

ARTIFICIAL NIGHT LIGHTING AND ANTHROPOGENIC NOISE ALTER ANIMAL ACTIVITY,
BODY CONDITION, SPECIES RICHNESS, AND COMMUNITY STRUCTURE

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ABSTRACT

Artificial night lighting and anthropogenic noise alter animal activity, body condition, species richness, and community structure

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Sensory pollution from artificial night-lighting and anthropogenic noise have increased at a dramatic rate over the last several decades. Alterations to the sensory environment have been found to affect wildlife in a wide variety of ways including behavioral changes, physiological responses, changes in species interactions, and altered community structure. Increased levels of light and noise pollution can originate from many sources including roads, energy development and infrastructure, and urbanization. Even remote or protected areas are not immune to the effects of increased sensory disturbances with 63 percent of protected areas within the United States found to have been exposed to a doubling of background noise levels due to anthropogenic activity and skyglow, the scattering of artificial light by the atmosphere, extending hundreds of kilometers from the source. Despite a large body of work investigating the effects of light or noise pollution acting alone, relatively few studies have examined the effects of both stimuli acting together even though they frequently co-occur. Better understanding how these stressors, especially when present simultaneously, are affecting ecosystems is critical to ongoing mitigation and conservation efforts.

In Chapter 1, we investigated the effects of increased levels of light and noise pollution, both singularly and in tandem, on pinyon mouse (*Peromyscus truei*) activity and body condition. Using a full factorial study design allowed us to isolate the effects of both stimuli when acting alone as well as any potential interactions between the two when both were present. We used standard trapping methods across a gradient of light, noise, and both combined while also accounting for variations in moonlight, vegetative structure, and weather. We found that an increased level of artificial night-lighting resulted in lower trap success of pinyon mice while there was no effect of noise on trap success. There was no effect of elevated light levels on body condition but there was a negative effect of noise on body condition early in the season. Later in the season, neither light nor noise influenced body condition. No interactive effects between light and noise were found.

In Chapter 2, we studied the effects of anthropogenic light and noise, singularly and in tandem, on species richness and community structure using camera traps in a manipulative field experiment. We investigated these effects at both the species level and the taxonomic level (nocturnal mammals, diurnal mammals, lagomorphs, birds, mesocarnivores, and ungulates). We showed that both light and noise pollution did alter species richness and that these effects can differ depending on the scale of observation. Increased levels of night-lighting had a scale-dependent effect on species richness such that increases in light levels had a negative effect on richness at the camera level, but light-treated sites had the highest estimated cumulative richness. In contrast, noise was found to have a negative effect on richness for birds. When both stimuli were present, the addition of night-lighting mitigated the effects of noise for birds. For community structure, noise-treated sites were the most dissimilar from other treatments, indicating that increased levels of anthropogenic noise likely have the largest effect on community structure in this study. We also found evidence of a possible rescue effect of light that counteracts the negative effect of noise. That is, combined treatment sites were significantly dissimilar from both light and noise sites but not from the control sites.

Together, our results provide evidence that alterations to the sensory environment from anthropogenic activity can affect wild animal populations in multiple ways. As human development increases to meet the demands of growing human populations, more ecosystems will be exposed to increased levels of sensory disturbance, making the understanding of how these changes affect wildlife critical to ongoing conservation efforts.

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CHAPTER 1

NIGHT LIGHTING AND ANTHROPOGENIC NOISE ALTER THE ACTIVITY AND BODY CONDITION OF PINYON MICE (*PEROMYSCUS TRUEI*)

1.1 INTRODUCTION

Human development has grown at a dramatic rate over the last century, accompanied by a substantial increase in the amount of artificial night lighting and anthropogenic noise (reviewed in Swaddle et al. 2015). Alterations to the sensory environment from light or noise pollution have been shown to have significant effects on a wide range of animals including changes in behavior (Bird et al. 2004, Shannon et al. 2014), physiology (Du et al. 2010, Gaston et al. 2013), and community structure and species interactions (Jung et al. 2020, Francis et al. 2012, Davies et al. 2012). Anthropogenic noise has become highly pervasive throughout North America, even within protected areas: 63 percent of protected areas within the United States have experienced a doubling of background noise levels due to anthropogenic noise (Buxton et al. 2017, 2019). There has been a similar dramatic increase in the amount of artificial light. More than 80 percent of the world's human population lives under light-polluted skies (Falchi et al. 2016) and skyglow, the scattering of light by the atmosphere, can extend dozens to hundreds of kilometers from the source (Kyba and Hölker 2013). Many natural systems are predominantly organized by daily and seasonal cycles of light and dark (Kronfeld-Schor et al. 2013) and any disturbance or alteration to these cycles could have wide-ranging ecological effects.

One way in which animals may respond to altered sensory environments is through risk avoidance behavior in response to perceived predation risk (reviewed in Frid and Dill 2002). Many studies have found a reduction in the activity of small mammals in response to increased levels of ambient light (reviewed in Prugh and Golden 2014). For example, Bird et al. (2004) found that beach mice (*Peromyscus polionotus leucocephalus*) removed fewer seeds from resource patches as the intensity of light at the resource patch increased, likely due to an increased perceived risk associated with foraging in brightly lit areas. Additionally, other *Peromyscus* species shift their activity away from open areas to areas with dense cover in the presence of increased simulated moonlight, which has also been interpreted as a response to

perceived risk of predation (Blubaugh et al. 2017). The decision to engage in foraging activity represents a tradeoff between the physiological demands of resource acquisition and the risk of predation or injury (MacArthur and Pianka 1966). These responses suggest that alterations to the sensory environment can influence the tradeoff between physiological demands of resource acquisition and risk of predation by changing the real or perceived predation risk of an area. Importantly, perceived risk does not necessarily reflect actual risk as shown by a recent meta-analysis that found the presence of an actual predator did not have as strong of an effect on foraging activity relative to habitat structure (Verdolin 2006). Some limited evidence suggests that an increase in light intensity represents an increase in actual predation risk rather than just perceived risk. Clarke (1983) found that an experimental increase in the amount of light within a flight chamber led to decreased activity of deer mice (*Peromyscus maniculatus*) and higher capture rates and greater predation efficiency by short-eared owls (*Asio flammeus*). While the results of this study provide evidence of increased predation risk from brightly lit conditions, there remains a need for field-based, manipulative experiments to fully assess the effects of light on activity levels that could reflect changes in perceived predation risk in a natural setting.

As with artificial light, animals respond to changes in the acoustic environment in a variety of ways. Increased levels of artificial noise can mask important signals used in both inter- and intra-specific communication (Barber et al. 2010). For instance, noise can interfere with predator detection of adventitious acoustic cues generated by prey, resulting in reduced hunting success (Mason et al. 2016, Senzaki et al. 2016). The same is likely true for a variety of interactions in which one species takes advantage of public information through eavesdropping on other species. However, the degree to which community dynamics and ecosystem function are influenced by community members' ability to detect and use public information remains poorly understood (Danchin et al. 2004). Despite the potential negative effects of elevated ambient noise levels, it is also possible for animals to experience benefits from increased human activity through predator shielding (Berger 2007). Past work in New Mexico has shown that Woodhouse's scrub jays (*Aphelocoma woodhouseii*), a major nest predator, strongly avoid noisy sites and that

songbird nest success is increased due to their avoidance (Francis et al. 2009). Some species even preferentially nest close to noise, potentially to avoid predation (Francis et al. 2009, 2011).

Despite many studies examining the effects of elevated levels of light and noise separately, far fewer have examined the effects of both stimuli acting together despite the fact that they frequently co-occur (reviewed in Halfwerk and Slabbekoorn 2015, Swaddle et al. 2015, Dominoni et al. 2020). From the few that have evaluated both stimuli together, it appears that light and noise can interact to influence anti-predator behavior (Chan et al. 2010) and host-parasite interactions (McMahon et al. 2017), but that noise and not light influences the timing of dawn song in rufous-collared sparrows (*Zonotrichia capensis*) (Dorado-Correa et al. 2016). These studies suggest that there is much to learn from studies that consider multiple sensory stressors at once, as knowledge of whether responses to one stimuli dominate or if the responses reflect additive, synergistic or antagonistic effects (reviewed in Piggott et al. 2015) will be essential for proper mitigation measures.

In this study, we sought to determine if and how artificial night lighting, anthropogenic noise and the combined stimuli influence activity and body condition of pinyon mice (*Peromyscus truei*). We used a study system that allowed us to isolate the effects of increased light and noise from one another and from additional potentially confounding variables. Because past studies have shown that rodent activity decreases with increased light exposure (e.g. Kramer and Birney 2001, Sone 2002, Bird et al. 2004), we expected that trap success would decline with increased light exposure. In contrast, we expected to see an increase in trap success with increases in noise levels because past work in this system found an increased number of detections of *Peromyscus* mice consuming and harvesting piñon (*Pinus edulis*) seeds in noisy relative to quiet areas (Francis et al. 2012), perhaps due to a reduction in predation risk and/or a release from competition with species that are more sensitive to noise such as Woodhouse's scrub jays (Francis et al. 2009) or other avian competitors. Because of the opposing predictions for the effects of noise and light on trap success, we expected co-occurrence of the two stimuli to have opposing effects on trap success and lead to intermediate levels of trap success that should be similar to those at quiet and dark traps. Additionally, if noise releases *Peromyscus* mice from

predation and interspecific competition with noise-sensitive avian species, body condition of individuals from noiser areas could be higher than those of individuals captured in quieter areas. If overall activity, including foraging activity, decreases with increased exposure to light, animals captured in brightly lit areas could have lower body conditions than animals captured in darker areas. Finally, we expected exposure to increased levels of both light and noise to lead to intermediate body condition values due to the opposing effects of light and noise.

1.2 MATERIALS AND METHODS

1.2.1 Study area overview

Our study took place within the Rattlesnake Canyon Habitat Management Area (RCHMA) located in northwestern New Mexico (Figure 1.1). This area is managed by the Bureau of Land Management (BLM) and consists mostly of mixed pinyon pine (*Pinus edulis*) - juniper (*Juniperus osteosperma*) woodland interspersed with patches of great basin sagebrush (*Artemisia tridentata*) shrublands. Within this landscape there are numerous natural gas wells and corresponding infrastructure (e.g., roads, pipelines, etc.). Some well pads are paired with a large compressor, creating high amplitudes of industrial noise that run for 24 hours a day, 365 days a year, except for short periods of maintenance, creating a mosaic of quiet wells that lack noise-generating compressors and noisy wells with compressors. Although wells with and without compressors differ in anthropogenic noise, previous work has shown that they do not differ in major vegetation features (Francis et al. 2009, 2012) and also do not systematically differ in human visitation or the presence of other major infrastructure on the well pad. Because night lighting of well pads is rare within RCHMA and none of our sites were illuminated prior to the start of the experiment, we were afforded the opportunity to experimentally manipulate lighting conditions at both quiet and noisy sites. This allowed us to create a full-factorial study design consisting of six locations (henceforth termed “clusters” as described below and in Figure 1.1), each with four different sites (treatments): light alone, noise alone, light and noise together, and a quiet, dark control. By using existing compressors as a noise source, this design allowed us to test the effect of the introduction and addition of light as a novel stimulus whereas any effects from noise would be

due to chronic, long-term exposure. To control for landscape-scale variation in environmental variables, sites were geographically demarcated into clusters such that each of the six geographic clusters included one site of each treatment type (Total 24 sites grouped into six clusters, with four treatments per cluster; Figure 1.1). Sites were a minimum of 375 meters apart.

Prior to any trapping, for each experimentally illuminated site a total of five light towers were placed at randomly assigned directions and distances between 75 and 150 meters from the center of the well pad, defined as the location of the compressor on noisy sites and the pump jack or well head on quiet sites (Figure 1.2A). Each light tower consisted of a 3-meter metal pole to which two 400 lumen, white, 54 LED flood lights with 6V/6W polysilicon solar panels were attached to power the lights over the duration of the study during all nighttime hours.

1.2.2 Trapping protocol

Trapping began on 6 April 2019 and occurred in two distinct sessions: three clusters from 6 April 2019 - 5 May 2019 and the remaining three clusters from 30 June 2019 - 24 July 2019. We also re-trapped one of the original three clusters a second time during the second session. At each light tower at the lit sites, trap stations were placed at a distance of two, eight, ten, and 15 meters from the base of the towers at 90 degrees from one another and a minimum of 5 meters from one another in a design that optimized exposure to a gradient of light exposure levels (Figure 1.2b). This design was replicated at each of the five light towers giving a total of 20 stations and 40 traps per site. At dark sites, the pattern of trap placement was replicated on sampling locations that were 72 degrees from one another and located at a randomly generated distance between 75 and 150 m from the center of the well pad (Figure 1.2a). This pattern was repeated at each of the six clusters giving a total of 120 stations and 240 traps per treatment.

Each of the chosen locations was trapped for a total of three sequential days per trapping session. Folding Sherman live traps were baited with rolled oats shortly before sunset and checked the subsequent morning just after sunrise. A small amount of synthetic batting was added to each trap to provide insulation for captured animals during cold nights. Upon checking traps, we transferred any captured animals from the trap into a clear, plastic bag. We tagged

each animal with a uniquely coded numeric metal fingerling ear tag for re-identification. We identified each individual to species and determined sex, breeding condition, and life history stage (adult, subadult, or juvenile) through visual inspection. We also measured mass to the nearest gram with a Pesola spring scale along with head and body length, tail length, hindfoot length, and ear length with a ruler (mm). We then released each animal at the point of capture. We repeated all measurements on any recaptured animals. Non-target species that were captured, such as chipmunks and rabbits, were not processed and were immediately released at the point of capture. Traps that were closed upon arrival but contained no animals were recorded as tripped traps.

During the first three-day trapping session at each site, the lights remained off. This allowed us to assess baseline activity prior to introducing lights to the system. Lights were turned on three days after the final day of the first session of trapping and remained on for the remainder of the study. A followup three-day trapping session was performed at each of the three initial clusters ten days after the first session concluded and 7 days after the lights were turned on. Late-season trapping began on 30 June 2019 and continued through to the end of July. Only one three-day trapping session per site was conducted during these surveys because lights had already been installed and turned on. Trapping protocols and methods remained consistent with early season trapping. All trapping and handling protocols received approval from the Institutional Animal Care and Use Committee (protocol 1903).

1.2.3 Variable measurements

Although our sites were established as controls, lit, noisy or both, noise and light were quite variable on sites where they occurred, necessitating quantification of received levels at trap stations. Noise measurements were taken at each trap location using a Larson Davis Model 831 Type 1 Sound Level Meter. Measurements were taken with the microphone held approximately 0.5 meters above the ground. Care was taken to ensure that the ambient noise level during the measurement was representative of the overall noise environment and did not include any sporadic noise sources, such as airplane flyovers or high winds, that could increase the

measured noise level. At each trap, a measurement was taken for one minute with the average noise level in both A-weighted and Z-weighted equivalent noise level (L_{eq}) being recorded. A-weighting is based on perceived loudness by the human ear such that frequencies between 10 Hz and 20 kHz that are less readily transduced by the ear will bear less weight in the sound level measurement. Z-weighting, on the other hand, is a flat, unweighted response between 10 Hz and 20 kHz. Although longer or additional measurements would be ideal to characterize noise levels at each location, previous work in this system suggests that short measurements capture general ambient noise conditions in this system (Kleist et al. 2018). See supplemental Table S1 for a summary of noise measurements.

