Effects of Urban Lighting at Night on Daytime Songbird Aggression

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Abstract

Many animals require sleep for daily functions. In spring, songbirds expend a great deal of energy early in the day by singing to attract mates and aggressively protecting territory. Some evidence suggests that artificial lighting at night (ALAN) in the environment of wild birds increases their nighttime activity that, in turn, contributes to sleep loss. This study investigated how ALAN affects northern cardinal (*Cardinalis cardinalis*) response to experimental aggressive intrusion by conspecifics. The hypothesis tested is that high ALAN near cardinal roosting spots would cause those individuals to have less energy for daytime aggressive behaviors. After selecting known dark and bright urban roosting locations, ALAN was measured at specific sites with active cardinal territories during nighttime hours. Observers returned in the morning to present cardinal territorial songs using standardized call playback protocols. Aggressive behaviors of responding cardinals were recorded and used to quantify aggression intensity. Standard aggression measures included response latency, distance from bird to speaker, number of songs, hops, and flip flops. An aggression index was obtained using factor analysis which confirmed that aggressive responses featured short latency and approach distances, few chips, and many songs, flip flops, and hops. Analysis of variance revealed that cardinals roosting in high ALAN engaged in significantly more aggressive morning responses; directly contradicting predictions and previously published findings. One possible explanation for this result is that high ALAN might improve sleep in cardinals. To test this, autonomous recording units (ARUs) were placed in study locations to record nighttime calling behaviors in high and low ALAN. Insufficient data were obtained to clarify whether nighttime activity was reduced significantly by ALAN exposure. However, results showed that nighttime activity by cardinals is strongly influenced by moonlight, and that determination of the influence of ALAN on nighttime and daytime avian behavior must include measures of lunar illumination.

Keywords: *Cardinalis cardinalis*, artificial lighting, playback experiments, territoriality, avian behavior, anthropogenic effects

Introduction

Sleep is vital for animal performance, both physical and cognitive (Craven et al., 2022). Loss of sleep affects many behaviors that define success, such as activity levels, and factors that reduce sleep quality are of increasing interest in wildlife conservation (Roth et al., 2010). When

birds lack motivation to sing, they are less willing to spend energy on more complex songs and more rigorous social interaction required to maximize their fitness (Mussoi et al., 2022). Disturbed sleep can impact birds's ability to recognize and understand conspecific and heterospecific songs (Johnsson et al., 2022), which could impair territory defense and ability to attract mates (Nowicki & Searcy, 2004), or ability to eavesdrop on alarm calls from other birds and escape predators (Magrath et al., 2015). Laboratory study suggests that longer periods of light stimulation can trigger increased nighttime physical activity (Wikelski et al., 1999), which can contribute to sleep loss (Aulsebrook et al., 2021), but how sleep loss influences the behavior of wild, urban birds remains unclear. This study asks: does artificial lighting at night (ALAN) affect avian response to conspecific calls?

Intimidating potential threats to an adult's territory is necessary to protect nests (Hinde, 1956) and increase the chance of their offspring's survival. Because some avian species use vocalization to declare territories and warn away potential intruders, playback studies can be used to prompt aggressive responses (Hyman, 2003; Searcy & Beecher, 2009; Searcy et al., 2006). Previous songbird studies have deployed song playback trials to characterize the aggressive behavior consistent for that species and observe the methods birds use to defend their territory (Moran et al., 2018). Playback trials will be used to 1) determine what specific behaviors the urban northern cardinal (*Cardinalis cardinalis*) uses aggressively and 2) measure differences in aggressive responses between ALAN levels.

Our study species was the northern cardinal, a diurnal songbird chosen for its high abundance, visibility, and territoriality (Lemon, 1968). Northern cardinals live throughout the Eastern United States, Canada, and Mexico with an expanding range. Duetting and mate selection begins in the winter months and continues through spring (Lemon, 1968). Males (and, to a lesser extent, females) act territorial during this time. Northern cardinals roost in dense vegetation in urban or rural areas and are typically non-migratory (Bent & Austin, 1968). Previous studies have found that migratory species adapt more successfully to different sleeping hours than non-migratory species (Aulsebrook et al., 2021) and have suggested that the timing of non-migratory species' activity can be influenced by ALAN (Singh et al., 2021). Northern cardinal populations are common, and they are generalists that occupy all manner of habitats in and outside of human-disturbed landscapes, making them an ideal study species.

