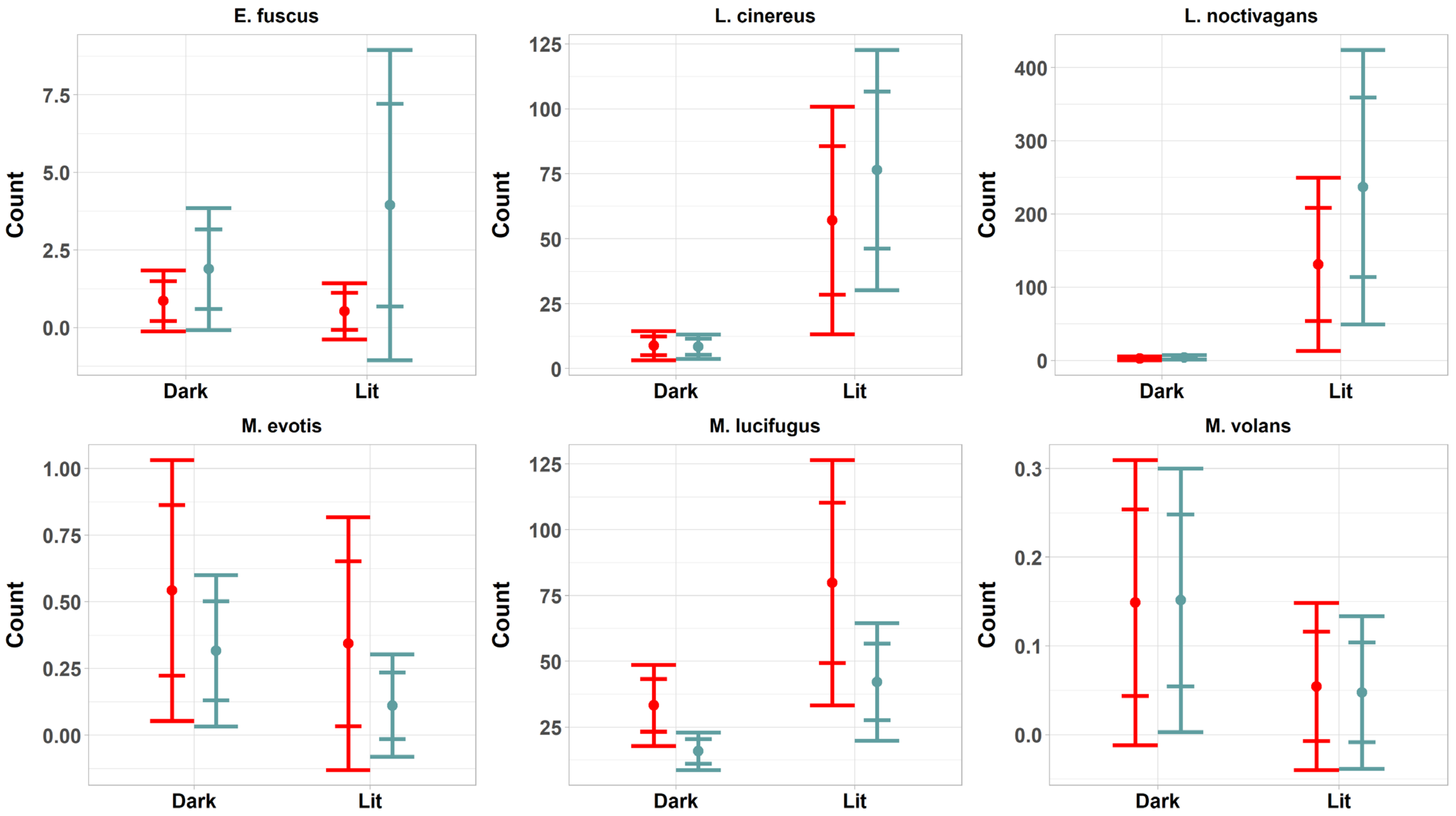

Figure 2.4. Bat activity prediction plots. Models for species-specific bat activity measured via passive acoustic monitors were used to predict the number of call sequences that would be recorded under multiple lighting conditions. All model parameters were held at their median values except light color and site classification, and model-based predictions were made for all combinations of light color and site classification. Inner and outer error bars represent 80% and 95% confidence intervals, respectively.