Light measurements were taken using a Konica-Minolta T-10A Illuminance Meter at all illuminated trap locations, but not dark locations, because light levels on moonless nights were below the response minimum of the unit (i.e., 0.01 lux). As such, light levels at dark locations were assigned lux values of zero. All light measurements took place a minimum of one hour after sunset to ensure no residual sunlight was detected. For each measurement, the light meter was placed flat on the ground facing up. An acclimation period of three seconds was used before recording the lux level. See supplemental Table S1 for a summary of light measurements.

To investigate how different habitat types could influence pinyon mouse abundance and activity, land cover data were obtained from the 2016 U.S. National Land Cover Database (Homer et al. 2015), providing 30 m resolution of major land cover classes. The trap location coordinates were overlaid onto the land cover data and the land use type of the grid in which each point occurred was extracted using the *extract* function in the Raster package version 3.0-12 in *R* (Hijmans et al. 2019). Within the study area the most common land cover classes were mixed evergreen forest and shrubland. Two categories of developed land (low and moderate intensity) were combined into a single development category.

To investigate potential effects that weather related variables had on trap success we obtained local weather data through a NOAA Geostationary Operational Environmental Satellites (GOES) Data Collection Platform (DCP), which was located just northeast of the study area (36.9769°, -107.62830°) and ranged from approximately 2.75 to 12.85 kilometers from our sites.

Hourly weather data were obtained for each night that trapping occurred. We obtained both categorical and continuous data on the moon phase for each trap night using the lunar package version 0.1-04 in *R* (Lazaridis 2014). Specifically, for each night, the moon phase was determined as a four-level factor, a six-level factor, and a numerical variable representing the percent face of the moon. The duration of time that the moon was above the horizon was calculated using the moon rise/set and sunrise/set times which were obtained through the suncalc package version 0.5.0 in *R* (Thieurmél and Elmarhraoui 2019). The duration of each night was also calculated. We created a moon index by first calculating the proportion of the night that the moon was above the horizon then by multiplying that number by the numerical moon phase variable. This created a new variable that ranged from zero, which could represent a new moon or moon below the horizon at night, to one, which represented a full moon in the sky for the entire night (Figure 1.3b).

1.3 DATA ANALYSIS

1.3.1 Activity

We used binomial generalized linear mixed-effects models to analyze trap success using the *glmer* function from the lme4 package version 1.1-21 in *R* (Bates et al. 2019). Each trap was assigned a one if an animal was captured or zero if the trap was empty for each night that the trap was deployed at each trap station (4,800 trap nights total). Trap location nested within site were treated as random effects for all models to account for the nested nature of the study design. Cluster was initially also included as a random effect, with both site and trap location nested within cluster. However, estimated variance of cluster was equal to zero and it was removed as a random effect from subsequent models (Bates et al. 2018). Trap rates were calculated as the number of captures per night divided by the total number of traps deployed per night.

In our first step of model selection, we evaluated the support of individual variables pertaining to three broad hypotheses of how environmental factors, including noise and light, influence small mammal activity and, hence, trap success (see below and Tables 1, 2). Because trapping occurred in two distinct sessions, we included a predictor classifying each trap night as

either early or late season. We included season and minimum overnight temperature as variables in models for all of the hypotheses because although they were not explicitly related to our study objectives, past studies suggest they have an important influence on *Peromyscus truei* activity (Marten 1973, Scheibe 1984). For each hypothesis category we used the *dredge* function from the package MuMIn version 1.43.15 (Bartoń 2019) in *R* to select the best fitting models containing the subset of variables pertaining to each category. Models were ranked by AICc to determine which models were most competitive and were considered highly competitive if the $\Delta\text{AICc} \leq 2$ from the top model.

We considered several competing models representing moonlight. Competing models were created for each of the moon variables (4- and 6-level factors and numerical) interacting with moon duration, plus a fourth model using the calculated moon index variable which incorporated both the moon phase and duration. All models also contained the environmental variables of minimum overnight temperature and season. We built a model reflecting variation in vegetation using the land cover data, minimum overnight temperature, and season. Finally, we built models pertaining to our main objectives that included either LAeq or LZeq with an interaction with lux, plus season and minimum overnight temperature.

Parameters that 1) appeared in highly competitive models (i.e., $\leq 2 \Delta\text{AICc}$ from the top model) for each of the individual hypotheses and 2) had 85% confidence intervals (CIs) that did not contain zero were considered to have an effect and included in the final omnibus model. To investigate potential interactions between variables, we also explored interactions between lux and moon phase, lux and noise, lux and land cover, land cover and moon phase, noise and land cover, and moon phase and noise. For models including categorical moon phase variables, we switched the reference state (i.e., new moon to full moon) to obtain estimated differences across all phases. Finally, to assess the strength of predictor effects, we considered those with 85% CIs that did not cross zero as having evidence of an effect that warranted consideration for inference and those with 95% CIs that did not overlap zero as having more precise evidence of effect.

To evaluate whether the inclusion of the tripped traps in the original analyses affected the results in any significant way, all of the analyses were rerun using a dataset that excluded all

tripped traps. The results of these analyses were consistent with the original models containing the tripped traps. As such, the models presented in the results include all traps. Finally, to determine whether analysis of unique individuals may differ from overall activity, we also ran the analysis with all recaptured individuals removed from the analysis so that each individual was only represented once in the dataset.

1.3.2 Body condition

We used linear mixed-effects models to analyze body condition using the *lmer* function from the lme4 package version 1.1-21 in *R* (Bates et al. 2019). Because variation in anthropogenic noise was a relatively permanent feature in our study design, we first assessed the body condition of animals captured only during the initial trapping sessions before lights were turned on to assess the singular effect of noise on body condition. To assess the effects of both light and noise, we then built models using only late-season captures because, at that point, lights had been turned on for a minimum of eight weeks. To assess body condition, we constructed a scaled-mass index (SMI) using the weight and head-and-body length of each captured individual (Peig and Green 2009). This was done by 1) creating a log-log plot of mass versus length; 2) fitting a line to the mass and length data and using the resultant slope divided by the Pearson's correlation coefficient r as the power function in the SMI formula; 3) calculating the mean length which is used as a constant in the SMI equation; and 4) calculate the SMI for each individual. We also created a new variable, class, that combined the age and breeding condition for each individual into three categories: non-adults, non-breeding adults, and breeding adults. Any females captured that appeared pregnant were removed from the analyses. Two competing models, one using LAeq and one using LZeq, were created to determine which noise measurement best fit the data. For the early-season analysis, models were then constructed using the scaled-mass index as a response with the noise levels and land cover classification of the trap location as well as the sex and class of the individual trapped. For the late-season analysis, models were constructed using the same variables with the addition of the lux value measured at each trap. No non-adult animals were captured during the early season trapping

sessions so the class variable consisted of only two levels, breeding adult and non-breeding adult, for this analysis. To investigate potential interactions between variables, several post hoc models were constructed to investigate potential effects between noise and sex, noise and landcover, sex and class, and sex and landcover (Table S3). We also evaluated the interaction between lux and noise, lux and landcover, and lux and sex for the late-season analysis (Table S3). As with trap success, we used 85% and 95% CIs for inference on the presence and precision of effects.

For all analyses, we evaluated model performance by simulating scaled residuals and visualizing qqplots using the DHARMA package version 0.2.7 (Hartig 2019). We also used the *check_collinearity* function in the performance package version 0.4.6 (Lüdecke et al. 2020) in R to inspect final models for potential problems with multicollinearity, but found all models to have variance inflation factor values < 5, suggesting no issues of multicollinearity (Dormann et al. 2007). All analyses were performed using R (R Core Team 2019). In the results, we present parameter estimates from the top-ranked model in which that parameter appeared, but also report other highly competitive models (i.e. $\Delta AICc \leq 2$).

1.4 RESULTS

Four species of interest were captured during the field season: Pinyon mice (*Peromyscus truei*; captures = 374, individuals = 191), deer mice (*Peromyscus maniculatus*; captures = 38, individuals = 24), brush mice (*Peromyscus boylii*; captures = 3, individuals = 1), and Mexican woodrats (*Neotoma mexicana*; captures = 5, individuals = 3). Of these, only pinyon mice occurred in high enough abundance for formal analysis. Mean trap rate of pinyon mice (number captured per day divided by total number of traps set) was 7.8% (range: 1.9% - 15.0%).

1.4.1 Activity

Of the competing models containing the various moonlight variables, the model that contained the 6-level categorical moon phase variable was the most competitive and was therefore used in further analyses. Model selection resulted in two highly competitive models and

both contained moon phase (Table 3). Because moon phase had an effect on trap success, it was included in the omnibus model. Model selection of the land cover model resulted in two highly competitive models. The top ranked model was the fully parameterized model containing season, minimum overnight temperature, and land cover while the second-ranked model contained only season and temperature variables (Table 3). Because both season and minimum overnight temperature had an effect on trap success, they were included in the omnibus model. Because land cover did not have an effect on trap success, it was not included in further models. Model selection of the competing disturbance models resulted in two highly competitive models (Table 3). The top ranked model contained lux plus the environmental variables while the second also included LZeq. Because lux had an effect on trap success, it was included in the omnibus model. Because neither of the noise variables had an effect on trap success, they were not included in further models.

Model selection of the omnibus model that included season, minimum overnight temperature, lux, and moon phase resulted in two models with strong support (i.e., $\Delta AICc \leq 2$) (Table 4). In both models, lux and moon phase were the only variables to have an effect on trap success and the only variables to appear in all competitive models. None of the interactions had effects with 85% CIs that did not overlap zero and none of the post hoc models were competitive based on AICc scores.

All supported models suggested that the lux level had a negative effect on trap success ($\beta = -0.62$, 95% CI = -1.24, -0.01; Figure 1.3a) such that the probability of capturing a pinyon mouse decreased by 0.316 with each increase in lux by one. Relative to a new moon, trap success was lower during a waxing crescent (reference state new moon: $\beta = -0.68$, 95% CI = -1.26, -0.09), but not during a waxing gibbous (reference state new moon: $\beta = -0.25$, 95% CI = -0.75, 0.26), full moon (reference state new moon: $\beta = -0.23$, 95% CI = -0.68, 0.22), or waning gibbous (reference state new moon: $\beta = 0.57$, 95% CI = -0.05, 1.20; Figure 1.3a, Table 1.5). Once the moon reached a waning crescent phase, trap success began to increase (reference state new moon: $\beta = 0.67$, 95% CI = 0.11, 1.24; Figure 1.3a, Table 1.5).

To aid in the interpretation of these changes in trap success across the lunar cycle, to our top supported model we substituted an ordinal rank variable for moon phase and modeled the ordinal rank as a third-order polynomial in a *post hoc* analysis. To create the ordinal variable, the moon phases were ranked from one to eight where one denoted the new moon, five represented the full moon, and eight was equal to the waning crescent. This model was competitive with the top-ranked model with 6 categories of moon phase ($\Delta\text{AICc} = 0.39$) and facilitated visualization of changes in trap success across the lunar cycle (Figure 1.3c). Both approaches revealed that there was a pattern of a decrease in trap success with the initial appearance on moonlight, followed by an increase back to original levels as the moon continued to increase. This was then followed by an increase in trap success as the moon began to wane again. For all models, trap success did not differ strongly between early and late season trapping sessions ($\beta = -0.03$, 95% CI = -0.41, 0.34) and the effect of minimum overnight temperature was negligible ($\beta = 0.003$, 95% CI = -0.01, 0.02).

Model selection of the omnibus model using only newly captured individuals resulted in seven competitive models, four of which were highly competitive (Table S2). Results were qualitatively very similar to the models built with all captures. The effect size was nearly the same as the model with all captures, although the precision of the estimate was lower ($\beta = -0.59$, 85% CI = -1.12, -0.05; Table S2). There was also a positive effect of minimum overnight temperature, but the effect size was very small ($\beta = 0.01$, 85% CI = 0.004, 0.025; Table S2) and there were some differences in the effect of moonlight (Table S2).

1.4.2 Body condition

Among models explaining body condition for the early-season analysis, the model built using the LAeq variable (AICc = 202.42) was more competitive than the model built using the LZeq variable (AICc = 206.26). Of the interactions tested, only the interaction between sex and land cover had an effect (Table S3). Therefore, we included this interaction in our omnibus model. Model selection of the omnibus model resulted in two highly competitive models (Table 6). From the top ranked model, LAeq had a negative effect on body condition ($\beta = -0.15$, 95% CI = -

0.24, -0.05), males had higher body condition than females (reference state female: $\beta = 1.81$, 95% CI = 0.44, 3.18), and animals trapped in shrubland areas had higher body condition than those trapped in woodland areas (reference state woodland: $\beta = 1.91$, 95% CI = 0.63, 3.20) (Figure 1.4a). Class had no effect on body condition (reference state breeding adult: $\beta = 0.54$, 95% CI = -0.75, 1.84; Table 1.6).

For the late-season body condition analysis, the model built using the LAeq variable (AICc = 466.16) was more competitive than the model built with the LZeq variable (AICc = 467.35). Of the interactions tested, only the interaction between sex and class and the interaction between LAeq and landcover had an effect (Table S3). Therefore, we included these interactions in our omnibus model. Model selection of the omnibus model resulted in a total five highly competitive models (Table 1.6). The top-ranked model was the model containing only the random effects. None of the variables in the highly competitive models had an effect on body condition (Table 1.6).

1.5 DISCUSSION

Despite the growing volume of work on the effects of light and noise pollution, most previous studies have focused on investigating the effects of only one of these stimuli (reviewed in Dominoni et al. 2020, Swaddle et al. 2015). Our findings are important in that they represent one of the few studies to investigate the effects of both light and noise pollution simultaneously (see also, Chan et al. 2010, reviewed in Dominoni et al. 2020) and are the first to experimentally investigate effects of the combined stimuli on a mammal. Furthermore, they add to the small but growing body of research on the effects of anthropogenic noise on small mammals (e.g., Shier et al. 2012, Francis et al. 2012). Specifically, although we found no interaction between the two stimuli, we found that light pollution reduced trap success and noise pollution had a negative effect on body condition on pinyon mice.