We hypothesized that high ALAN near cardinal roosting spots would cause those individuals to have less energy for daytime aggressive behaviors. The critical test was territorial playback trials in low-ALAN areas versus high-ALAN areas. The primary prediction was that cardinals in high-ALAN territories would display a fewer number of aggressive behaviors and vocalizations in response to playbacks. The rationale of this prediction explained that during laboratory studies, birds suffering from 12-hour nighttime periods of sleep loss had less motivation to use reduced energy budgets on vocalizations (Johnsson et al., 2022). Alternative hypotheses that could influence behavioral responses included anthropogenic noise, which was a confounding variable that was measured at the time of playback trials for inclusion in the statistical analyses. Previous research has observed increasing disruption in avian communication with increasing anthropogenic noise (Francis et al., 2011) making it a key variable to measure while attempting to characterize any impacts on behavior from ALAN levels. Vital results of this study include the importance of considering alternative anthropogenic variables and both natural and manmade light sources when attempting to qualify the effects of ALAN on avian behaviors.
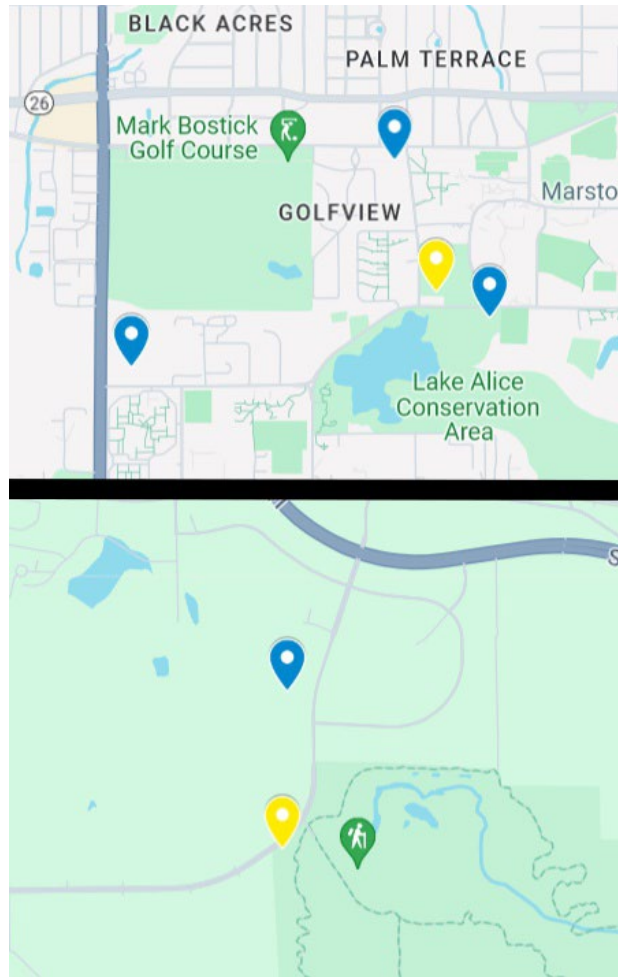
Methods

Research Design

The primary assumption of this study was that high ALAN near cardinal roosts disrupted their sleep, and this was tested using autonomous recording units (ARUs) to record the nighttime vocal activity of birds in high and low ALAN areas. If aggression is related to sleep quality, we would expect that the most aggressive birds would have better quality sleep during the night and would be less active (and calling less) in that period. Further assumptions included that playback trials conducted at different relative locations within a territory (i.e. trials done at the border of a territory versus the center of another) all prompted the same response intensity and birds slept at their morning locations (playbacks were spaced according to average northern cardinal territory size). Some environmental variables were controlled (canopy cover, habitat type, and distance to nearest road) to minimize their effects on results, while others (noise, temperature, moon luminosity, date, and time) were recorded to incorporate into the data analysis.

Study Area

This study was conducted across multiple urban locations on the University of Florida campus in north central Florida, United States as well as nearby rural locations around San Felasco Hammock Preserve State Park. Roads on campus and surrounding Gainesville, Florida were scouted for hardwood forest locations that 1) were 50 meters from the road, 2) had approximately 50% canopy cover, 3) had either no nearby artificial sources of light (for low ALAN sites; 0-2 lux) or had a nearby source of ALAN (for high ALAN sites; 2-4 lux), 4) were at least 200 meters other sites, and 5) were accessible day and night.

After identifying potential sites, *C. cardinalis* recordings were played to visually determine the presence of at least 1 adult cardinal. After final site selection, playback trials were conducted. ARUs (Wildlife Acoustics' Song Meter Mini 1) were deployed at playback trial sites and collected data across 17 days. Playback sampling occurred at three urban and two rural locations (Figure 1) and ARU sampling occurred at four urban locations and four rural locations (Figure 2). Cardinal home territories are on average 80-100 meters wide (Bent & Austin, 1968), which informed the minimum distance between different sampling locations (150 meters).