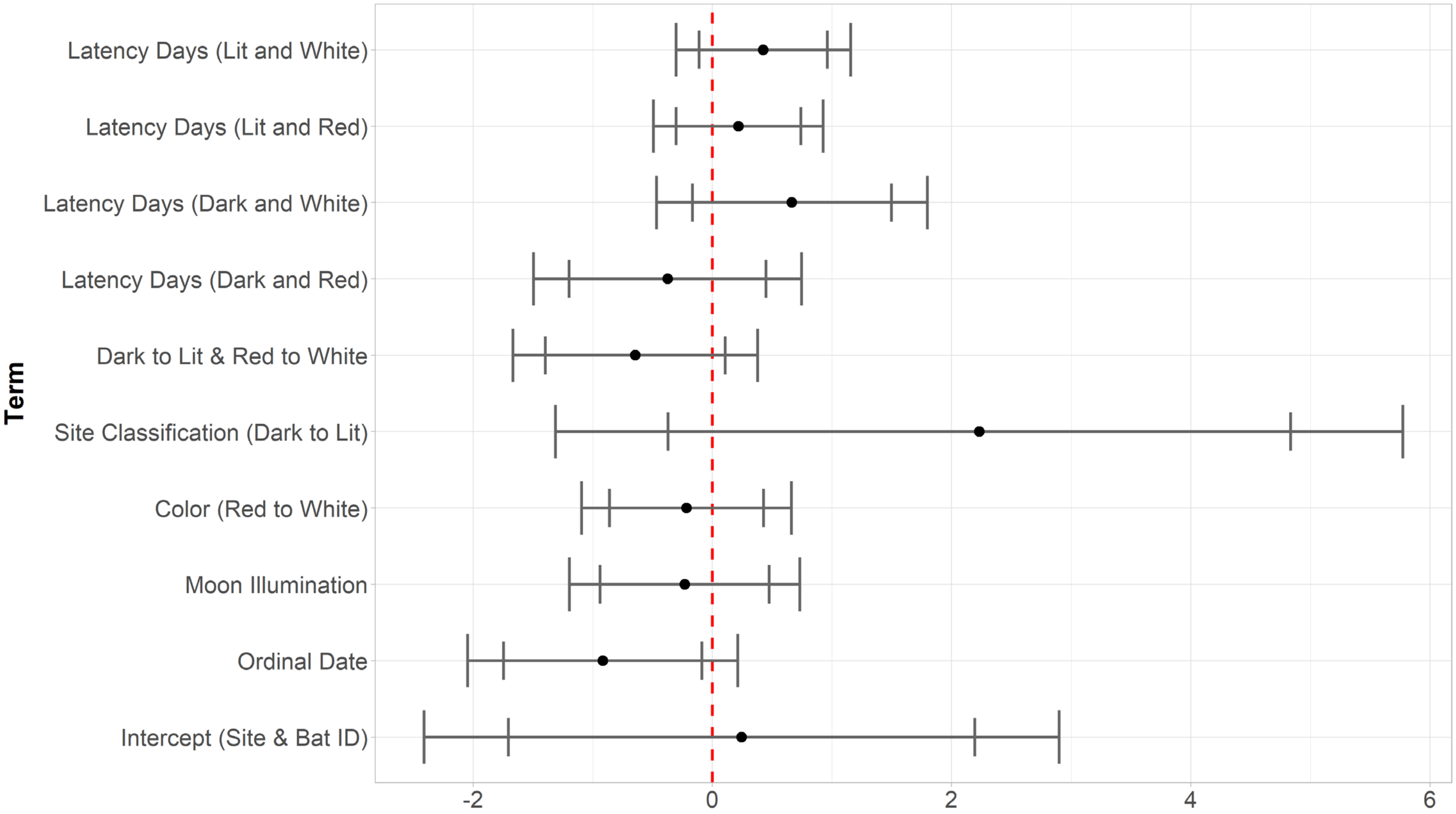

Figure 2.5. **Bat lightscape use model results plot. Following the model construction and selection process for *M. lucifugus* radio telemetry monitoring data, we used EcoCountHelper's "EffectsPlotter" function to visualize scaled parameter estimates with 85% and 95% confidence intervals.**

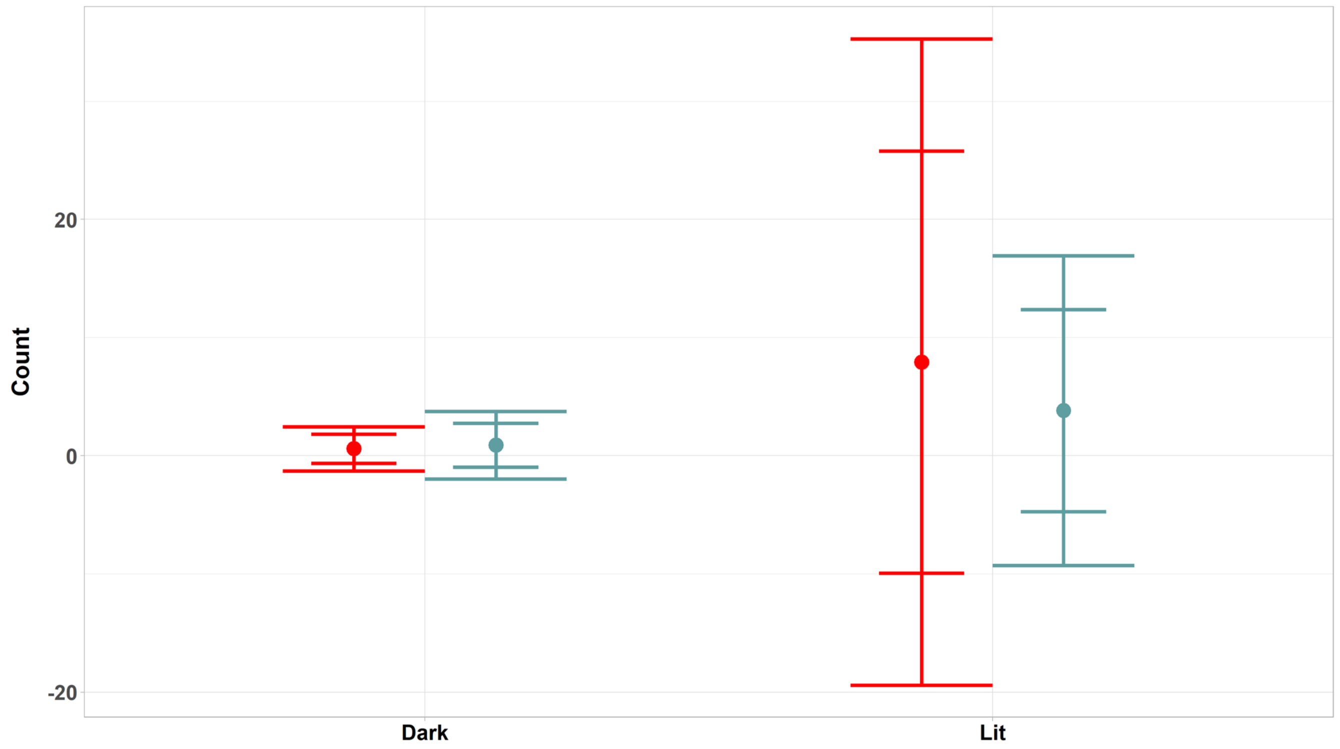

Figure 2.6. **Bat lightscape use prediction plot. Models for *M. lucifugus* activity measured via passive telemetry receivers were used to predict the number of radio tag detections that would be recorded under multiple lighting conditions. All model parameters were held at their median values except light color and site classification, and model-based predictions were made for all combinations of light color and site classification. Inner and outer error bars represent 80% and 95% confidence intervals, respectively.**