In our study, reduced trap success under high light conditions could be interpreted to reflect both numerical and functional responses in different contexts. Numerical responses could include changes in abundance or density while functional responses indicate changes in

behavior, including activity. Trap success has been used in previous studies as a proxy for activity levels (e.g. Price et al. 1984, Upham and Hafner 2013); however, the degree to which trap success reflects all aspects of activity is still unclear (Prugh and Brashares 2010). Nevertheless, evidence suggests that rodent trap success generally corresponds to relative area use (Price 1977), but other factors, such as individual variation in willingness to enter traps or the visibility of traps under different light conditions, could act as confounding variables. Here, our methods cannot clearly distinguish between numerical and functional responses. However, responses to particular predictors can be interpreted with greater certainty. For instance, it is unreasonable to assume that the density or abundance of pinyon mice (i.e., a numerical response) fluctuates with the lunar cycle. As such, changes in trap success during different moon phases are likely driven by functional responses. Reduced trap success with elevated light exposure likely reflects avoidance of those areas. Over time, this behavioral response of avoiding lit areas could lead to a change in the abundance or density of pinyon mice, especially since anthropogenic light, unlike natural moonlight, is temporally constant in intensity every night in our system. Therefore, although our results provide some evidence of the effect of light on apparent activity levels, more fine scale activity data are likely needed to fully assess whether these sensory stressors have population-level effects in pinyon mice.

It is worth noting that in our study design, noise had been present on the landscape for a long period of time whereas light was introduced by us at the beginning of the experiment. As such, we could be measuring responses at different points along the response/habituation timeline for these two stimuli. Nevertheless, by the end of the study, light was a chronic feature. Understanding how responses to sensory pollution potentially change over time is another area of needed research. Also, the wavelength of artificial light varies from that of natural light and *Peromyscus* mice have been shown to respond differently to different wavelengths of light (Bird et al. 2004). Given the recent move towards cheaper, cool LEDs for lighting, which emit a broad spectrum of wavelengths, it is especially important to understand how organisms respond to different wavelengths of light (Pawson and Bader 2014). However, despite these differences between natural and artificial light, we found that artificial light had a similar effect size on trap

success as did moonlight; a one lux increase in artificial light was roughly equivalent to the effect of waxing crescent relative to a new moon (Figure 1.3a, 1.3d). When considering only newly captured individuals, effects were largely equivalent, though the precision of the estimated effect was lower.

Previous studies have shown that rodents decrease activity under increased light conditions (Kramer and Birney 2001, Sone 2002, Bird et al. 2004), which likely reflects the improvement in hunting success under bright conditions among visually orienting predators (Clarke 1983). Supporting the influence of ambient light on small mammal activity, we not only found a strong influence of artificial lighting but also a strong influence of natural light from the moon, providing support for the risk avoidance hypothesis (Frid and Dill 2002). Relative to the new moon, which reflects the darkest conditions in the lunar cycle, trap success decreased with a waxing moon. However, as the moon continued to grow, trap success increased again, such that there was no difference in trap success between nights with a new moon and those with a full moon. Subsequent to a full moon, trap success further increased as moonlight illuminance decreased with the waning moon.

Pinyon mice are known to cache seeds (Hollander and Vander Wall 2004) and this stored food resource could allow them to minimize foraging activity when perceived predation risk is high. It is unknown whether these food caches are of limited size and therefore can only sustain an individual through part of the lunar cycle. If caches are limited, once they are depleted, individuals would need to emerge and resume foraging under lit conditions that are typically avoided due to elevated perceived predation risk. High trap success during the full and waning moon phases provides some support for this possibility. Additionally, it is possible that individual foraging decisions could be informed by present perceptions of risk relative to the most immediate past perceptions of risk. In the context of moonlight, this possibility is supported by the incremental decline in trap success during a waxing moon, which could correspond to incremental increases in perceived predation risk, and the increase in trap success during a waning moon, which could correspond to incremental decrease in perceived predation risk. Such a possibility could explain why trap success was different during waxing and waning moon

phases despite moonlight levels being roughly equivalent during these phases (Figure 1.3b). Thus, relative changes in moonlight, available caches, and metabolic needs could all influence activity patterns. Giving up density experiments that manipulate cache availability and accessibility over the lunar cycle may be a promising approach to testing these possibilities. Nevertheless, should the link between relative changes in moonlight, available caches and metabolic needs gain additional support through further study, it could help resolve conflicting results based solely on more simplified moon phase classifications (Prugh and Golden 2014).

In contrast to our predictions based on results from a previous study in this system that found an increase in foraging activity among *Peromyscus* mice at noisier sites relative to quiet ones (Francis et al. 2012), our results did not show any effect of noise on trap success. However, we did find that body condition declined as noise levels increased, which was opposite of our prediction (Figure 1.4b). One possible explanation for this finding could be changes in foraging behavior driven by alterations in the acoustic environment. However, if this were the case, we would expect lower trap success in noisy areas, which was not what we found. A study investigating the effects of noise from wind turbines on California ground squirrels (*Otospermophilus beecheyi*) found no difference in time spent above ground between quiet and noisy sites, but individuals in the noisy sites increased vigilance and tended to spend more time closer to their burrows (Rabin et al. 2006). Similarly, experimental exposure to sounds of rushing rivers, which are spectrally similar to anthropogenic noise, increased vigilance and decreased movement in the same species (Le et al. 2019). In these studies, increased vigilance and decreased movements were interpreted to reflect noise-induced increases in perceived predation risk and come at the cost of decreases in foraging activity. The decline in body condition among pinyon mice in our study could reflect the cost of elevated vigilance, although an increased reliance on visual surveillance for predators under low light conditions may not fully compensate for lost surveillance through audition.

Perhaps a more likely explanation is a direct, physiological effect of the noise itself. Increases in low frequency noise can have physiological effects on rodents by triggering stress responses (Du et al. 2010) and altering organ tissue (Branco et al. 2004), even if the frequency of

the noise is below the range at which the rodents can likely hear (see below). A similar pattern of reduced body condition or changes in stress hormones in noisy areas has been found in multiple bird species as well, providing further evidence that elevated levels of ambient noise can induce negative, physiological effects (Phillips et al. 2018, Kleist et al. 2018). If these or similar direct, physiological effects occur in natural systems from noise levels and frequencies that pinyon mice can or cannot detect, it could result in an equal use ecological trap where individuals do not avoid habitat that is ultimately deleterious (Hale and Swearer 2016). It is not clear how sensitive *Peromyscus* mice are to low frequency noise, with the hearing ability of other mice species having been shown to drop off at lower frequencies (Heffner and Masterton 1980, Heffner et al. 2001). Further research should attempt to determine whether lower body condition in noise exposed pinyon mice results from changes in behavior due to perceptions of risk, direct effects of noise on individual physiology or a combination of the two. Improved understanding of *Peromyscus* hearing sensitivities will be necessary to evaluate these possibilities.

Unlike our results from the early-season body condition analysis, there was no effect of either light or noise on body condition later in the season, in contrast to our predictions. The lack of an effect of noise on body condition later in the season could perhaps reflect the reduced metabolic costs of being active during the mild nights of the late season compared to the cold nights of the early season. The lack of an effect of light on body condition could be explained by the fact that, in this study system, light levels were much more variable across the landscape, possibly allowing mice to avoid the most brightly lit areas while still being able to forage effectively.

Besides the results pertaining to our hypotheses about noise and light exposure, we also found that individuals captured in shrubland areas had higher body condition scores than individuals captured in woodlands during the early part of the season. Pinyon mice have been shown to have a varied diet consisting of small arthropods, fungi, mammalian remains, and seeds of various plant species (Bradford 1974, Hoffmeister 1981, Maser and Maser 1987). Although we do not have any data on the arthropod and fungi communities in our system, perhaps shrubland areas offer a wider variety of food resources for pinyon mice, resulting in higher body condition.

The lack of a difference in body condition between land cover types later in the season could reflect increased primary productivity providing ample food resources across all habitat types during spring and summer months relative to late winter when food resources are scarce. Our results also suggest that males have higher body condition scores than females early in the season. For other rodent species, males have higher overall body weights upon spring emergence than females (Boswell et al. 1994). For males, the greatest energetic cost of reproduction comes early in the breeding season in the form of male-male competition and increased exploratory behavior to find mates whereas for females, the greatest energy demands come later in the season during gestation and lactation (Kenagy et al. 1989). It is possible that similar phenological differences explain the difference documented for males and females at the beginning of our field season.

1.6 CONCLUSION

Our results provide evidence that light and noise pollution from anthropogenic sources can affect both pinyon mouse behavior and body condition. Although our study did not uncover any antagonistic, additive, or synergistic effects (i.e. evidenced by an interaction) between light and noise for pinyon mice in our system, more work should be done examining both of these stimuli at once given the propensity of these stimuli to co-occur in space and time (reviewed in Swaddle et al. 2015, Dominoni et al. 2020). As the human population grows, more ecosystems will be exposed to increasing levels of anthropogenic noise and light making the understanding of how these stressors affect wildlife critical to ongoing conservation and management strategies.

Table 1.1: Names and descriptions of covariates included in trap success and body condition models.

Variable	Description	Direction of Predicted Effect
Seas	Season of trap night, early vs late	+
Tmin	Minimum overnight temperature	+
Lux	Light level measured at trap location	-
Laeq	A-weighted noise level at trap location	+
Lzeq	Z-weighted noise level at trap location	+
LC	Landcover classification of trap location	+ (woodland)
MP4	4-level, categorical moon phase	- (increased light)
MP6	6-level, categorical moon phase	- (increased light)
MIllum	Numerical moon phase	- (increased light)
MDur	Duration during night moon above horizon	-
MIndex	Index created from moon phase and duration	-
Sex	Sex of the individual captured	+ (males)
Class	Juvenile, breeding adult, or non-breeding adult	+ (breeding adults)

Table 1.2: Working hypotheses and candidate models for analysis of trap success. Random effects (μ) for all models were trap location nested within site. See Table 1.1 for full description of variables.

Hypothesis	Models
Moon	Seas + Tmin + MDur * MP4 + μ
	Seas + Tmin + MDur * MP6 + μ
	Seas + Tmin + MDur * Mllum + μ
	Seas + Tmin + MIndex + μ
Landcover	Seas + Tmin + LC + μ
Disturbance	Seas + Tmin + LZeq * Lux + μ
	Seas + Tmin + LAeq * Lux + μ
Null	μ

Table 1.3: All supported models ($\Delta\text{AICc} \leq 4$) for all hypotheses. Bolded variables had 85% CIs that did not overlap zero. Variables bolded and italicized had 95% CIs that did not cross zero. K is the number of parameters in the model, AICc is the Akaike's Information criteria adjusted for small sample size, ΔAICc is the change in AICc from the top model, and w is the model weight. See Table 1.1 for an explanation of variable names. All models included trap station nested within site as a random effect (μ).

Hypothesis	Model	K	AICc	ΔAICc	w
Moon	<i>MP6</i> + μ	8	2412.31	0.00	0.50
	<i>MP6</i> + Seas + μ	9	2414.00	1.69	0.21
	<i>MP6</i> + Tmin + μ	9	2414.44	2.13	0.17
	<i>MP6</i> + Seas + Tmin + μ	10	2415.14	2.83	0.12
Landcover	LC + <i>Seas</i> + <i>Tmin</i> + μ	7	2433.81	0.00	0.63
	<i>Seas</i> + <i>Tmin</i> + μ	5	2434.92	1.11	0.36
Disturbance	<i>Lux</i> + <i>Seas</i> + <i>Tmin</i> + μ	6	2430.41	0.00	0.62
	<i>Lux</i> + LZeq + <i>Seas</i> + <i>Tmin</i> + μ	7	2431.91	1.50	0.29

Table 1.4: All supported models ($\Delta\text{AICc} \leq 4$) for the analysis of trap success. Bolded variables had 85% CIs that did not overlap zero. Variables bolded and italicized had 95% CIs that did not cross zero. K is the number of parameters in the model, AICc is the Akaike's Information criterion adjusted for small sample size, ΔAICc is the change in AICc from the top model, and w is the model weight. See Table 1.1 for an explanation of variable names. All models included trap station nested within site as a random effect (μ).

Model	K	AICc	ΔAICc	w
<i>Lux + MP6</i> + μ	9	2406.8	0.00	0.47
<i>Lux + MP6</i> + seas + μ	10	2408.6	1.82	0.19
<i>Lux + MP6</i> + TMin + μ	10	2408.9	2.14	0.16
<i>Lux + MP6</i> + seas + TMin + μ	11	2409.6	2.79	0.12
μ	3	2457.21	50.41	0.00

Table 1.5: Effect size and 95% confidence intervals of comparison between different moon phases from the top ranked model. Reference moon phase is shown in italics.

Moon Phase	β	Lower	Upper
<i>New</i> – Waxing crescent	-0.68	-1.26	-0.09
<i>New</i> – Waxing gibbous	-0.24	-0.75	0.26
<i>New</i> – Full	-0.23	-0.68	0.22
<i>New</i> – Waning crescent	0.67	0.11	1.24
<i>Full</i> – Waning gibbous	0.80	0.15	1.46
<i>Full</i> – Waning crescent	0.90	0.31	1.50
<i>Waxing crescent</i> – Waning crescent	1.35	0.93	1.77

Table 1.6: All supported models ($\Delta AICc \leq 4$) for the body condition analyses. Bolded variables had 85% CIs that did not overlap zero. Variables bolded and italicized had 95% CIs that did not cross zero. K is the number of parameters in the model, AICc is the Akaike's Information criterion adjusted for small sample size, $\Delta AICc$ is the change in AICc from the top model, and w is the model weight. See Table 1.1 for an explanation of variable names. Early-season models included trap station as a random effect, late-season models included cluster as a random effect (μ).