Figure 1. Map of low-ALAN (blue) and high-ALAN (yellow) playback trial locations.
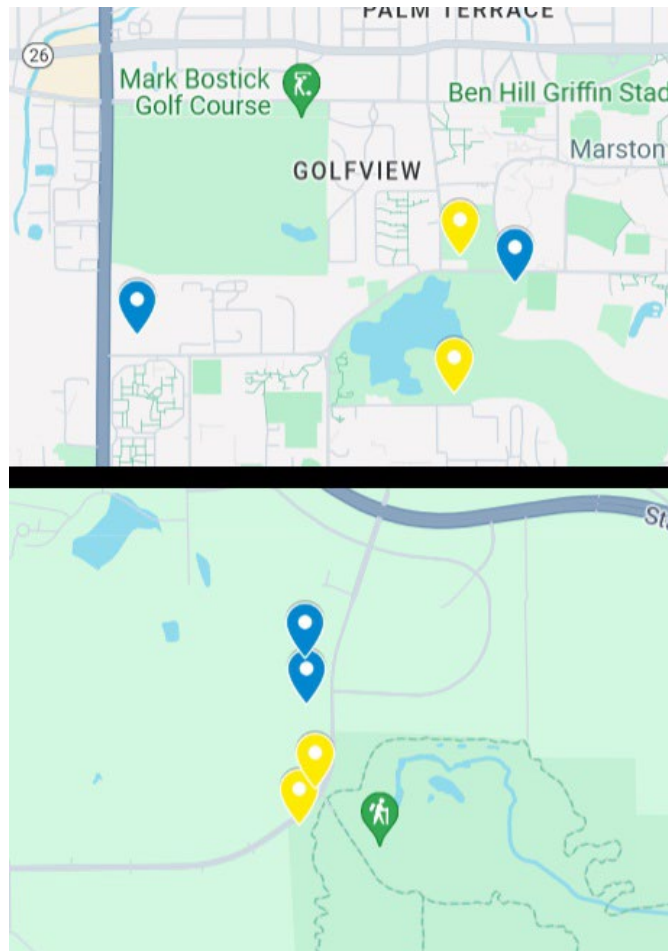
Figure 2. Map of low-ALAN (blue) and high-ALAN (yellow) ARU sampling locations.

Playback Methods

All locations were visited at night to measure ALAN (in lux, using a LX1330B Digital Light Meter) and the average noise in decibels over two minutes. Playbacks were conducted primarily in the morning with some afternoon and evening trials. American green tree frog (*Hyla cinerea*) calls served as a control. Northern cardinal songs were played from the Merlin Bird ID app. The chosen species' recordings (either *H. cinerea* or *C. cardinalis*) were played for at least three minutes and responding behaviors were recorded until individuals ceased responding. If no individuals responded within 3 minutes, the trial ended. A cardinal response ended when they left a 20-meter radius of the speaker. We recorded and categorized response behaviors (Table 1) (Grade & Sieving, 2016), the number of cardinals within 20 meters, sex, age, and all environmental variables. There was a minimum of 15 minutes between playbacks. The time,

date, moon luminosity (*Daily Moon Guide*, n.d.), temperature, cloud cover (%), and humidity (%) were all recorded at the time of each playback session.

Table 1. Overview of responding behaviors and how they were measured.

Aggressive Behavior	Behavior Description	Measurement
Singing	Individual emits a vocal singing response	Total number of occurrences during response
Flip flops	Bird rapidly switches body direction back and forth	Total number of occurrences during response
Hops	Bird makes a short jump or flight between branches	Total number of occurrences during response
Chipping	Bird makes loud, rapid chips	Total number of occurrences during response
Response latency	Length of time between playback begins and response begins	Seconds
Approach distance	Shortest observed distance between bird and speaker	Meters

Note. From "When the birds go unheard: highway noise disrupts information transfer between bird species," by Grade & Sieving, 2016, (https://doi.org/10.1098/RSBL.2016.0113).

ARU Methods

Autonomous recording units (ARUs) were deployed at the chosen locations to record bird activity at night. Each ARU recorded 5 minutes each hour from 6:00 PM to 6:00 AM. Bird activity was measured as the number of chips per unit time (Pérez-Granados et al., 2019). Avisoft-SASLab Pro software was used to control the sampling frequency of each sample and generate spectrogram images for visual identification of cardinal chips.

Data Analysis

Four distinct analyses were conducted on the aggression and ARU data. First, we assessed what factors were associated with response/non-response to playbacks. Not all playbacks attracted a bird, and so the response variable here was binary. A logistic regression analysis was run to determine the probability of response to different environmental variables.