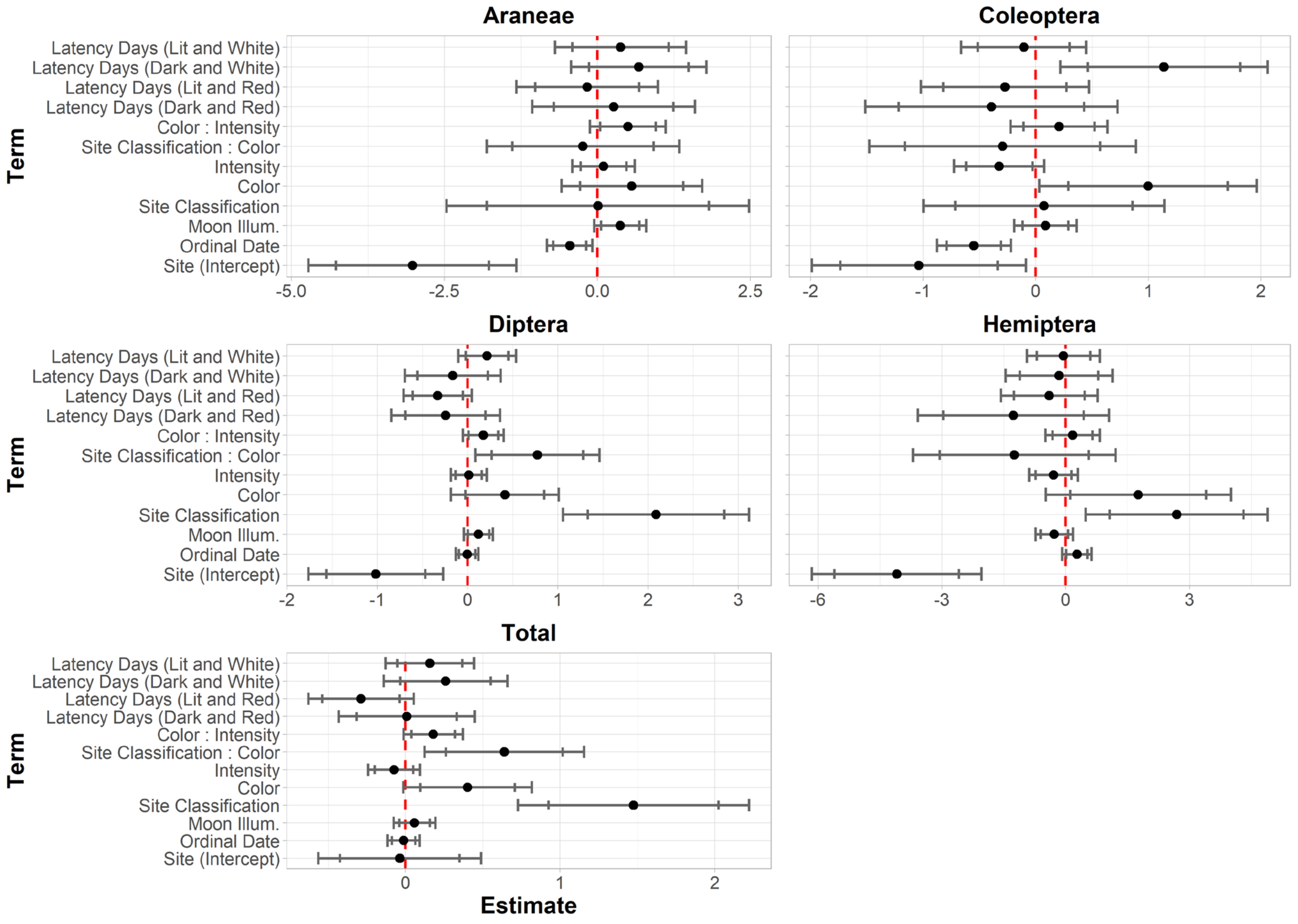

Figure 2.7. 2019 insect lightscape use model results plot. Following the model construction and selection process, we used EcoCountHelper's "EffectsPlotter" function to visualize scaled parameter estimates with 85% and 95% confidence intervals. Each plot represents an order-level model, with the associated species indicated by subplot titles. The "Total" subplot represents results for models with all insect counts aggregated by site-night.

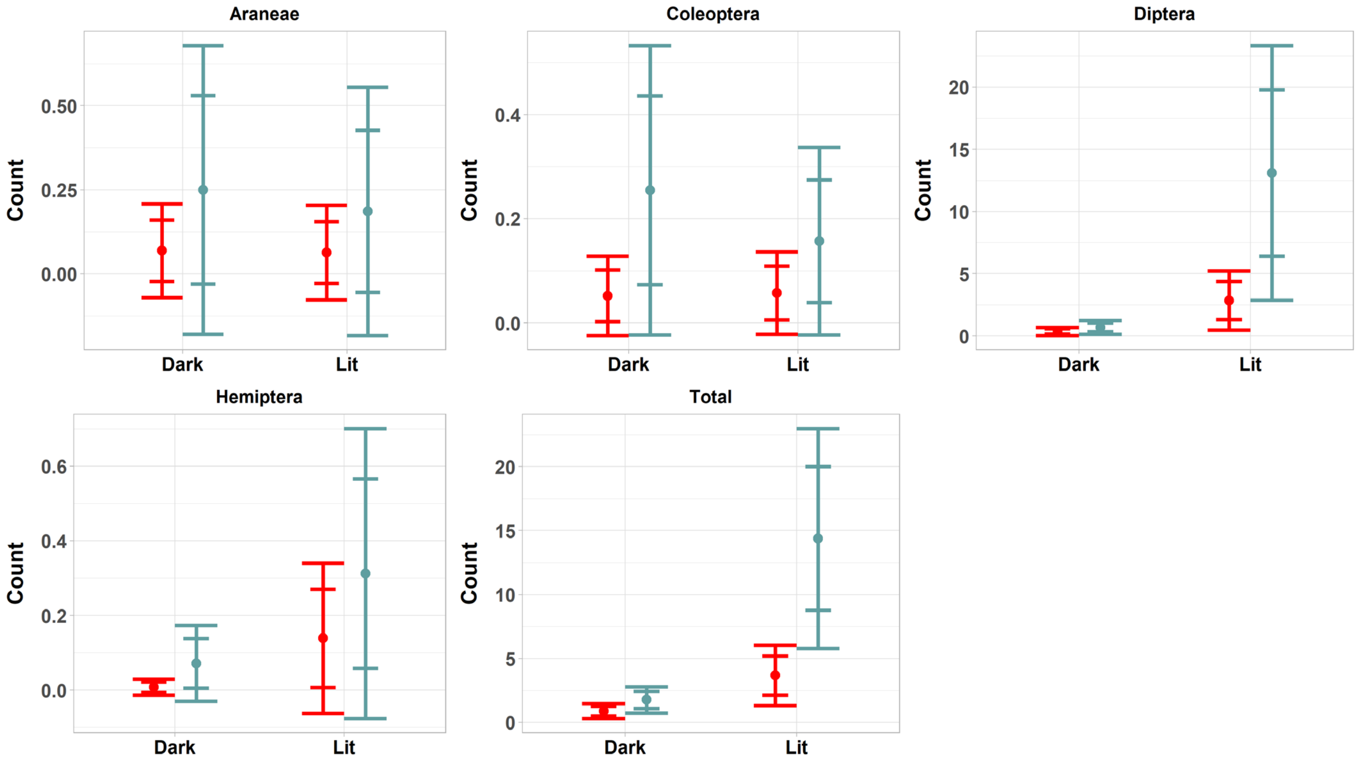

Figure 2.8. **2019 insect lightscape use prediction plot. Models for order-specific insect captures (and all orders combined) measured via flight intercept traps were used to predict the number of insects that would be captured under multiple lighting conditions. All model parameters were held at their median values except light color and site classification, and model-based predictions were made for all combinations of light color and site classification. Inner and outer error bars represent 80% and 95% confidence intervals, respectively.**