Analysis	Model	K	AICc	$\Delta AICc$	w
Early season	Laeq + Sex + LC + μ	6	200.18	0.00	0.33
	Laeq*Sex + LC + μ	7	201.28	1.10	0.19
	Laeq + Sex + LC + Class + μ	7	202.42	2.24	0.11
	Laeq*Sex + LC + Class + μ	8	203.33	3.15	0.07
	Laeq + LC + μ	5	203.47	3.29	0.06
	Laeq*Sex + μ	6	200.83	3.36	0.06
	μ	3	208.13	7.95	0.01
Late season	μ	3	454.60	0.00	0.18
	LAeq + μ	4	455.86	1.25	0.09
	Sex + μ	4	456.00	1.40	0.09
	Lux + μ	4	456.31	1.71	0.07
	LC + μ	4	456.57	1.97	0.07
	LAeq + Sex + μ	5	456.96	2.36	0.05
	LAeq + Lux + μ	5	457.43	2.83	0.04
	LAeq + LC + LAeq*LC + μ	6	457.69	3.09	0.04
	Lux + Sex + μ	5	457.92	3.32	0.03
	LAeq + LC + μ	5	457.96	3.36	0.03
	Sex + LC + μ	5	458.04	3.44	0.03
	Lux + LC + μ	5	458.44	3.84	0.03
	Class + μ	5	458.53	3.93	0.03

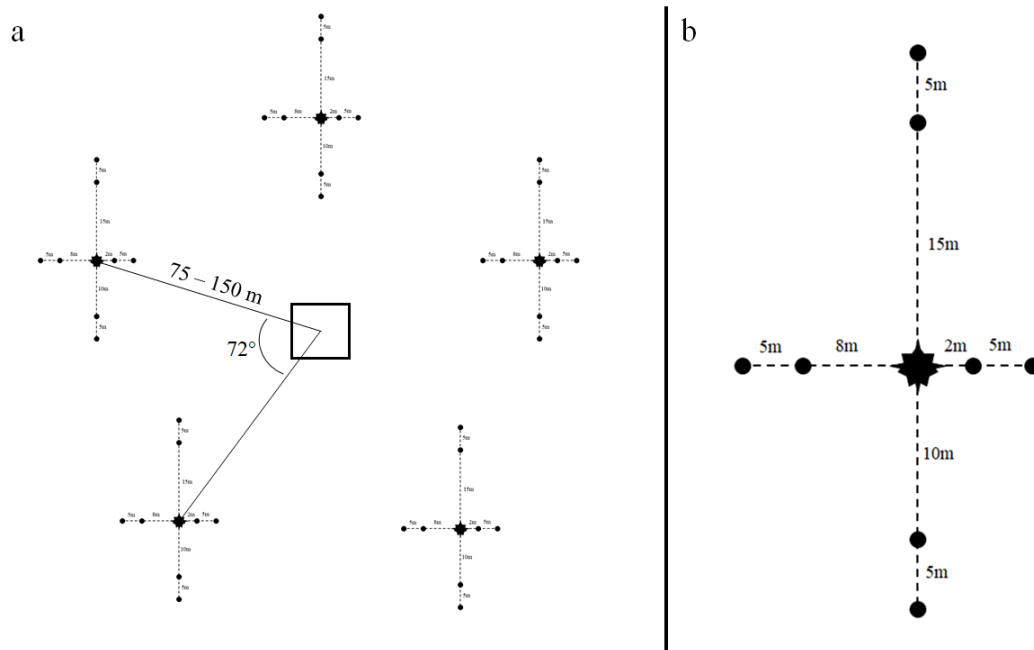


Figure 1.2: (a) Layout of trapping arrays at each site surrounding well pad (square). (b) Trap array design at each sampling location. At lit sites, the center point was established at pre-existing light tower locations. Distances are not shown to scale.

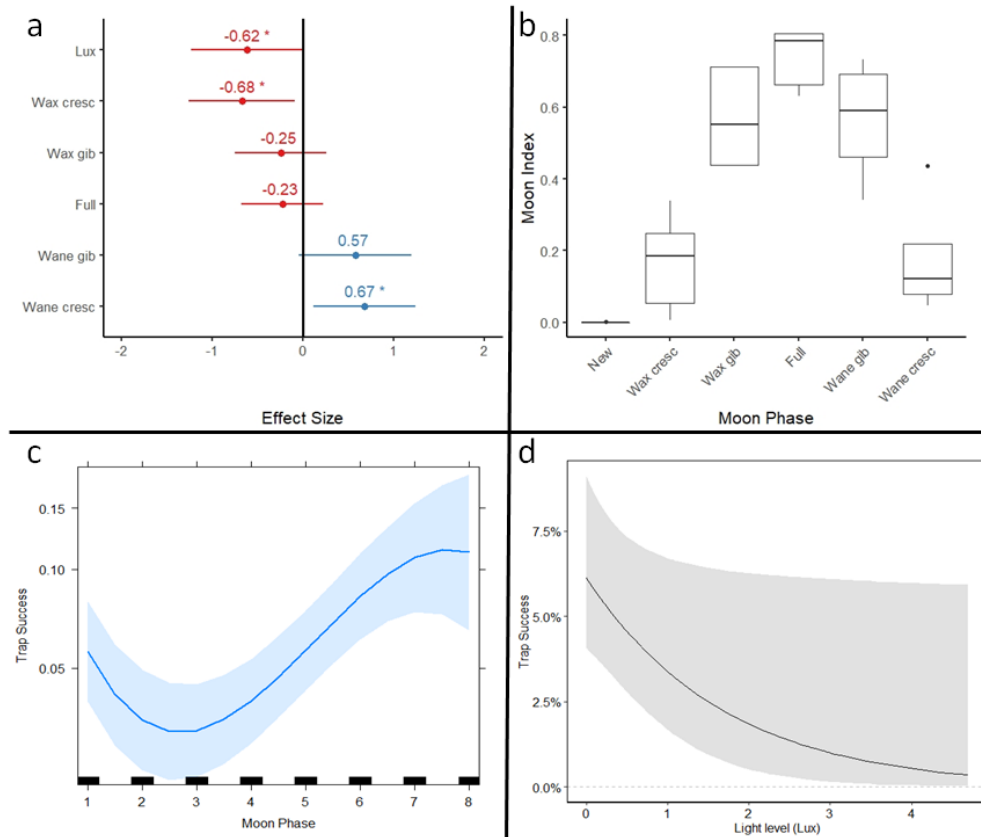


Figure 1.3: (a) Effects plot of top-ranked model from Table 1.4. Effect sizes (β) and 95% confidence intervals shown. For moon phase effects, new moon is the reference phase. Asterisks indicate confidence intervals that do not cross zero. (b) Plot of moon index vs moon phase. (c) Plot of trap success from model using the polynomial moon phase variable. For the moon phases, rank 1 is a new moon, rank 5 is a full moon, and rank 8 is a waning crescent. Shaded area indicates the 95% confidence band. (d) Plot of trap success vs light level from top-ranked model in Table 1.4.

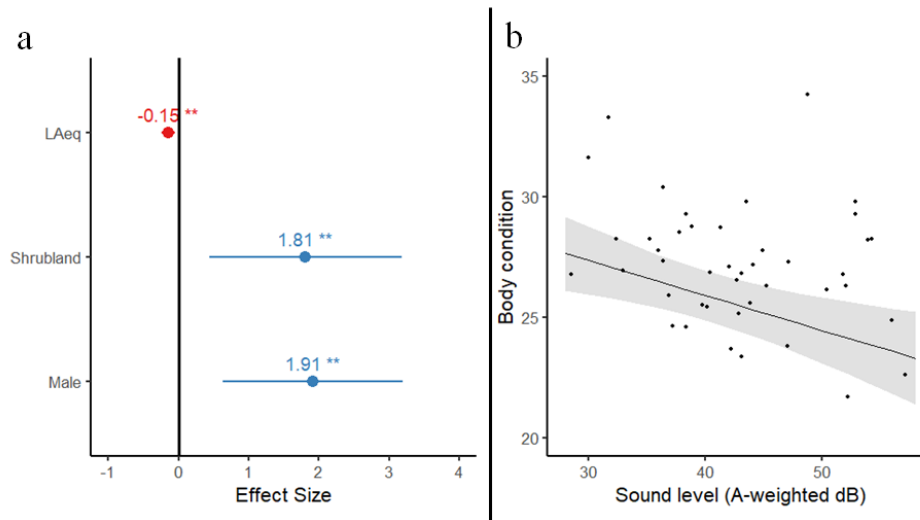


Figure 1.4: (a) Effects plot of top-ranked model from Table 1.6. Effect sizes (β) and 95% confidence intervals shown. For land cover, woodland is the reference state. Asterisks indicate confidence intervals that do not cross zero. (b) Plot of body condition vs noise from top-ranked model in Table 1.6.

CHAPTER 2

ARTIFICIAL LIGHT AT NIGHT AND ANTHROPOGENIC NOISE ALTER VERTEBRATE SPECIES RICHNESS AND COMMUNITY STRUCTURE

2.1 INTRODUCTION

Urbanization has increased dramatically over the last several decades (Angel, Parent, Civco, Blei, & Potere, 2011; Seto, Güneralp, & Hutyrá, 2012) and is one of the main drivers of habitat loss and fragmentation (Liu, He, & Wu, 2016; McDonald, Kareiva, & Forman, 2008) and threats to biodiversity around the world (McKinney, 2008; Seto et al., 2012). In addition to physical alterations to natural land cover, the sensory environment has fundamentally changed due to urbanization via artificial night-lighting, anthropogenic noise, and other pollutants (Halfwerk & Slabbekoorn, 2015; Swaddle et al., 2015). Previous research involving the effects of increased light and noise on wildlife have focused primarily on behavioral responses (e.g., Amichai & Kronfeld-Schor, 2019; Morris-Drake, Bracken, Kern, & Radford, 2017; Shannon, Angeloni, Wittemyer, Fristrup, & Crooks, 2014), but changes to reproductive success (e.g., Habib, Bayne, & Boutin, 2007; Halfwerk, Holleman, Lessells, & Slabbekoorn, 2011) and physiology (e.g., Du et al., 2010; Kleist, Guralnick, Cruz, Lowry, & Francis, 2018) have also received some attention. A number of studies have also examined community-level consequences, such as how interactions among species change with alterations to light and noise regimes (e.g., Francis, Ortega, & Cruz, 2009; H. Jung, Sherrod, LeBreux, Price, & Freeberg, 2020; Yurk & Trites, 2000), how resulting communities are structured (e.g., Francis et al., 2009; Meyer & Sullivan, 2013; Schoeman, 2016) or whether light or noise influences patterns of species richness (e.g., Davies, Bennie, & Gaston, 2012; Meyer & Sullivan, 2013; Proppe, Sturdy, & Clair, 2013). Most of these examples have focused on responses of a limited number of species or taxa. More importantly, however, the community-level consequences of co-exposure to noise and light have received almost no attention despite the fact that they often co-occur (reviewed in Dominoni et al., 2020). To our knowledge, the only study to evaluate community structure resulting from the combined effects of light and noise evaluated winter bird community assemblages along urban gradients where many other human stressors that can influence bird distributions co-occur (Ciach & Fröhlich, 2017). As

such, there remains the need for further research into the combined effects of light and noise pollution at the community-level, especially through manipulative field experiments that eliminate or otherwise minimize confounding human stressors.

Although the weight of evidence suggests that noise and light pollution have negative consequences for wildlife and their supporting ecological communities (reviewed in: Dominoni et al., 2020; Francis & Barber, 2013; Gaston, Bennie, Davies, & Hopkins, 2013), substantial variation exists in species-specific responses to altered sensory environments. For example, research involving ecological consequences of energy-sector noise found that Woodhouse's scrub jays (*Aphelocoma woodhouseii*) strongly avoided noisy sites while both black-chinned hummingbirds (*Archilochus alexandri*) and house finches (*Carpodacus mexicanus*) nested almost exclusively in noisy areas (Francis et al., 2009). A recent meta-analysis revealed similar divergent responses among mammals to natural photoperiod regimes (reviewed in Prugh and Golden 2014). Given species-specific variation in responses to these stimuli, at the community level noise and light pollution could act as environmental filters by excluding less tolerant species, reducing overall species richness and resulting in community homogenization. However, it is possible that some species are able to exploit areas experiencing sensory disturbance, such as through predator shielding (Berger, 2007), and thus overall species richness in these areas could increase. The degree and direction in which light and noise pollution, both independently and together, affect species richness, and whether those effects can result in community-wide changes, remains an area in need of further research.

In this study we investigated if and how artificial night-lighting, anthropogenic noise pollution, and the combination of the two influences species richness and community structure of vertebrates in a mixed juniper (*Juniperus osteosperma*) - pinyon pine (*Pinus edulis*) woodland. To do this, we isolated the effects of light and noise in a unique study system in northwest New Mexico where we were able to exclude or control for confounding factors often associated with these stimuli along urban gradients (i.e., roads, human structures, human presence). Previous work in this system took advantage of the presence of natural gas wells with and without noise-generating compressors to isolate the effects of noise (e.g., Francis, Kleist, Ortega, & Cruz, 2012;

Francis et al., 2009; Kleist et al., 2018). Here, we leveraged this unique system to explore exposure to noise and light by adding light towers to both noisy and quiet sites, allowing us to create a full factorial study design that provides the opportunity to study the effects of both light and noise alone as well as the combination of both stimuli.

Here we used camera traps to test the hypothesis that elevated levels of light and noise would alter both species richness and community structure. Because past studies have found numerous negative effects of exposure to increased levels of both light (e.g., Bird et al., 2004; Clarke, 1983) and noise (e.g., Habib et al., 2007; Senzaki, Yamaura, Francis, & Nakamura, 2016), species richness should decrease with experimental exposure to these stimuli when present alone. Additionally, potential additive or synergistic effects of co-exposure to light and noise may result in larger declines in species richness than either stimulus alone. Thus, we predicted that species richness measured at individual camera traps would decline with increases in noise and light levels and that species richness would be lowest with co-exposure to high noise and light levels. This pattern should also be apparent in terms of cumulative richness across treatment types, where quiet and dark sites would have the highest cumulative richness, and sites exposed to noise and light together would have the lowest cumulative richness, and those exposed to noise or light would have intermediate levels of cumulative richness. For community turnover, because past work has found a negative effect of both light (Meyer & Sullivan, 2013) and noise (Ciach & Fröhlich, 2017; Proppe et al., 2013) on richness, communities on sites where both stimuli are present should differ the most strongly from communities on dark, quiet sites due to more sensitive species being excluded and species compositions becoming more homogeneous. Because some species are more sensitive to one stimulus than the other (Francis, Ortega, & Cruz, 2011) or even benefit from some amount of sensory disturbance (González-Bernal, Greenlees, Brown, & Shine, 2016; Minnaar, Boyles, Minnaar, Sole, & McKechnie, 2015), sites treated with only light or noise should have intermediate levels of community dissimilarity compared to control sites and those with both noise and light.

2.2 MATERIALS AND METHODS

2.2.1 Site description

The study took place within the Rattlesnake Canyon Habitat Management Area (RCHMA) in northwestern New Mexico, an area consisting of mixed juniper (*Juniperus osteosperma*) - pinyon pine (*Pinus edulis*) woodland and great basin sagebrush (*Artemisia tridentata*) shrublands. See section 1.2.1 for a thorough site description. Briefly, our sites were located at gas wells with and without noise-generating compressors. To some of these sites we added light towers, creating a full-factorial study design with four treatments: light alone, noise alone, light and noise combined, and a dark, quiet control. Sites were grouped into six geographically distinct “clusters” to control for landscape-level variation in environmental variables. See section 1.2.3 for description of variable measurements.

2.2.2 Camera deployment

Cameras were deployed at each cluster for a total of three consecutive nights. Once cameras were collected from one cluster, they were moved to the next cluster for three nights. This pattern was repeated until all clusters had been sampled. Cameras were first deployed on 27 May 2019 and collected on 25 June 2019. Ten cameras were deployed at each site (40 per cluster) for a total of 720 camera trap nights across the duration of the study. Bushnell Trophy Cam HD 20-megapixel no glow infrared trail cameras were used and set to take three images per trigger. At lit sites, cameras were placed near pre-existing light towers and at least 25 meters apart (Figure 2.2a). Mean distance from cameras to closest light tower was 11.4 meters (range = 1.3 to 25.8 meters). At dark sites, the method of camera placement was replicated at locations 72 degrees from one another and located at random distances between 75 and 150 meters from the center of the well pad, matching placement on lit sites (Figure 2.2b).

Cameras were baited with a handful of rolled oats provided at zero and 48 hours after deployment. Cameras were collected the morning after the third night as close to sunrise as possible. All captured images were analyzed individually, and for each detection, the species of the animal, time of the detection, and number of images per detection were recorded. We were

not able to reliably identify mice in the genus *Peromyscus*, woodrats in the genus *Neotoma*, or bluebirds in the genus *Sialia* to species from images, thus they were grouped by genus. Physical trapping conducted the same season in this system suggests that the majority of *Peromyscus* mice present were likely pinyon mice (*Peromyscus truei*; 90% of captures) with some deer mice (*Peromyscus maniculatus*; 9% of captures) and brush mice (*Peromyscus boylii*; 1% of captures) present as well while woodrats were likely Mexican woodrats (*Neotoma mexicana*) (Willems et al., in review). Bluebirds were either Western bluebirds (*Sialia mexicana*) or mountain bluebirds (*Sialia currucoides*). Detections that were not able to be reliably identified to species or genus were dropped from all analyses.

2.3 DATA ANALYSIS

2.3.1 Species richness

We compared species richness across treatments using two approaches. First, we compared apparent species richness at the camera-trap level using generalized linear mixed-effect models. To do this we initially created models using the observed species richness at each camera as a response with the treatment, measured lux and Laeq values, land cover classification, average Julian date, and our created moonlight index for each camera as explanatory variables and site nested within cluster as random effects. However, we encountered issues with model convergence using the moonlight index variable. Therefore, we re-ran the models using the percent moon face variable instead. Second, we used the *specaccum* function from the package ‘vegan’ (Oksanen et al. 2019) to create site-level and treatment-level (i.e., pooling all sites per treatment) rarefaction curves, which were not asymptotic (see below), suggesting undetected species remained. Because of known problems comparing richness across locations with incomplete sampling or different sampling effort (Gotelli & Colwell, 2001), we also calculated cumulative richness estimates for each treatment using first order jackknife and bootstrap estimators using the *specpool* function in the package ‘vegan’ (Oksanen et al., 2019). We concluded that estimated richness differed between treatments if the standard error of the two treatments did not overlap. These analyses were performed for all species combined and

separately for all mammalian species and all bird species. For the camera-level observed species richness analyses, the models of all-species richness and mammalian richness were under-dispersed. Therefore, models were built using the Conway-Maxwell Poisson family with the *glmmTMB* function from the 'glmmTMB' package in R (Magnusson et al. 2020). The models of bird species richness were not under-dispersed, so we used Poisson error. We initially used the control treatments as the reference for the treatment factor when determining if there was a significant treatment effect on richness. For well supported models we then changed the reference state to the noise treatment to determine if richness on noisy sites differed from richness on other treatments.

2.3.2 Community structure

We analyzed community turnover at the camera level in three ways: 1) by presence/absence of each species because individuals were unmarked, and to reflect functional influence on the community; 2) the number of detections per species; and 3) by species pooled into broader taxonomic groups (nocturnal rodents, diurnal rodents, birds, lagomorphs, herps, ungulates, and mesocarnivores). Because analyses of beta diversity require communities of at least 1 species, 80 of the 240 camera-trap locations, which had no detections, were removed from the analysis ($n = 160$). For each of these approaches we ranked several dissimilarity metrics (euclidean, manhattan, gower, altGower, canberra, clark, kulczynski, horn, binomial, jaccard, and bray) with the *rankindex* function from the 'vegan' R package (Oksanen et al., 2019) to determine which index best captured the dissimilarities among treatments. For the presence-absence analysis, we used the binary form of the best fitting index. We then used the *adonis* function in *vegan* (Oksanen et al., 2019) to perform PERMANOVA on the best-ranked index with the treatment, measured LAeq and lux values, land cover classification, average Julian date, and average percent moon face for each camera as explanatory variables. We also included the interaction between treatment and percent moon face, lux and percent moon face, as well as LAeq and lux. We followed this analysis with pairwise comparisons for all treatments to investigate potential differences between specific treatment types. Finally, we also performed an

indicator species analysis using the *multipatt* function from the 'indicspecies' R package (Cáceres, Jansen, & Dell, 2020) to characterize any associations among species or taxa and specific treatments.

All analyses were performed using *R* (R Core Team, 2019). For all analyses, we considered parameters with apparent trends and 85% CI that did not cross zero or where $p \leq 0.15$ were considered to have evidence of a potential effects that warranted consideration for inference while parameters with a 95% CI that did not cross zero or a $p \leq 0.05$ were considered to have more precise evidence of an effect (Kleist, Guralnick, Cruz, Lowry, & Francis, 2018; Ware, McClure, Carlisle, & Barber, 2015). In the results, we report parameter estimates and confidence intervals from the top-ranked model in which that parameter appeared but also report other highly competitive models (i.e. $\Delta AICc \leq 2$).

2.4 RESULTS

Due to technical issues with some cameras (i.e. battery failure, memory card errors, etc), our final sample size was 685 camera nights (maximum possible = 720) across 233 cameras. In total, 5,583 detections of 25 species were made across all cameras. By far the most commonly detected species were *Peromyscus* mice ($n = 4,106$), along with desert cottontails (*Sylvilagus audubonii*; $n = 348$), least chipmunks (*Neotamias minimus*; $n = 301$), Woodhouse's scrub jays (*Aphelocoma woodhouseii*; $n = 244$), and rock squirrels (*Otospermophilus variegatus*; $n = 162$) also being commonly detected (Figure 2.3). See Table S2.2 for a full breakdown of species detected. Detections where the identity could not be determined (e.g., 20 unidentified birds, 1 unidentified bat, and 84 unidentified animals) were excluded from further analyses.

2.4.1 Species Richness

For all-species richness, none of the included variables had an effect and the null model was top-ranked (Table 2.1; Figure 2.4a). For mammalian species, increases in light caused a decrease in richness ($\beta = -0.20$, 85% CI = -0.36, -0.05; Table 2.1; Figures 2.4b, 2.5) while increased moonlight caused a strong decrease in richness ($\beta = -0.20$, 95% CI = -0.35, -0.05;

Table 2.1; Figures 2.4b, 2.5). For bird species richness, the top-ranked model was the null model including only the random effects (Table 2.1; Figure 2.4c). From the rest of the highly competitive models (i.e. $\Delta AICc \leq 2$), the treatment in which the camera was located was the only variable to have an effect (Table 2.1; Figure 2.4c). Relative to those on control sites, cameras on noisy sites had on average 70% lower observed bird species richness, but the confidence in the difference was less precise (reference state control: $\beta = -1.22$, 85% CI = -2.32, -0.28). There was no difference in observed bird species richness at cameras on lit (reference state control: $\beta = 0.08$, 85% CI = -0.65, 0.80) or combined (reference state control: $\beta = 0.14$, 85% CI = -0.59, 0.84) sites relative to those on control sites (Table 2.1; Figures 2.4c, 2.6). Relative to noise sites, there was greater bird species richness at both combined (reference state noise: $\beta = 1.36$, 85% CI = 0.42, 2.44; Figure 2.6) and lit (reference state noise: $\beta = 1.30$, 85% CI = 0.36, 2.39; Figure 2.6) sites.

Individual-based rarefaction and richness estimators both suggest that cumulative richness was higher on light-treated sites than any other sites, with estimated richness on light sites nearly double that of the noisy sites (Figure 2.7, Table S2.3). Although noise-treated sites appear to have lower cumulative richness than all other treatment types based on rarefaction and bootstrapped richness estimator, there was no difference between estimated cumulative richness on control and noise-treated sites using the jackknife estimator (Figure 2.7, Table S2.3).

Rarefaction and richness estimators also suggest that there were no differences in cumulative richness between combined and control sites for either estimator (Figure 2.7, Table S2.3).

For mammals, rarefaction curves and richness estimators suggest that the light-treated sites had the highest cumulative species richness with all other treatments not differing from one another, with richness on light sites about 1.5 times higher than on noisy sites (Figure 2.8a,b, Table S2.4). For birds, the estimated cumulative species richness of the light and combined treatments were not different from each other and were about 1.5 times higher than the noise treatment for both estimators (Figure 2.9a,b, Table S2.5). For both estimation methods, the combined treatment had higher estimated richness than the control treatment but light and control treatments did not differ. For the bootstrap estimator, the estimated richness on the noise

treatment was lower than all others whereas for the jackknife estimator, control and noise treatments did not differ (Figure 2.9b, Table S2.5).

2.4.2 Community Structure

Community turnover analyses using PERMANOVA based on species presence/absence, species detections, and taxa detections were highly consistent with one another. Specifically, treatment and percent moon face had a significant effect in all analyses (Table 2.2). In both the species and taxa detections analysis, lux had a significant effect with there also being a significant interaction between treatment and percent moon face for the species level detections analysis as well as a significant effect of Julian date (Table 2.2). For all pairwise treatment comparisons, the noise treatments differed significantly from all other treatments (Table 2.3). In addition, for both species detections and species presence/absence, the combined and light treatments were significantly different (Table 2.3).

Results of the indicator species analysis for species presence/absence, species detections, and taxa detections were consistent with one another. For both species detections and presence/absence, Woodhouse's scrub jays (*Aphelocoma woodhouseii*) were positively associated with light treatments, wild turkeys (*Meleagris gallopavo*) were positively associated with combined treatments, and grey foxes (*Urocyon cinereoargenteus*) were positively associated with noise treatments (Table 2.4). Desert cottontails (*Sylvilagus audubonii*) were positively associated with control treatments for the species detections analysis and with control, light, and combined treatments for the species presence/absence analysis (Table 2.4). No significant associations were detected for taxonomic groupings except that mesocarnivores were positively associated with noise treatments while birds were positively associated with both combined and light treatments (Table 2.4).

2.5 DISCUSSION

Although evidence for the effects of noise and light pollution are growing (reviewed in Dominoni et al., 2020; Halfwerk & Slabbekoorn, 2015; Swaddle et al., 2015), to our knowledge,

no study has examined the combined effect of both on vertebrate community structure in an experimental context. Results from our manipulative field experiment demonstrate that both artificial night-lighting and anthropogenic noise can alter both species richness and community structure. They also show that these effects can differ depending on the scale of observation and that their combined influence can result in unexpected patterns. Our results partially matched our predictions that both light and noise would negatively affect species richness, such that noise had a negative effect on richness for some species whereas light had a positive effect for others. Specifically, we found that increased levels of anthropogenic noise resulted in reduced species richness and altered community structure and that the addition of night-lighting mitigated these effects for birds. We also found that increased levels of night-lighting had a scale-dependent effect on species richness such that increases in light level had a negative effect on richness at the camera level but light-treated sites had the highest estimated cumulative richness.

For both total species richness and mammalian species richness, at the camera level we found a negative effect of lux, matching our prediction. Increased levels of artificial night lighting have been shown to have a wide range of negative effects including increased predation risk (Clarke, 1983) and reduced foraging behavior (Bird et al., 2004; Blubaugh, Widick, & Kaplan, 2017), which could cause animals to avoid areas that are most brightly lit. Despite the potential negative effects of increased night-lighting, comparisons of observed and estimated cumulative species richness across treatments revealed higher species richness on light-treated sites, which was in contrast to our prediction that increased levels of light would result in reduced species richness.

There are no simple explanations for the difference in camera-level and cumulative species richness, but they could potentially result from a combination of responses, such as avoidance of the brightest conditions and attraction to low light areas for foraging. Increased levels of artificial night lighting have been shown to attract insects (reviewed in Owens and Lewis 2018) and insects were observed in high densities surrounding our lights at night (J. Willems, personal observation). Additionally, a number of insectivorous taxa take advantage of this phenomenon, including bats (Jung & Kalko, 2010; Minnaar, Boyles, Minnaar, Sole, & McKechnie,

2015), spiders (Heiling, 1999), and toads (González-Bernal et al., 2016), although foraging in brightly lit areas does not always increase foraging efficiency (Yuen & Bonebrake, 2017). A similar phenomenon has been documented with harbor seals (*Phoca vitulina*), which have higher hunting success on juvenile salmonids under bright, artificial lights than under natural lighting conditions (Yurk & Trites, 2000). There is also evidence that increased night lighting can lead to temporal niche expansion among diurnal species, allowing them to forage under lit conditions during nighttime hours (Amichai & Kronfeld-Schor, 2019; Leveau, 2020). This combination of increased prey abundance and/or density along with the potential for an increased amount of foraging time per day under dim lighting conditions could lead to greater foraging success and/or efficiency for species occurring in areas experiencing increased levels of light at night. Thus, it is possible that a tradeoff between the negative effects of increased light, such as increased predation risk (Clarke, 1983) and sleep disruption (Raap, Pinxten, & Eens, 2015), and the positive effects of potentially increased food resources, could explain why we found lower species richness at the cameras under the brightest artificial light conditions but the highest cumulative species richness at light treatment sites. These results highlight the importance not only of considering scale when investigating the effects of sensory pollutants, but also of weighing both positive and negative outcomes of exposure to these stimuli.

For bird species richness, there was less of a discrepancy between the results based on the camera-level analyses and comparisons of cumulative richness across treatments. Results from the camera-level analysis partially matched our predictions in that richness was lower on noise treatment sites compared to all other treatments, but observed richness at cameras on light and combined sites did not differ from one another and were both higher than control and noise sites, which contrasted with our predictions. In terms of cumulative richness, control sites had higher cumulative bird richness than noise sites for one richness estimator while cumulative richness was indistinguishable between the two using the second estimator. The measured lux and Laeq values at each camera had no effect on bird richness, also in contrast to our prediction. Past studies have found that noise can have a negative effect on bird species richness and abundance (Arevalo & Newhard, 2011; Bayne, Habib, & Boutin, 2008; Ciach & Fröhlich, 2017)

and research in the same study system as ours suggests that noise filters bird communities non-randomly based on the frequency of their vocalizations (Francis, Ortega, et al., 2011). Although a negative effect of noise was found, as indicated by low bird species richness at noisy sites at both scales, the addition of light seems to act as a rescue effect because bird species richness at combined sites was equal to that of light alone sites and higher than that of the noise alone sites. It is possible that the addition of light could serve to offset some of the negative effects of increased levels of noise. As discussed above for richness patterns among all species and mammals, the presence of increased invertebrate food resources and/or increased foraging opportunities due to an increased effective daylength at lit sites could offset the negative effects of increased background noise for many species. Supporting this possibility, there is some evidence that alterations to the natural light-dark cycle dominate or override behavioral alterations to acoustic regimes. A recent lab-based study with great tits (*Parus major*) found that individuals exhibited similar behavior patterns when exposed to both light and noise as individuals who were exposed to only light (D. Dominoni, Smit, Visser, & Halfwerk, 2020). Finally, the lack of a scale-dependent response to noise such as that observed for light could be due to the fact that, in our study system, light levels attenuated at much shorter distances than did compressor noise. This resulted in considerable heterogeneity in light levels at sites treated with light. Sites surrounding compressors experience a gradient in sound levels, but levels remain well above ambient levels until at least 350 m from compressors (Francis, Paritsis, Ortega, & Cruz, 2011). Future research should focus on the relative role of spatial heterogeneity in noise and light exposure that may permit individuals to exploit benefits provided by these stimuli, such as increased prey densities and extended foraging time (Amichai & Kronfeld-Schor, 2019; González-Bernal et al., 2016; Jung & Kalko, 2010), but still avoid deleterious effects, such as sleep disruption and hormone dysregulation (Kleist et al., 2018; Raap et al., 2015).