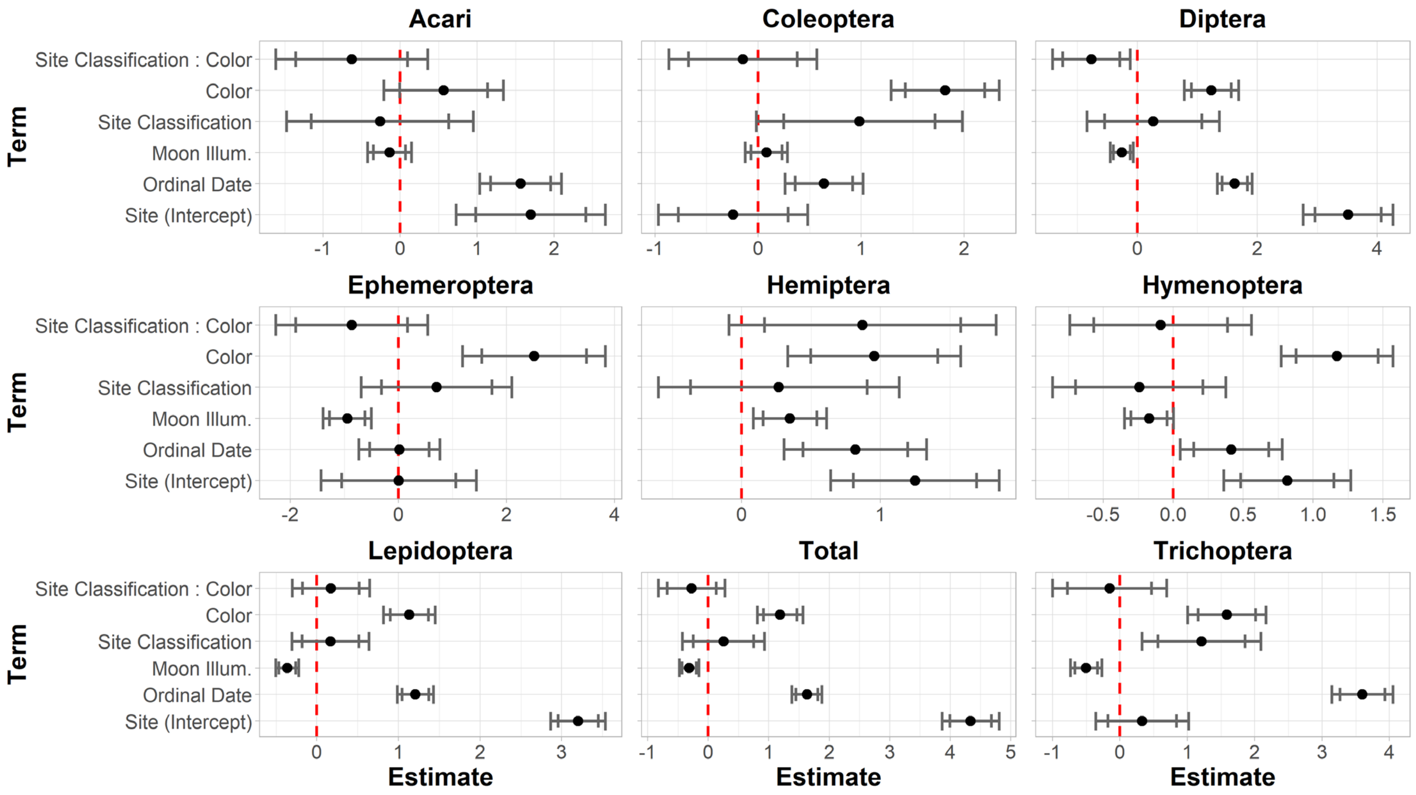

Figure 2.9. 2020 insect lightscape use model results plot. Following the model construction and selection process, we used EcoCountHelper's "EffectsPlotter" function to visualize scaled parameter estimates with 85% and 95% confidence intervals. Each plot represents an order-level model, with the associated species indicated by subplot titles. The "Total" subplot represents results for models with all insect counts aggregated by site-night.

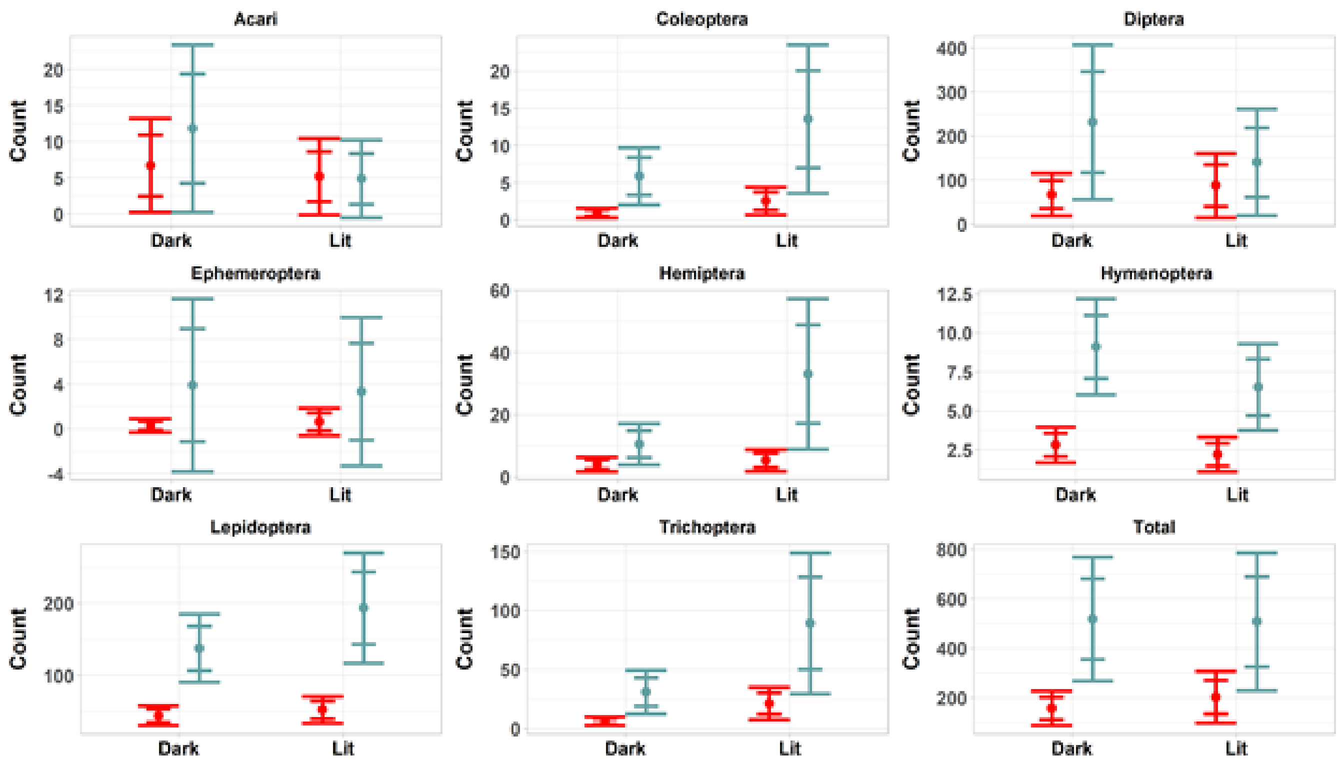

Figure 2.10. 2020 insect lightscape use prediction plot. Models for order-specific insect captures (and all orders combined) measured via UV bucket traps were used to predict the number of insects that would be captured under multiple lighting conditions. All model parameters were held at their median values except light color and site classification, and model-based predictions were made for all combinations of light color and site classification. Inner and outer error bars represent 80% and 95% confidence intervals, respectively.

Tables

Table 2.1. Model results for species-specific bat activity measured with passive acoustic monitoring. GLMMs using a log-link were fit for each bat species detected using passive acoustic monitoring. All terms containing colons represent interaction terms between the two variables on either side of the colon. 95% confidence intervals for each parameter estimate are listed parenthetically.

Species	Term	Estimate	Std. Error	z value	p
E. fuscus	Site (Intercept)	0.71 (-0.01/1.44)	0.370	1.931	0.054
	Ordinal Date	-0.32 (-0.61/-0.03)	0.148	-2.146	0.032
	Year	0.31 (-0.15/0.78)	0.235	1.338	0.181
	Moon Illum.	-0.85 (-1.16/-0.54)	0.158	-5.385	$7.25\text{x}10^{-8}$
	Site Classification	0.71 (-0.39/1.8)	0.558	1.266	0.206
	Color	0.4 (0.08/0.72)	0.164	2.433	0.015
	Intensity	-0.26 (-0.73/0.22)	0.244	-1.048	0.295
	Site Classification : Color	-0.51 (-1.01/-0.02)	0.252	-2.042	0.041
	Color : Intensity	0.1 (-0.41/0.6)	0.259	0.376	0.707
	Latency Days (Dark & Red)	-0.16 (-0.67/0.35)	0.260	-0.613	0.540
	Latency Days (Lit & Red)	-0.87 (-1.72/-0.03)	0.431	-2.027	0.043
	Latency Days (Dark & White)	0.03 (-0.42/0.47)	0.227	0.126	0.900
	Latency Days (Lit & White)	0.36 (-0.21/0.92)	0.290	1.226	0.220
L. cinereus	Site (Intercept)	2.09 (1.69/2.5)	0.205	10.222	$1.57\text{x}10^{-24}$
	Ordinal Date	1.85 (1.69/2.02)	0.085	21.797	$2.50\text{x}10^{-105}$
	Year	0.13 (-0.09/0.35)	0.114	1.148	0.251
	Moon Illum.	0.05 (-0.1/0.2)	0.078	0.665	0.506
	Site Classification	2.08 (1.47/2.69)	0.310	6.695	$2.15\text{x}10^{-11}$
	Color	-0.05 (-0.23/0.12)	0.090	-0.579	0.563
	Intensity	0.48 (0.25/0.7)	0.115	4.127	$3.68\text{x}10^{-5}$
	Site Classification : Color	-0.1 (-0.36/0.17)	0.136	-0.699	0.484
	Color : Intensity	-0.58 (-0.84/-0.32)	0.134	-4.331	$1.48\text{x}10^{-5}$
	Latency Days (Dark & Red)	-0.21 (-0.5/0.07)	0.145	-1.471	0.141

Species	Term	Estimate	Std. Error	z value	p
	Latency Days (Lit & Red)	-0.34 (-0.7/0.02)	0.183	-1.851	0.064
	Latency Days (Dark & White)	0.05 (-0.19/0.3)	0.124	0.421	0.674
	Latency Days (Lit & White)	0.19 (-0.06/0.44)	0.128	1.460	0.144
L. noctivagans	Site (Intercept)	1.58 (1.04/2.12)	0.274	5.768	$8.03\text{x}10^{-9}$
	Ordinal Date	1.68 (1.48/1.88)	0.102	16.547	$1.67\text{x}10^{-61}$
	Year	0.05 (-0.25/0.35)	0.155	0.321	0.748
	Moon Illum.	-0.65 (-0.85/-0.45)	0.101	-6.398	$1.57\text{x}10^{-10}$
	Site Classification	3.23 (2.42/4.04)	0.414	7.805	$5.97\text{x}10^{-15}$
	Color	0.11 (-0.11/0.33)	0.114	0.951	0.342
	Intensity	0.25 (-0.05/0.55)	0.154	1.650	0.099
	Site Classification : Color	-0.16 (-0.5/0.18)	0.172	-0.932	0.352
	Color : Intensity	-0.01 (-0.34/0.32)	0.167	-0.062	0.951
	Latency Days (Dark & Red)	-0.4 (-0.75/-0.05)	0.177	-2.258	0.024
	Latency Days (Lit & Red)	-0.07 (-0.47/0.32)	0.204	-0.367	0.713
	Latency Days (Dark & White)	-0.24 (-0.55/0.08)	0.163	-1.446	0.148
	Latency Days (Lit & White)	0.31 (0/0.63)	0.161	1.939	0.053
M. evotis	Site (Intercept)	-0.52 (-1.04/0.01)	0.267	-1.938	0.053
	Ordinal Date	0.53 (0.13/0.92)	0.203	2.596	0.009
	Year	-0.22 (-0.68/0.25)	0.238	-0.913	0.361
	Moon Illum.	-0.19 (-0.5/0.11)	0.156	-1.241	0.215
	Site Classification	-0.83 (-1.66/-0.01)	0.420	-1.979	0.048
	Color	0.03 (-0.28/0.33)	0.156	0.181	0.857
	Intensity	-0.33 (-0.79/0.14)	0.238	-1.375	0.169
	Site Classification : Color	-0.52 (-1.2/0.17)	0.351	-1.469	0.142
	Color : Intensity	0.24 (-0.31/0.79)	0.280	0.863	0.388
	Latency Days (Dark & Red)	0.28 (-0.17/0.73)	0.228	1.234	0.217
	Latency Days (Lit & Red)	0.5 (-0.23/1.24)	0.376	1.341	0.180