In addition to changes in species richness, we found that alterations to the sensory environment changed community composition. Analyses of all three approaches we used to quantify beta-diversity (i.e., species total detections, species presence/absence, taxa total detections) revealed community dissimilarity among treatments. For all analyses the noise

treatments were significantly dissimilar from all other treatments (Table 5), indicating that increased noise levels likely have the largest effect on community composition in this system. This is in contrast to our prediction that control and combined sites would be most dissimilar. Species are known to show differing sensitivities to noise pollution, which could allow certain species to be more resilient to acoustic disturbances than others. One such example is that bird species with lower frequency vocalizations have been found to be more sensitive to anthropogenic noise pollution, likely due to masking of important intraspecific cues (Francis, Ortega, et al., 2011; Goodwin & Shriver, 2011; Rheindt, 2003). Alterations to the acoustic environment have also been shown to alter the ways in which species interact, which could lead to the reduction or exclusion of some species from areas with high amounts of sensory disturbance. For example, previous work in this system found that the avoidance of noise by Woodhouse's scrub jays (*Aphelocoma woodhouseii*), an important nest predator, led to increased nest success of songbirds in noisier areas (Francis et al., 2009). However, the authors also found that both black-chinned hummingbirds (*Archilochus alexandri*) and house finches (*Carpodacus mexicanus*) were strongly associated with noisy sites (Francis et al., 2009). These sorts of species-specific responses to alterations of the acoustic environment could explain why we found that noise treatment sites differed in community composition from the other treatment sites.

As with the analyses of bird species richness, the beta diversity analyses suggest a possible rescue effect of light that counteracts the negative effect of noise. For both species-level detections and presence-absence, the combined treatment sites were significantly dissimilar to both the light and noise sites but not from the control sites. For taxon-level detections, the combined treatment sites were significantly dissimilar from the noise sites but not from control or light sites. Perhaps the addition of light serves to offset some of the negative effects of noise through similar mechanisms as discussed above. If that were the case, increased levels of light and noise could effectively cancel out each other, resulting in the community structure being the same as at control sites. Indeed, we found no differences in community structure between combined and control sites. Importantly, however, the mere presence of taxa in areas exposed to both stimuli does not provide a complete picture of their singular or combined effects. For

instance, western bluebirds (*Sialia mexicana*) experience an equal use ecological trap with noise in that they do not avoid noise in nest site selection (Kleist, Guralnick, Cruz, & Francis, 2017), but experience stress hormone dysregulation and increased hatching failure with noise exposure (Kleist et al., 2018). Understanding whether the presence of light in noisy environments provides benefits that outweigh these and other costs of noise is an important area for future research.

Results of the indicator species analysis provide insights into possible biological explanations behind the observed changes in community structure in response to altered sensory environments. Our results showed that desert cottontails (*Sylvilagus audubonii*) seemed to avoid noise treatments where grey foxes (*Urocyon cinereoargenteus*) were indicator species. Rabbits are a major prey for these foxes (Cunningham, Kirkendall, & Ballard, 2006). Perhaps foxes are able to take advantage of acoustic cover in areas with elevated ambient noise levels, which could result in increased predation success, causing rabbits to preferentially avoid noisy areas due to increased predation risk. Past work in this system also found that Woodhouse's scrub jays (*Aphelocoma woodhouseii*) strongly avoid noisy sites (Francis et al., 2009) whereas our results found they seem to be attracted to lit sites. Similar to our results involving richness and community turnover, the contrasting responses to the two stimuli among Woodhouse's scrub jays highlights the nuances to species responses to human-altered environments.

In addition to the clear difference in community composition on noisy sites relative to other treatments, we also found differences in light levels to explain community turnover for both the species and taxa-level total detections analyses. Altered communities due to illumination is supported by past studies that found divergent responses of nocturnal species to changing levels of illumination from moonlight (Kronfeld-Schor et al., 2013; Prugh & Golden, 2014) and from our own finding of community turnover with percent moon face. There was also a significant interaction between treatment and percent moon face for the species-level total detections analysis, suggesting community turnover in response to moonlight differed among treatments. Many natural systems are strongly influenced by both daily and seasonal light-dark cycles (Kronfeld-Schor et al., 2013) and high levels of artificial light at night could serve to override or mask these natural cues. Species are known to respond differently to changing levels of

moonlight with some reducing activity during the brightest phases and others increasing activity (reviewed in Prugh & Golden, 2014). As such, any disturbance of the natural moonlight cues by light pollution could have significant effects on species interactions and, ultimately, community structure. Our results also indicate that there are potentially some benefits to species when both light and noise pollution are present. As such, animals living in habitats experiencing increased levels of anthropogenic noise could experience some benefits during the brightest moon phases which could help to, at least temporarily, offset the negative effects of increased noise levels. How natural fluctuations in moonlight intensity potentially interact with both light and noise pollution is an area in need of further research.

2.6 CONCLUSION

Our results provide evidence that alterations to the sensory environment from artificial night-lighting and anthropogenic noise pollution can have effects on both species richness and community structure. Counter to our expectations, multiple lines of evidence also suggest light exposure may rescue communities from the negative effects of noise. We also found that the effect of light pollution on species richness was scale-dependent, with increased light levels having a negative effect on richness at the camera level but a positive effect in terms of cumulative richness across all light-exposed sites. These results highlight both the need to continue research into the combined effects of light and noise pollution at the community level and the importance of considering scale when investigating sensory disturbances. Because the intensity and spatial extent of sensory disturbances from human activities will continue to increase, understanding how natural systems respond to the singular and combined influence of these novel stressors will be critical to ongoing management and conservation efforts.

Table 2.1: All supported models ($\Delta AICc \leq 2$) for observed species richness analyses. Bolded variables had 85% CIs that did not overlap zero. Variables bolded and italicized had 95% CIs that did not cross zero. K is the number of parameters in the model, AICc is the Akaike's Information criterion adjusted for small sample size, $\Delta AICc$ is the change in AICc from the top model, and w is the model weight. All models included site nested within cluster as random effects (μ).

Analysis	Model	K	AICc	$\Delta AICc$	w
All species	μ	4	573.05	0.00	0.09
	M_Illum + μ	5	573.40	0.35	0.08
	Lux + μ	5	574.07	1.03	0.05
	JDay + Lux + μ	6	574.21	1.16	0.05
	M_Illum + Lux + μ	6	574.49	1.44	0.04
	JDay + μ	5	574.99	1.95	0.03
Mammals	Lux + <i>M_Illum</i> + μ	6	437.92	0.00	0.11
	Lux + <i>M_Illum</i> + JDay + μ	7	439.37	1.45	0.05
	Lux + <i>M_Illum</i> + Lux*M_Illum + μ	7	439.45	1.53	0.05
	Lux + <i>M_Illum</i> + LC + μ	7	439.73	1.81	0.04
Birds	μ	3	227.15	0.00	0.09
	M_Illum + μ	4	228.15	0.99	0.06
	<i>Treatment</i> + μ	6	228.27	1.12	0.05
	LC + μ	4	228.75	1.60	0.04
	JDay + μ	4	228.81	1.66	0.04

Table 2.2: Results of PERMANOVA analysis. Bolded variables had p-values ≤ 0.15 . Variables bolded and italicized had p-values ≤ 0.05 . The diversity metric for each analysis is listed as are the degrees of freedom, sum of squares, mean squares, F-statistic, partial R², and p-value for each variable.

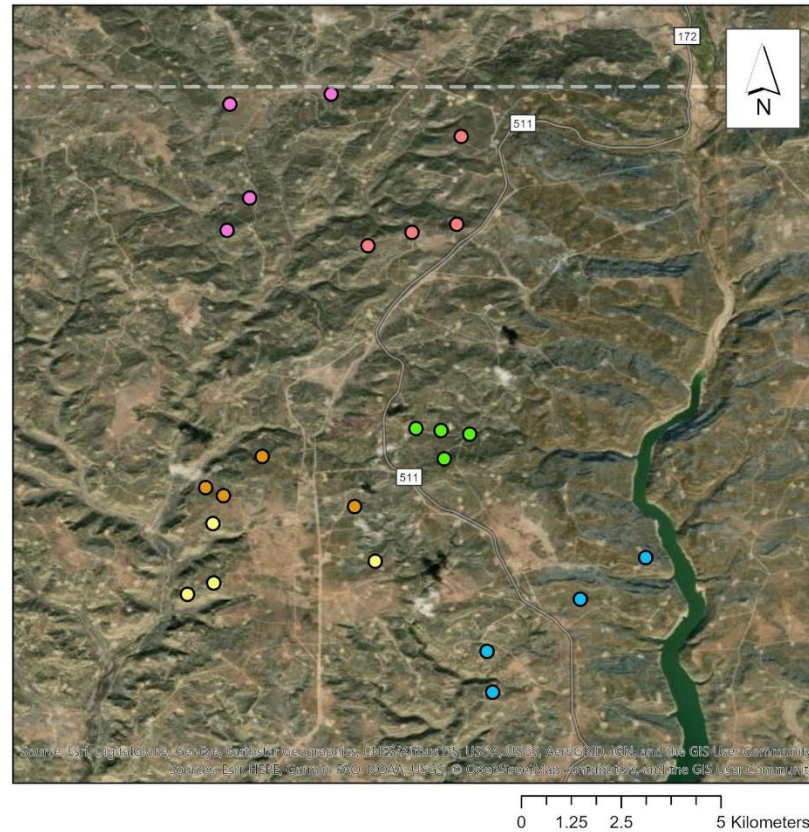
Analysis	Diversity Metric	Variable	df	Sums of Squares	Mean Squares	F Model	R ²	p
Species Detections	Clark	<i>Treat</i>	3	2.220	0.740	1.939	0.035	0.002
		Laeq	1	0.380	0.380	0.995	0.006	0.387
		<i>Lux</i>	1	0.543	0.543	1.423	0.009	0.089
		<i>M_Illum</i>	1	1.569	1.569	4.110	0.025	0.001
		Landcover	1	0.363	0.363	0.952	0.006	0.454
		<i>JDay</i>	1	0.668	0.668	1.750	0.010	0.042
		<i>Treat * M_Illum</i>	3	1.510	0.503	1.319	0.024	0.066
		Lux * M_Illum	1	0.307	0.307	0.805	0.005	0.692
Species Presence/Absence	Canberra	Lux * Laeq	1	0.493	0.493	1.295	0.008	0.165
		<i>Treat</i>	3	1.841	0.614	2.348	0.042	0.002
		Laeq	1	0.202	0.202	0.773	0.005	0.628
		Lux	1	0.244	0.244	0.932	0.006	0.427
		<i>M_Illum</i>	1	1.700	1.700	6.506	0.039	0.001
		Landcover	1	0.185	0.185	0.709	0.004	0.691
		JDay	1	0.251	0.251	0.959	0.006	0.396
		Treat * M_Illum	3	0.880	0.293	1.123	0.020	0.296
Taxa Detections	Kulczynski	Lux * M_Illum	1	0.144	0.144	0.552	0.003	0.724
		Lux * Laeq	1	0.372	0.372	1.426	0.008	0.155
		<i>Treat</i>	3	1.591	0.530	2.584	0.045	0.020
		Laeq	1	0.030	0.030	0.145	0.001	0.837
		<i>Lux</i>	1	0.537	0.537	2.615	0.015	0.062
		<i>M_Illum</i>	1	1.648	1.648	8.029	0.047	0.001
		Landcover	1	0.153	0.153	0.745	0.004	0.357
		JDay	1	0.114	0.114	0.557	0.003	0.709
		Treat * M_Illum	3	0.451	0.150	0.732	0.013	0.608
		Lux * M_Illum	1	-0.224	-0.224	-1.091	-0.006	1.00
		Lux * Laeq	1	0.066	0.066	0.322	0.875	0.745

Table 2.3: Pairwise comparisons of treatments from PERMANOVA analysis. Bolded comparisons had p-values ≤ 0.15 . Comparisons bolded and italicized had p-values ≤ 0.05 . The diversity metric for each analysis is listed as are the F-statistic, partial R², and p-value for each variable.

Analysis	Diversity Metric	Comparison	F Model	R ²	p
Species Detections	Clark	Control – Light	0.851	0.010	0.591
		<i>Control – Noise</i>	2.553	0.029	0.005
		Control – Combined	1.035	0.013	0.370
		<i>Light – Noise</i>	2.314	0.028	0.016
		Light – Combined	1.378	0.019	0.140
		<i>Noise – Combined</i>	3.418	0.044	0.001
Species Presence/ Absence	Canberra	Control – Light	0.991	0.012	0.401
		<i>Control – Noise</i>	3.682	0.042	0.006
		Control – Combined	1.015	0.013	0.370
		<i>Light – Noise</i>	2.760	0.034	0.013
		Light – Combined	1.819	0.025	0.061
		<i>Noise – Combined</i>	4.226	0.053	0.001
Taxa Detections	Kulczynski	Control – Light	1.125	0.014	0.299
		<i>Control – Noise</i>	3.102	0.035	0.040
		Control – Combined	0.710	0.009	0.576
		<i>Light – Noise</i>	4.358	0.052	0.026
		Light – Combined	1.230	0.016	0.303
		<i>Noise – Combined</i>	5.857	0.070	0.003

Table 2.4: Results of indicator species analysis. IV is the indicator value for each species.