Species	Term	Estimate	Std. Error	z value	p
	Latency Days (Dark & White)	-0.17 (-0.62/0.28)	0.229	-0.726	0.468
	Latency Days (Lit & White)	0.01 (-0.93/0.96)	0.483	0.027	0.978
M. lucifugus	Site (Intercept)	2.69 (2.41/2.97)	0.142	18.922	7.58x10^{-80}
	Ordinal Date	0.35 (0.2/0.49)	0.075	4.645	3.40x10^{-6}
	Year	0.17 (-0.03/0.37)	0.102	1.702	0.089
	Moon Illum.	-0.1 (-0.23/0.03)	0.068	-1.486	0.137
	Site Classification	0.88 (0.45/1.3)	0.215	4.077	4.56x10^{-5}
	Color	0.11 (-0.05/0.26)	0.077	1.372	0.170
	Intensity	0.2 (-0.01/0.42)	0.109	1.865	0.062
	Site Classification : Color	-0.27 (-0.51/-0.03)	0.121	-2.242	0.025
	Color : Intensity	-0.22 (-0.46/0.02)	0.122	-1.780	0.075
	Latency Days (Dark & Red)	0.29 (0.08/0.51)	0.112	2.638	0.008
	Latency Days (Lit & Red)	0.3 (0.01/0.58)	0.144	2.045	0.041
	Latency Days (Dark & White)	-0.11 (-0.34/0.11)	0.114	-0.985	0.325
	Latency Days (Lit & White)	0.11 (-0.15/0.37)	0.133	0.833	0.405
M. volans	Site (Intercept)	-0.36 (-0.62/-0.09)	0.135	-2.638	0.008
	Ordinal Date	-0.3 (-0.62/0.03)	0.165	-1.807	0.071
	Year	0.23 (-0.19/0.65)	0.214	1.059	0.289
	Moon Illum.	-0.17 (-0.45/0.11)	0.141	-1.199	0.231
	Site Classification	-0.91 (-1.79/-0.02)	0.452	-2.007	0.045
	Color	0.28 (0/0.55)	0.142	1.940	0.052
	Intensity	0.22 (-0.29/0.72)	0.258	0.841	0.400
	Site Classification : Color	-0.52 (-1.27/0.23)	0.382	-1.368	0.171
	Color : Intensity	-0.31 (-0.86/0.24)	0.279	-1.106	0.269
	Latency Days (Dark & Red)	0.24 (-0.15/0.62)	0.196	1.204	0.228
	Latency Days (Lit & Red)	0.18 (-0.61/0.96)	0.399	0.439	0.661
	Latency Days (Dark & White)	0.22 (-0.09/0.53)	0.160	1.389	0.165

Species	Term	Estimate	Std. Error	z value	p
	Latency Days (Lit & White)	0.38 (-0.41/1.18)	0.404	0.950	0.342

Table 2.2. Model results for *Myotis lucifugus* lightscsape use. 95% confidence intervals for each parameter estimate are listed parenthetically.

Term	Estimate	Std. Error	z value	Pr(>|z|)
Intercept (Site & Bat ID)	0.24 (-2.41/2.9)	1.354	0.180	0.857
Ordinal Date	-0.92 (-2.04/0.21)	0.576	-1.589	0.112
Moon Illumination	-0.23 (-1.19/0.73)	0.491	-0.471	0.638
Color (Red to White)	-0.21 (-1.09/0.66)	0.448	-0.480	0.631
Site Classification (Dark to Lit)	2.23 (-1.31/5.77)	1.807	1.235	0.217
Dark to Lit & Red to White	-0.64 (-1.67/0.38)	0.522	-1.233	0.217
Latency Days (Dark and Red)	-0.37 (-1.5/0.75)	0.572	-0.654	0.513
Latency Days (Dark and White)	0.67 (-0.47/1.8)	0.577	1.154	0.249
Latency Days (Lit and Red)	0.22 (-0.49/0.93)	0.362	0.600	0.549
Latency Days (Lit and White)	0.43 (-0.3/1.16)	0.372	1.144	0.253

Table 2.3. ***Myotis lucifugus*** **telemetry detection metrics by individual ("Bat ID" column) and light treatment color ("Color" column). Mean nightly detections was calculated by dividing the number of total detections for an individual and color treatment by the number of days within the sampling period (August 19, 2019 – September 9, 2019).**

Bat ID	Color	Site-Nights Detected	Mean Nightly Detections	Std. Error
7	Red	2	0.02	0.02
	White	0	0	0
10	Red	17	6.27	2.49
	White	9	0.51	0.18
12	Red	1	0.01	0.01
	White	0	0	0
15	Red	4	0.68	0.37
	White	0	0	0
16	Red	1	0.02	0.02
	White	0	0	0
18	Red	16	2.13	0.6
	White	11	1.08	0.43
22	Red	0	0	0
	White	1	0.11	0.11
34	Red	14	2.08	0.69
	White	7	0.67	0.27
46	Red	3	0.92	0.76
	White	1	0.02	0.02
47	Red	10	7.47	3.21
	White	6	2.51	1.28
48	Red	29	42.01	15.24
	White	36	31.16	13.02
50	Red	3	0.78	0.67
	White	0	0	0
51	Red	18	6.71	2.83
	White	16	6.13	2.27
53	Red	1	0.01	0.01
	White	0	0	0
56	Red	2	0.03	0.02
	White	0	0	0

Table 2.4. Insect lightscape use model results using flight intercept trap data. GLMMs using log-links were fitted for each order captured in flight intercept traps. All terms containing colons represent interaction terms between the two variables on either side of the colon. 95% confidence intervals for each parameter estimate are listed parenthetically.