Analysis	Treatment	Species	IV	p
Species Detections	Control	Desert cottontail	0.386	0.04
	Light	Woodhouse's scrub jay	0.385	0.005
	Noise	Grey fox	0.265	0.03
	Combined	Wild turkey	0.378	0.005
Species Presence/ Absence	Light	Woodhouse's Scrub jay	0.322	0.035
	Noise	Grey fox	0.274	0.045
	Combined	Wild turkey	0.378	0.005
	Combined + Control + Light	Desert cottontail	0.344	0.045
Taxa Detections	Noise	Mesocarnivores	0.258	0.05
	Combined + Light	Birds	0.534	0.03



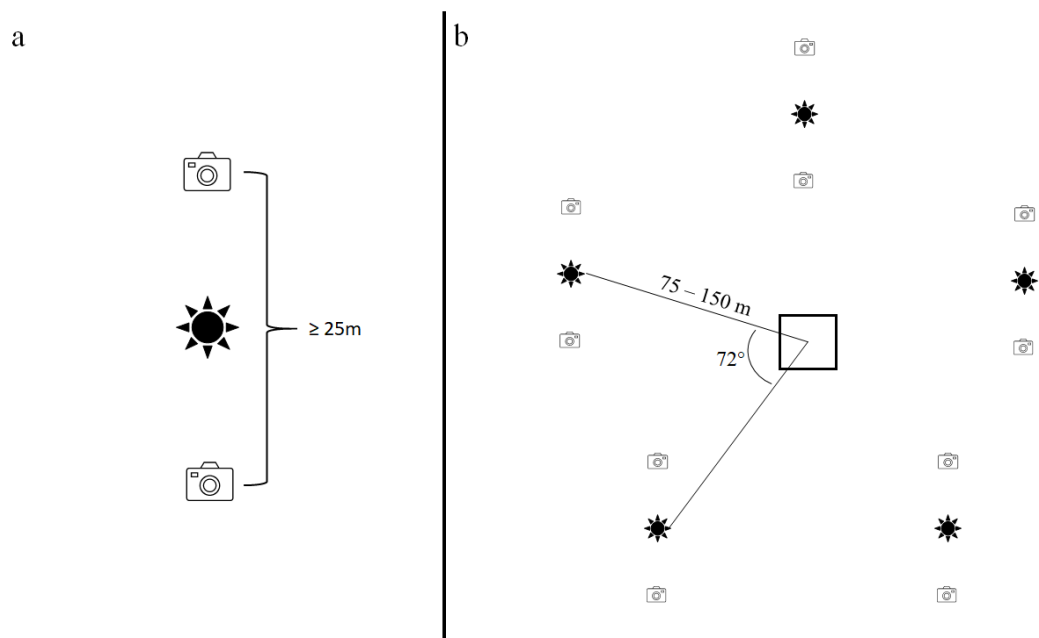


Figure 2.2: (a) Camera trap array design at each sampling location (5 per site). At lit sites, the center point was established at pre-existing light tower locations (star). (b) Layout of trapping arrays at each site surrounding well pad (square). Distances not shown to scale.

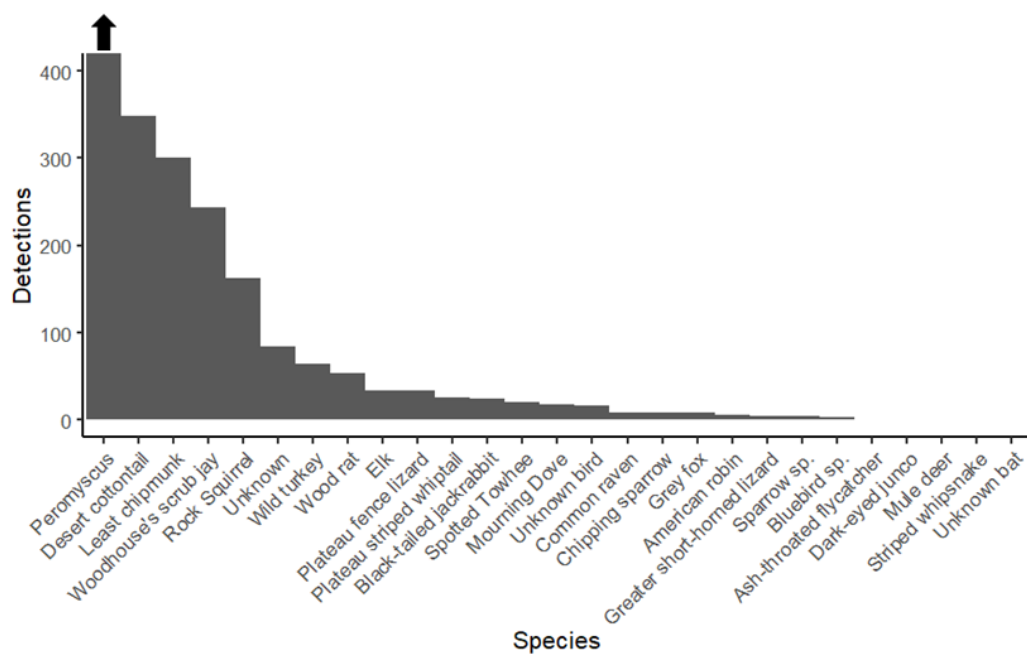


Figure 2.3: Total number of detections by species for all cameras. Note, y-axis has been cut off at 400 to aid in visualization of species with fewer detections. The total for *Peromyscus* detections was 4,106. See Table S2 for complete breakdown of species detected.

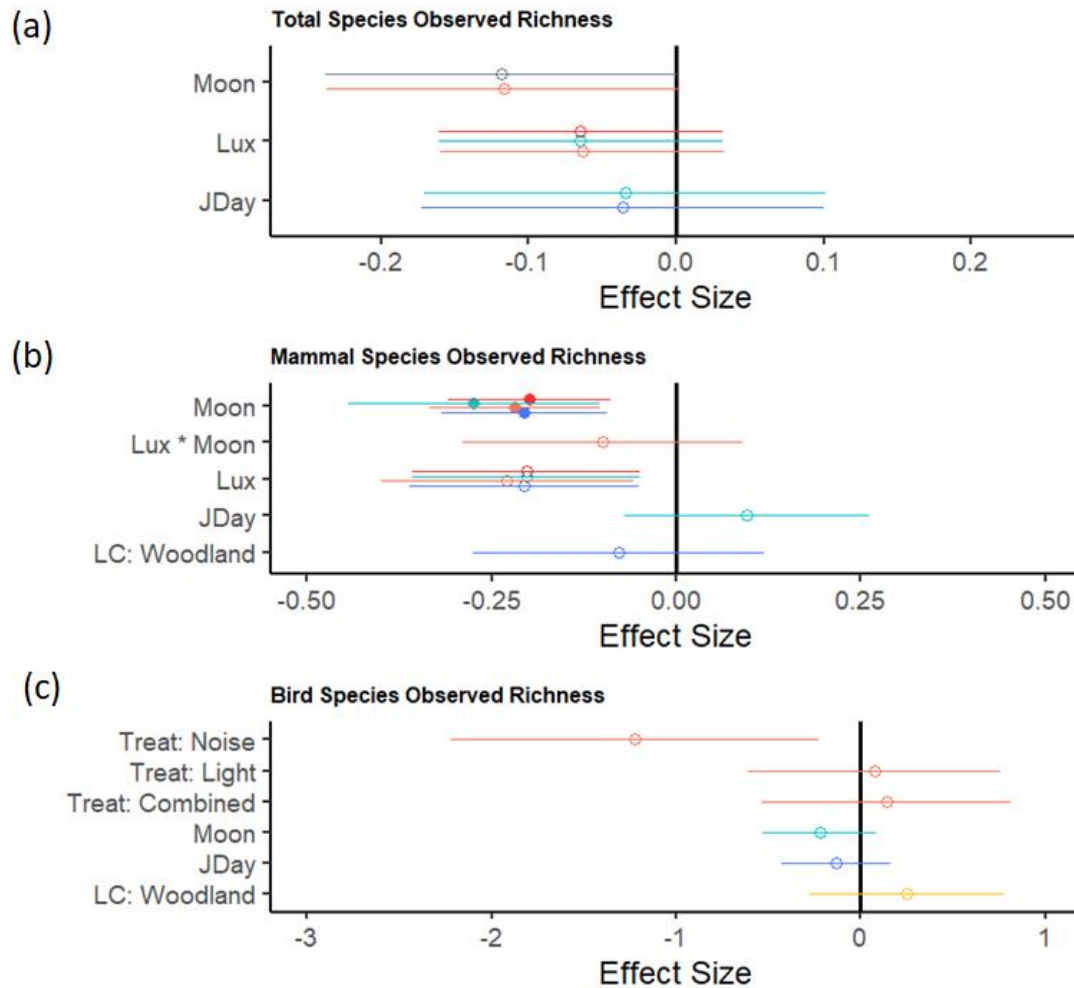


Figure 2.4: Results of all top-ranked models ($\Delta AICc \leq 2$) for observed species richness for (a) total richness, (b) mammal richness, and (c) bird richness. Each color indicates a different model. For all parameters, estimates and 85% CIs are shown. Solid circles indicate effects that are highly significant (95% CI does not cross zero). For treatment effects, control is the reference. For land cover effects, shrubland is the reference.

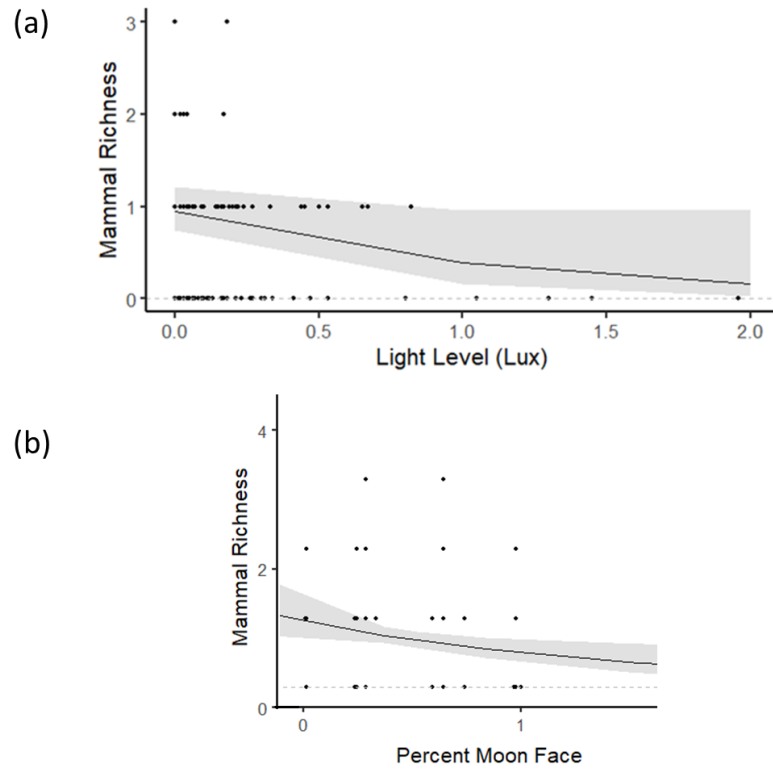


Figure 2.5: (a) Light level vs mammalian species richness from top-ranked model in Table 2.1. (b) Percent moon face vs mammalian richness from top-ranked model in Table 2.1.

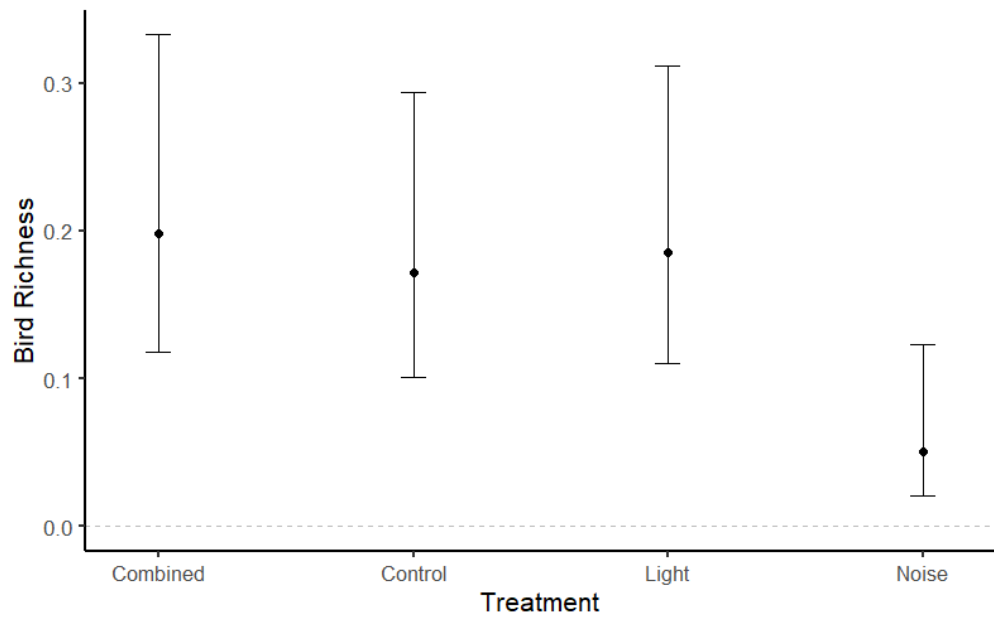


Figure 2.6: Observed bird species richness by treatment. Results shown from the top-ranked model containing a treatment effect in Table 2.1. Estimates and 85% CIs are shown.

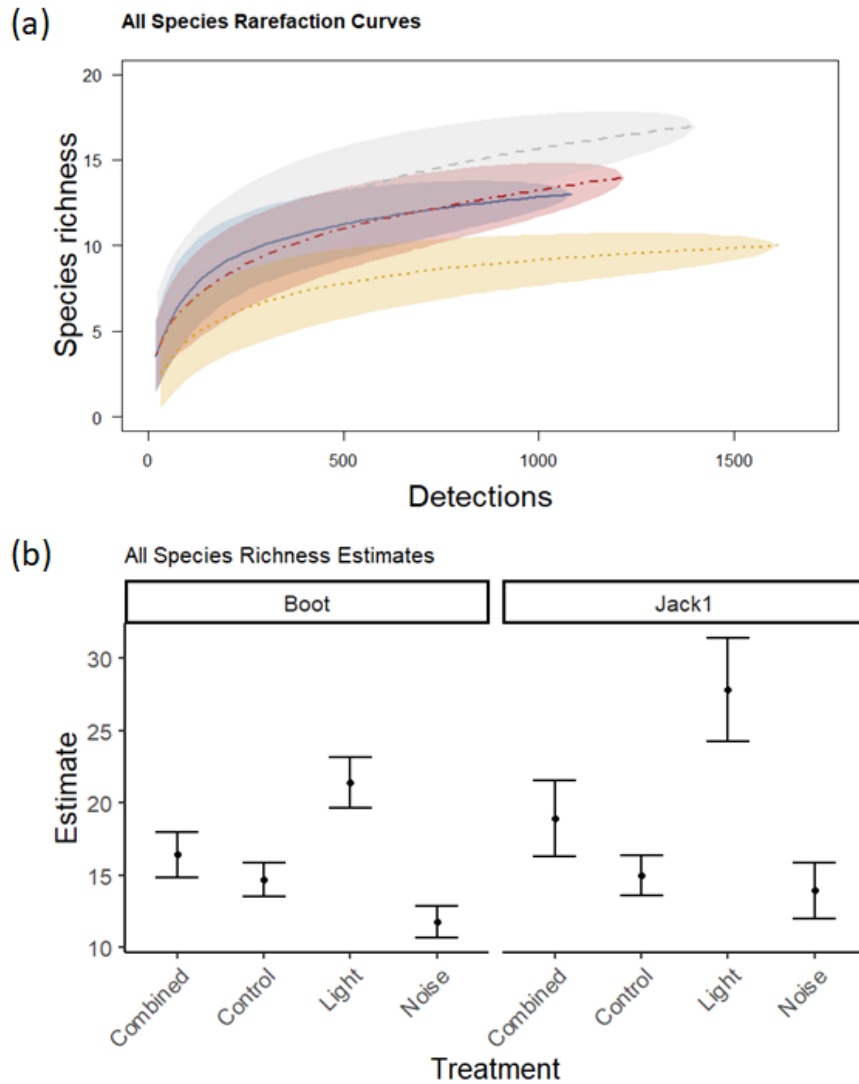


Figure 2.7: (a) Species accumulation curves for all species by treatment. Shaded areas represent 95% confidence intervals. Red is combined treatment, blue is control, grey is light, and orange is noise. (b) Total species richness estimates for each treatment, standard error bars shown.