Order	Term	Estimate	Std. Error	z value	Pr(>|z|)
Araneae	Site (Intercept)	-3.02 (-4.72/-1.32)	0.867	-3.487	0.0005
	Ordinal Date	-0.45 (-0.82/-0.08)	0.189	-2.408	0.016
	Moon Illum.	0.37 (-0.05/0.8)	0.217	1.707	0.088
	Site Classification	0.01 (-2.47/2.48)	1.262	0.005	0.996
	Color	0.56 (-0.59/1.71)	0.586	0.957	0.339
	Intensity	0.1 (-0.41/0.61)	0.260	0.385	0.700
	Site Classification : Color	-0.24 (-1.81/1.33)	0.802	-0.296	0.767
	Color : Intensity	0.5 (-0.12/1.12)	0.316	1.570	0.116
	Latency Days (Dark and Red)	0.26 (-1.07/1.59)	0.678	0.388	0.698
	Latency Days (Lit and Red)	-0.17 (-1.33/0.99)	0.590	-0.289	0.773
	Latency Days (Dark and White)	0.67 (-0.43/1.78)	0.564	1.193	0.233
	Latency Days (Lit and White)	0.38 (-0.7/1.45)	0.547	0.687	0.492
Coleoptera	Site (Intercept)	-1.04 (-1.99/-0.09)	0.485	-2.137	0.033
	Ordinal Date	-0.55 (-0.88/-0.22)	0.167	-3.284	0.001
	Moon Illum.	0.09 (-0.19/0.36)	0.142	0.612	0.541
	Site Classification	0.07 (-1/1.14)	0.546	0.134	0.893
	Color	1 (0.03/1.96)	0.492	2.027	0.043
	Intensity	-0.32 (-0.73/0.08)	0.205	-1.584	0.113
	Site Classification : Color	-0.29 (-1.48/0.89)	0.603	-0.488	0.626
	Color : Intensity	0.21 (-0.22/0.64)	0.219	0.944	0.345
	Latency Days (Dark and Red)	-0.39 (-1.51/0.73)	0.571	-0.688	0.492
	Latency Days (Lit and Red)	-0.27 (-1.02/0.47)	0.380	-0.718	0.473
	Latency Days (Dark and White)	1.14 (0.22/2.06)	0.470	2.424	0.015
	Latency Days (Lit and White)	-0.11 (-0.66/0.45)	0.284	-0.375	0.708
Diptera	Site (Intercept)	-1.02 (-1.76/-0.27)	0.381	-2.677	0.007
	Ordinal Date	-0.01 (-0.13/0.12)	0.063	-0.084	0.933
	Moon Illum.	0.12 (-0.04/0.28)	0.082	1.459	0.145
	Site Classification	2.09 (1.06/3.12)	0.526	3.971	$7.16\text{x}10^{-5}$
	Color	0.41 (-0.18/1.01)	0.304	1.354	0.176
	Intensity	0.01 (-0.19/0.21)	0.102	0.119	0.906

Order	Term	Estimate	Std. Error	z value	Pr(>|z|)
	Site Classification : Color	0.77 (0.09/1.46)	0.351	2.203	0.028
	Color : Intensity	0.17 (-0.05/0.4)	0.115	1.511	0.131
	Latency Days (Dark and Red)	-0.24 (-0.85/0.36)	0.308	-0.794	0.427
	Latency Days (Lit and Red)	-0.33 (-0.71/0.05)	0.193	-1.718	0.086
	Latency Days (Dark and White)	-0.17 (-0.7/0.37)	0.271	-0.608	0.543
	Latency Days (Lit and White)	0.22 (-0.11/0.54)	0.164	1.319	0.187
Hemiptera	Site (Intercept)	-4.09 (-6.15/-2.03)	1.051	-3.896	9.79×10^{-5}
	Ordinal Date	0.27 (-0.08/0.63)	0.180	1.515	0.130
	Moon Illum.	-0.28 (-0.73/0.18)	0.231	-1.193	0.233
	Site Classification	2.69 (0.49/4.9)	1.125	2.394	0.017
	Color	1.76 (-0.48/4)	1.144	1.539	0.124
	Intensity	-0.29 (-0.88/0.3)	0.300	-0.973	0.331
	Site Classification : Color	-1.24 (-3.7/1.21)	1.253	-0.991	0.322
	Color : Intensity	0.17 (-0.49/0.83)	0.336	0.507	0.612
	Latency Days (Dark and Red)	-1.27 (-3.58/1.05)	1.183	-1.069	0.285
	Latency Days (Lit and Red)	-0.39 (-1.57/0.78)	0.597	-0.661	0.509
	Latency Days (Dark and White)	-0.16 (-1.45/1.14)	0.661	-0.239	0.811
	Latency Days (Lit and White)	-0.05 (-0.93/0.83)	0.450	-0.117	0.907
Total	Site (Intercept)	-0.04 (-0.56/0.49)	0.269	-0.135	0.893
	Ordinal Date	-0.01 (-0.12/0.09)	0.053	-0.234	0.815
	Moon Illum.	0.06 (-0.08/0.19)	0.069	0.849	0.396
	Site Classification	1.48 (0.73/2.22)	0.382	3.865	0.0001
	Color	0.4 (-0.01/0.82)	0.212	1.893	0.058
	Intensity	-0.07 (-0.24/0.09)	0.086	-0.856	0.392
	Site Classification : Color	0.64 (0.12/1.16)	0.263	2.433	0.015
	Color : Intensity	0.18 (-0.01/0.37)	0.098	1.834	0.067
	Latency Days (Dark and Red)	0.01 (-0.43/0.45)	0.225	0.036	0.972
	Latency Days (Lit and Red)	-0.29 (-0.63/0.05)	0.174	-1.654	0.098
	Latency Days (Dark and White)	0.26 (-0.14/0.66)	0.204	1.271	0.204
	Latency Days (Lit and White)	0.16 (-0.13/0.44)	0.146	1.086	0.278

Table 2.5. 2020 insect lightscape use model results. GLMMs using log-links were fitted for each order captured in UV bucket traps. All terms containing colons represent interaction terms between the two variables on either side of the colon. 95% confidence intervals for each parameter estimate are listed parenthetically.

Order	Term	Estimate	Std. Error	z value	Pr(>|z|)
Acari	Site (Intercept)	1.7 (0.73/2.67)	0.496	3.425	0.001
	Ordinal Date	1.57 (1.04/2.1)	0.271	5.789	7.07x10^{-9}
	Moon Illum.	-0.14 (-0.42/0.15)	0.146	-0.947	0.344
	Site Classification	-0.26 (-1.48/0.95)	0.620	-0.421	0.674
	Color	0.57 (-0.21/1.34)	0.396	1.429	0.153
	Site Classification : Color	-0.63 (-1.62/0.36)	0.504	-1.248	0.212
Coleoptera	Site (Intercept)	-0.24 (-0.97/0.48)	0.370	-0.655	0.513
	Ordinal Date	0.64 (0.26/1.02)	0.193	3.311	0.001
	Moon Illum.	0.08 (-0.12/0.29)	0.104	0.777	0.437
	Site Classification	0.98 (-0.02/1.98)	0.510	1.928	0.054
	Color	1.81 (1.29/2.34)	0.267	6.782	1.19x10^{-11}
	Site Classification : Color	-0.15 (-0.86/0.57)	0.366	-0.402	0.688
Diptera	Site (Intercept)	3.51 (2.77/4.26)	0.382	9.197	3.68x10^{-20}
	Ordinal Date	1.63 (1.34/1.92)	0.148	10.973	5.13x10^{-28}
	Moon Illum.	-0.26 (-0.45/-0.06)	0.098	-2.611	0.009
	Site Classification	0.26 (-0.84/1.37)	0.563	0.469	0.639
	Color	1.24 (0.78/1.69)	0.231	5.348	8.88x10^{-8}
	Site Classification : Color	-0.77 (-1.41/-0.12)	0.330	-2.319	0.020
Ephemeroptera	Site (Intercept)	0.01 (-1.43/1.44)	0.733	0.007	0.994
	Ordinal Date	0.02 (-0.74/0.77)	0.384	0.044	0.965
	Moon Illum.	-0.95 (-1.39/-0.5)	0.228	-4.162	3.16x10^{-5}
	Site Classification	0.71 (-0.69/2.1)	0.711	0.993	0.321
	Color	2.51 (1.19/3.83)	0.674	3.721	0.0002
	Site Classification : Color	-0.87 (-2.27/0.54)	0.718	-1.205	0.228
Hemiptera	Site (Intercept)	1.25 (0.64/1.86)	0.309	4.039	5.37x10^{-5}
	Ordinal Date	0.82 (0.31/1.33)	0.262	3.129	0.002