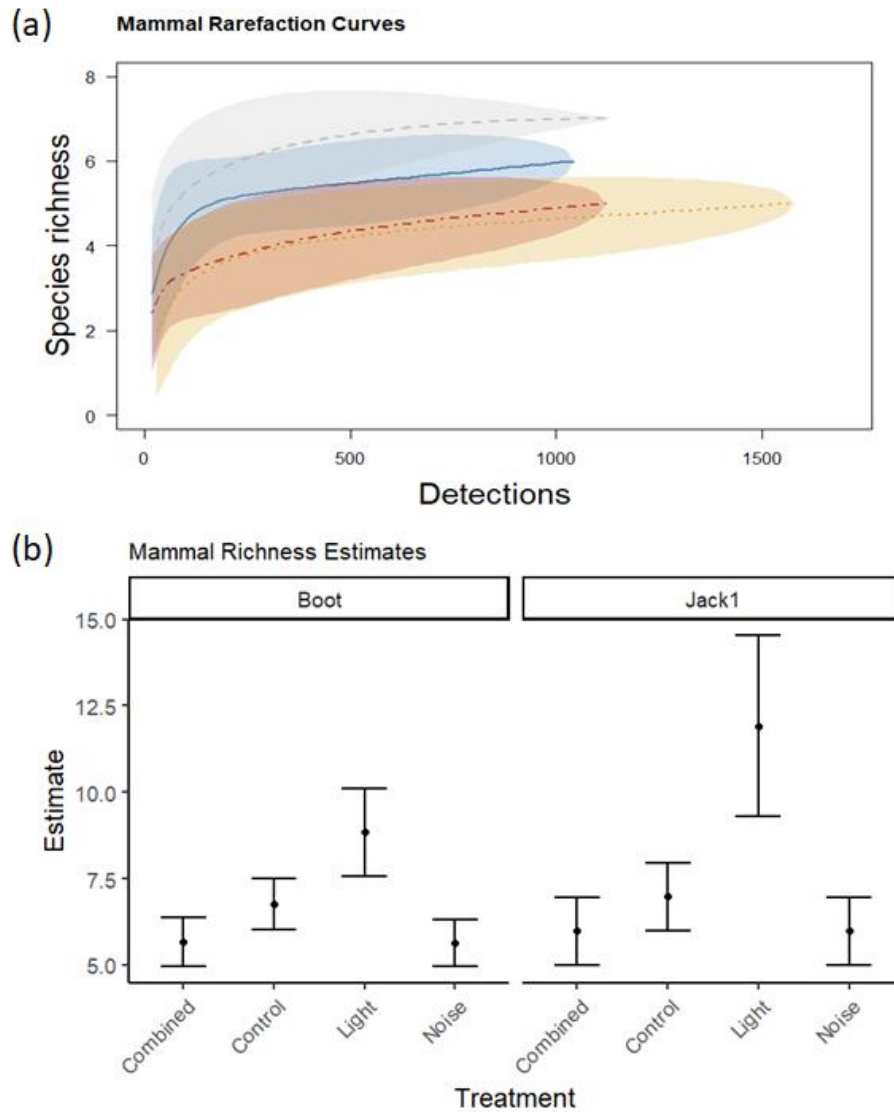


Figure 2.8: (a) Species accumulation curves for all mammal species by treatment. Shaded areas represent 95% confidence intervals. Red is combined treatment, blue is control, grey is light, and orange is noise. (b) Mammalian species richness estimates for each treatment, standard error bars shown.

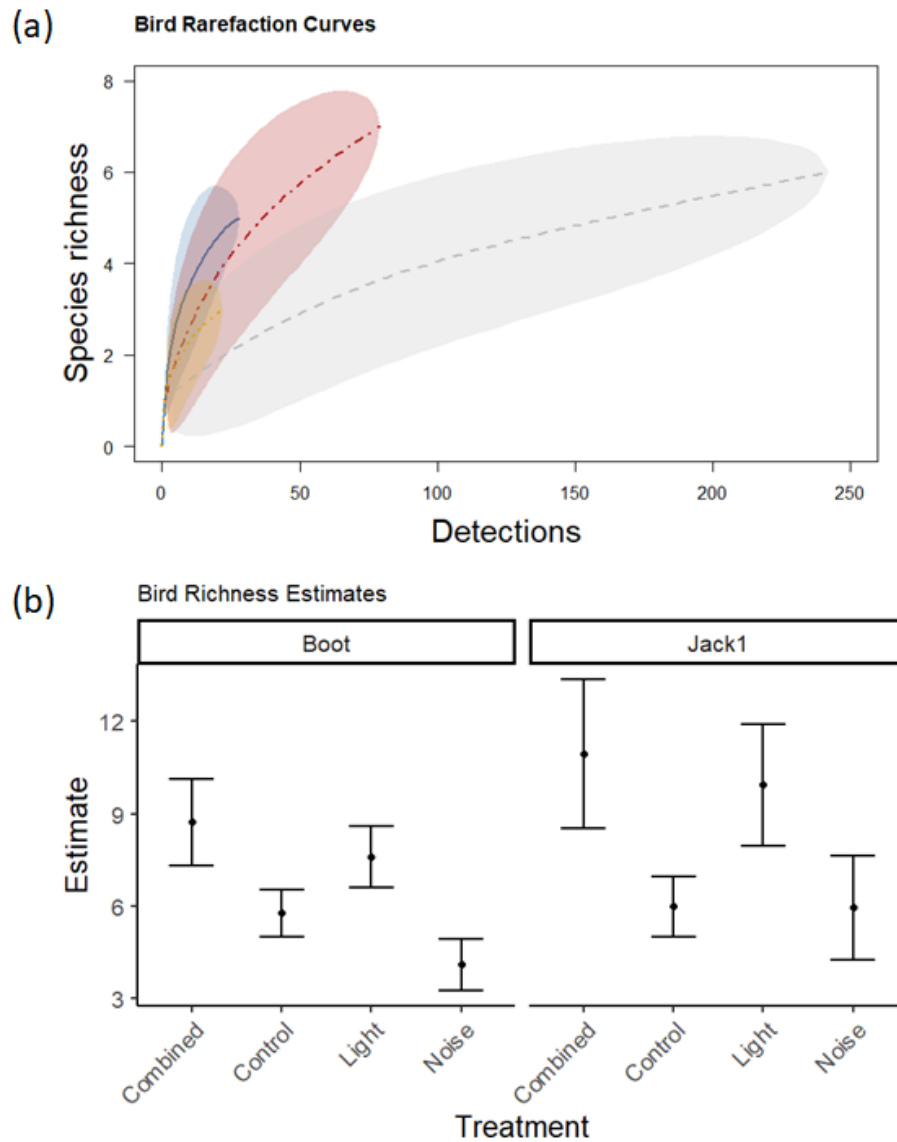


Figure 2.9: (a) Species accumulation curves for all bird species by treatment. Shaded areas represent 95% confidence intervals. Red is combined treatment, blue is control, grey is light, and orange is noise. (b) Bird species richness estimates for each treatment, standard error bars shown.

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APPENDIX

Table S1.1: Means and ranges of the noise and light measurements by treatment.

Treatment	LAeq		LZeq		Lux	
	Mean	Range	Mean	Range	Mean	Range
Control	40.25	25.7 – 68.3	65.99	53.5 – 81.4	0.00	0.00 – 0.00
Noise	47.81	35.0 – 63.4	73.90	60.2 – 87.1	0.00	0.00 – 0.00
Light	36.07	28.5 – 57.0	63.89	55.0 – 75.7	0.31	0.00 – 4.70
Combined	45.75	34.60 – 58.30	72.27	58.6 – 84.7	0.29	0.00 – 4.57

Table S1.2: Model selection results for trap success without recaptured individuals included. Models with $\Delta AICc \leq 4$ are shown and those with $\Delta AICc \leq 2$ were considered to have strong support. Bolded variables had 85% CIs that did not overlap zero. Variables bolded and italicized had 95% CIs that did not cross zero. K is the number of parameters in the model, AICc is the Akaike's Information criteria adjusted for small sample size, $\Delta AICc$ is the change in AICc from the top model, and w is the model weight. See Table 1 for an explanation of variable names. All models included trap station nested within site as a random effect (μ).

Model	K	AICc	$\Delta AICc$	w
<i>MP6 + Lux + TMin + μ</i>	10	1527.47	0.00	0.29
<i>MP6 + Lux + TMin + Seas + μ</i>	11	1528.16	0.69	0.21
<i>MP6 + Lux + μ</i>	9	1528.89	1.42	0.14
<i>MP6 + Lux + Seas + μ</i>	10	1529.41	1.94	0.11
<i>MP6 + TMin + μ</i>	9	1529.87	2.40	0.09
<i>MP6 + TMin + Seas + μ</i>	10	1530.50	3.03	0.06
<i>MP6 + μ</i>	8	1530.73	3.26	0.06
μ	3	1539.70	12.20	0.00

Table S1.3: Interactions tested for body condition models. ΔAICc is the change in AICc from the top-ranked model without any interactions. Parameters in bold had 85% CIs that did not contain zero. Bolded and italicized parameters had 95% CIs that did not contain zero.

Analysis	Interaction	ΔAICc
Early Season	<i>LAeq + Sex + LAeq*Sex</i>	0.65
	LAeq + LC + LAeq*LC	4.09
	Sex + Class + Sex*Class	10.79
	Sex + LC + Sex*LC	5.56
Late Season	LAeq + Sex + LAeq*Sex	4.39
	<i>LAeq + LC + LAeq*LC</i>	3.09
	Sex + Class + Sex*Class	6.01
	Sex + LC + Sex*LC	4.89
	LAeq + Lux + LAeq *Lux	5.09
	Lux + LC + Lux*LC	5.84
	Lux + Sex + Lux*Sex	4.93

Table S2.1: Means and ranges of light and noise measurements at cameras by treatment

Treatment	Lux		Laeq		Lzeq	
	Mean	Range	Mean	Range	Mean	Range
Control	0.00	0.0 – 0.0	42.63	31.4 – 65.3	65.88	58.5 – 78.4
Light	0.16	0.0 – 1.1	40.57	31.3 – 60.3	65.60	55.2 – 80.3
Noise	0.00	0.0 – 0.0	48.58	35.5 – 64.9	73.32	59.3 – 83.8
Combined	0.20	0.0 – 2.0	48.21	38.5 – 60.2	73.07	61.6 – 84.9

Table S2.2: Total number of detections per species or taxa, plus the number of unique camera locations where each species or taxa was detected.

Species	Detections	Cameras
Deermice (<i>Peromyscus</i> sp.)	4,106	122
Desert cottontail (<i>Sylvilagus audubonii</i>)	348	14
Least chipmunk (<i>Neotamias minimus</i>)	301	5
Woodhouse's scrub jay (<i>Aphelocoma woodhouseii</i>)	244	10
Rock squirrel (<i>Otospermophilus variegatus</i>)	162	7
Wild turkey (<i>Meleagris gallopavo</i>)	64	5
Woodrat (<i>Neotoma</i> sp.)	54	1
Elk (<i>Cervus canadensis</i>)	34	3
Plateau fence lizard (<i>Sceloporus tristichus</i>)	33	12
Plateau striped whiptail (<i>Aspidoscelis velox</i>)	26	21
Black-tailed jackrabbit (<i>Lepus californicus</i>)	25	3
Spotted towhee (<i>Pipilo maculatus</i>)	20	7
Mourning dove (<i>Zenaida macroura</i>)	18	1
Common raven (<i>Corvus corax</i>)	9	2
Chipping sparrow (<i>Spizella passerina</i>)	8	5
Grey fox (<i>Urocyon cinereoargenteus</i>)	8	5
American robin (<i>Turdus migratorius</i>)	6	4
Greater short-horned lizard (<i>Phrynosoma hernandesi</i>)	5	1
Bluebird (<i>Sialia</i> sp.)	3	3
Ash-throated flycatcher (<i>Myiarchus cinerascens</i>)	1	1
Mule deer (<i>Odocoileus hemionus</i>)	1	1
Dark-eyed junco (<i>Junco hyemalis</i>)	1	1
Striped whipsnake (<i>Masticophis taeniatus</i>)	1	1

Table S2.3: Total species richness estimates for each treatment. Jack1 is the first-order jackknife estimation and Boot is the bootstrap estimation. Est is the estimated species richness, SE is the standard error of the estimation.

Treatment	Boot			Jack1		
	Est	SE	Est SE	Est	SE	Est SE
Noise	11.80	1.09	10.70 – 12.89	13.93	1.96	11.96 – 15.89
Control	14.66	1.16	13.50 – 15.82	14.97	1.39	13.58 – 16.36
Light	21.42	1.74	19.68 – 23.16	27.81	3.55	24.26 – 31.36
Combined	16.40	1.55	14.85 – 17.96	18.92	2.61	16.31 – 21.52

Table S2.4: Mammal species richness estimates for each treatment. Jack1 is the first-order jackknife estimation and Boot is the bootstrap estimation. Est is the estimated species richness, SE is the standard error of the estimation.

Treatment	Boot			Jack1		
	Est	SE	Est SE	Est	SE	Est SE
Noise	5.64	0.68	4.96 – 6.32	5.98	0.98	5.00 – 6.96
Control	6.76	0.75	6.01 – 7.50	6.98	0.98	6.00 – 7.97
Light	8.84	1.27	7.57 – 10.11	11.92	2.61	9.31 – 14.52
Combined	5.67	0.71	4.96 – 6.39	5.98	0.98	5.00 – 6.97

Table S2.5: Bird species richness estimates for each treatment. Jack1 is the first-order jackknife estimation and Boot is the bootstrap estimation. Est is the estimated species richness, SE is the standard error of the estimation.

Treatment	Boot			Jack1		
	Est	SE	Est SE	Est	SE	Est SE
Noise	4.09	0.82	3.27 – 4.92	5.94	1.70	4.24 – 7.64
Control	5.77	0.76	5.01 – 6.53	5.98	0.98	5.00 – 6.97
Light	7.59	1.00	6.59 – 8.59	9.93	1.97	7.97 – 11.90
Combined	8.73	1.40	7.32 – 10.13	10.93	2.41	8.52 – 13.35