	Moon Illum.	0.35 (0.08/0.61)	0.135	2.581	0.010
	Site Classification	0.27 (-0.6/1.14)	0.443	0.605	0.545
	Color	0.96 (0.33/1.58)	0.318	3.007	0.003
	Site Classification : Color	0.87 (-0.09/1.83)	0.491	1.774	0.076
Hymenoptera	Site (Intercept)	0.82 (0.36/1.27)	0.232	3.516	0.0004
	Ordinal Date	0.41 (0.05/0.78)	0.186	2.225	0.026
	Moon Illum.	-0.17 (-0.35/0.00)	0.089	-1.937	0.053
	Site Classification	-0.24 (-0.86/0.38)	0.317	-0.769	0.442
	Color	1.17 (0.77/1.57)	0.204	5.734	$9.83x10^{-9}$
	Site Classification : Color	-0.09 (-0.74/0.56)	0.332	-0.271	0.786
Lepidoptera	Site (Intercept)	3.2 (2.87/3.54)	0.171	18.699	$5.02x10^{-78}$
	Ordinal Date	1.21 (0.99/1.43)	0.113	10.734	$7.02x10^{-27}$
	Moon Illum.	-0.36 (-0.5/-0.22)	0.072	-5.067	$4.04x10^{-7}$
	Site Classification	0.17 (-0.3/0.64)	0.241	0.697	0.486
	Color	1.13 (0.82/1.45)	0.162	7.002	$2.53x10^{-12}$
	Site Classification : Color	0.17 (-0.3/0.65)	0.242	0.714	0.476
Trichoptera	Site (Intercept)	0.33 (-0.36/1.02)	0.352	0.941	0.347
	Ordinal Date	3.6 (3.14/4.05)	0.232	15.491	$3.96x10^{-54}$
	Moon Illum.	-0.5 (-0.73/-0.27)	0.118	-4.236	$2.27x10^{-5}$
	Site Classification	1.21 (0.33/2.09)	0.450	2.693	0.007
	Color	1.59 (1.01/2.17)	0.296	5.362	$8.23x10^{-8}$
	Site Classification : Color	-0.15 (-1/0.69)	0.432	-0.356	0.722
Total	Site (Intercept)	4.34 (3.87/4.81)	0.240	18.091	$3.73x10^{-73}$
	Ordinal Date	1.63 (1.38/1.88)	0.127	12.848	$8.78x10^{-38}$
	Moon Illum.	-0.32 (-0.48/-0.15)	0.083	-3.817	0.0001
	Site Classification	0.25 (-0.42/0.93)	0.346	0.731	0.465
	Color	1.19 (0.81/1.57)	0.192	6.181	$6.36x10^{-10}$
	Site Classification : Color	-0.27 (-0.82/0.28)	0.281	-0.975	0.330

CONCLUSION

The research in this thesis is aimed at providing information for the management of bats and insects throughout Grand Teton National Park as well as the broader GYE. To better understand basic habit use patterns for the bat species of the park, we monitored bat activity using passive acoustic monitors and modeled nightly activity with respect to both natural and anthropogenic landscape features. We found that *E. fuscus* and *M. volans* had a positive relationship with porous buildings, *M. lucifugus* were more active nearby water sources, and *M. volans* activity was positively related to largely forested microhabitat. Additionally, the package we developed (EcoCountHelper) makes GLMM-based analyses that are often suitable for analyzing ecological count data (such as bat calls per site-night) more accessible to managers. Following our park-wide research, we monitored bat and insect activity while illuminating our study area with either red or white light to assess red light's ability to mitigate artificial light's impacts on bats and insects. We found that red light may not lead to more natural behavior from bats in Grand Teton, however red light reduced insect sample counts in lit areas compared to sample counts during white-lit treatments.

Perhaps our most important finding from our park-wide research was that bats increase activity in areas surrounding porous buildings that have the potential to allow bats to enter and roost within the structures. Due to the interdimensional nature of this finding (both natural and social implications), it is important that more information surrounding this issue be procured. Future research regarding bat habitat use should aim to assess mitigation techniques to manage the intersection between historically managed buildings, human-occupied structures, and bat roosting habitat. While we suggest sealing buildings of this nature to limit human-wildlife conflicts, this is only a temporary solution, and one that favors humans. Many bat populations in the park may rely on human-occupied structures for roosting, and attempting to exclude bats from these buildings may be futile and costly, or if successful, could displace bats to other buildings or leave the population at risk of not having adequate roosting habitat. To ensure human-bat conflicts are limited while also ensuring adequate roosting habitat for bats, a better understanding of methods for dissuading bats from roosting in human-occupied buildings, as well as alternative roost habitat improvements (e.g., bat boxes, unoccupied buildings intentionally maintained for bat roosting) are necessary.

Future work focusing on red light as a means of mitigating the effects of artificial light on bats and insects should expand on multiple aspects of our research. While we were able to show the effects of red light in a relatively short treatment period, this may not be entirely indicative of the effect sizes that would be observed if white lights were entirely replaced with red lights. Future research should attempt to implement longer treatment periods to ensure that bat populations have adequate time to manifest responses to changes in lighting. Additionally, the relatively close proximity of our dark control sites to our lit sites made immigration between dark and lit sites possible for individual bats, and thus we were forced to include complicated interaction terms in our models to account for non-independent activity between dark and lit sites. Additional research regarding the effect of artificial lighting on bats and insects that changes lighting treatments should attempt to ensure that dark controls are sufficiently far away from lit sites so that sites are properly independent.

Collectively, this work serves as a source of information not only for managers in Grand Teton National Park to conserve bat and insect populations, but also for land and wildlife managers throughout the greater GYE and other public land managers in areas with similar bat community assemblages. Furthermore, with an ever-growing wildland-urban interface and frequent interactions between humans and wildlife, our research highlights the need for more research exploring conservation tactics that balance the habitat needs of bats and insects with the desires of humans utilizing their habitat.

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