Secondly, a factor analysis was run in Stata 18.0 to calculate a single ordinated factor of aggression based on the observed behaviors (listed in Table 1) for the cardinals that responded. Thirdly, the factor scores for each bird were used as the response variable in a Poisson-distributed generalized linear model using ALAN, noise, and moon luminosity as predictor variables. Finally, to analyze the ARU samples, a multilevel mixed effect generalized linear model was conducted with the amount of chips per sample as the response variable and ALAN, average noise, and the time of night (in three-hour blocks) as predictor variables. To visualize the

influence of natural and artificial lighting, the total number of chips recorded was graphed in relation to moon luminosity, moon presence during the night, and ALAN.

Results

29 individual cardinals were observed across all attempted playback trials (n = 41). 19 individuals entered the 20-meter radius and responded vocally. The range of ALAN observed was 0-3.8 lux. Defined dark areas (ALAN < 2 lux) had an average of 0.37 lux. Defined bright areas (ALAN > 2 lux) had an average of 3.04 lux. The range of background noise recorded was 0-6 decibels.

Playback Trial Results

The results of the playback trials characterized an aggressive response and supported a difference in aggression levels between responses in low ALAN territories and high ALAN territories. Cardinals that roosted in dark areas (n = 11) had a higher mean response latency and approach distance. Lower-ALAN cardinals had a lower mean number of chips, songs, flip flops, and hops. Cardinals that roosted in bright areas (n = 8) had a lower mean response latency and approach distance. Higher-ALAN individuals had a higher mean number of chips, songs, flip flops, and hops (Table 2). Some playback trials using cardinal calls (n = 17) did not prompt a response and were not included in the aggression analysis. The probability of a response occurring decreased with time of day ($t(31) = -2.86$, $p = 0.004$) (Figure 3) and background noise ($t(31) = -1.63$, $p = 0.103$) (Figure 4). None of the control playback trials (n = 9) prompted a response.

Table 2. Mean quantities of each response variable per low and high ALAN levels.

ALAN level	Response latency (seconds)^	Approach distance (meters)^	Number of songs*	Number of flip flops*	Number of hops*	Number of chips^
Dark (< 2 lux)	84.73	7.75	2.27	1.45	6.82	36.91
Light (> 2 lux)	69.75	3.69	7.43	4.43	9.71	57.71

Note. * indicates variables increasing with the index of aggression, ^ indicates variables decreasing with the index of aggression.
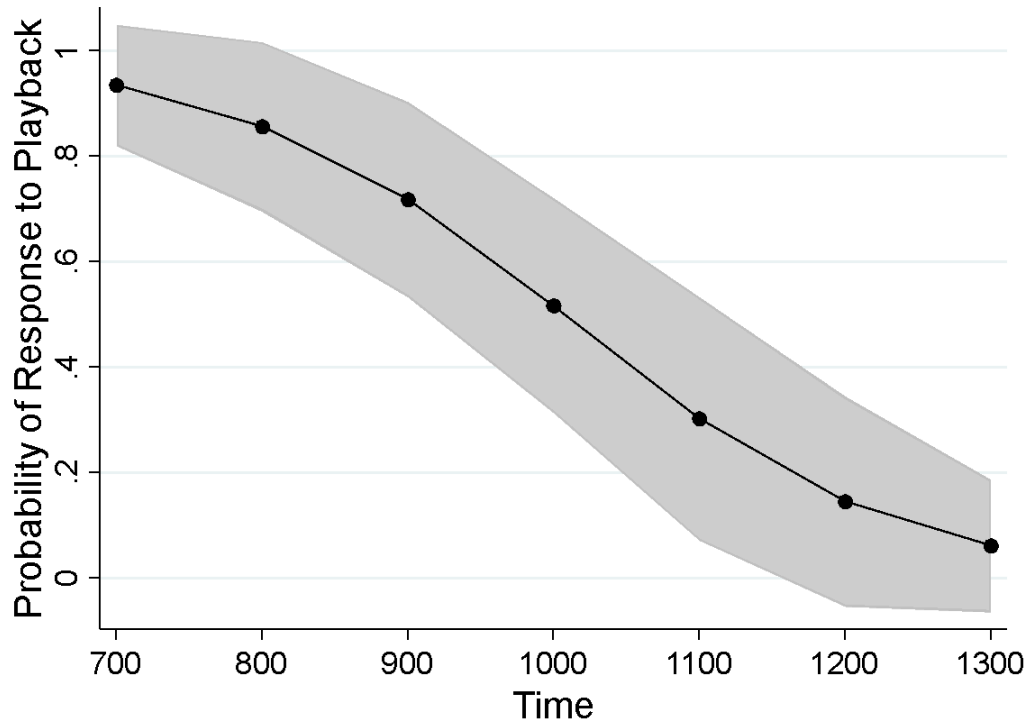
Figure 3. The time of day (*x*-axis; in 24-hour time) versus probability of bird response to playback (*y*-axis).
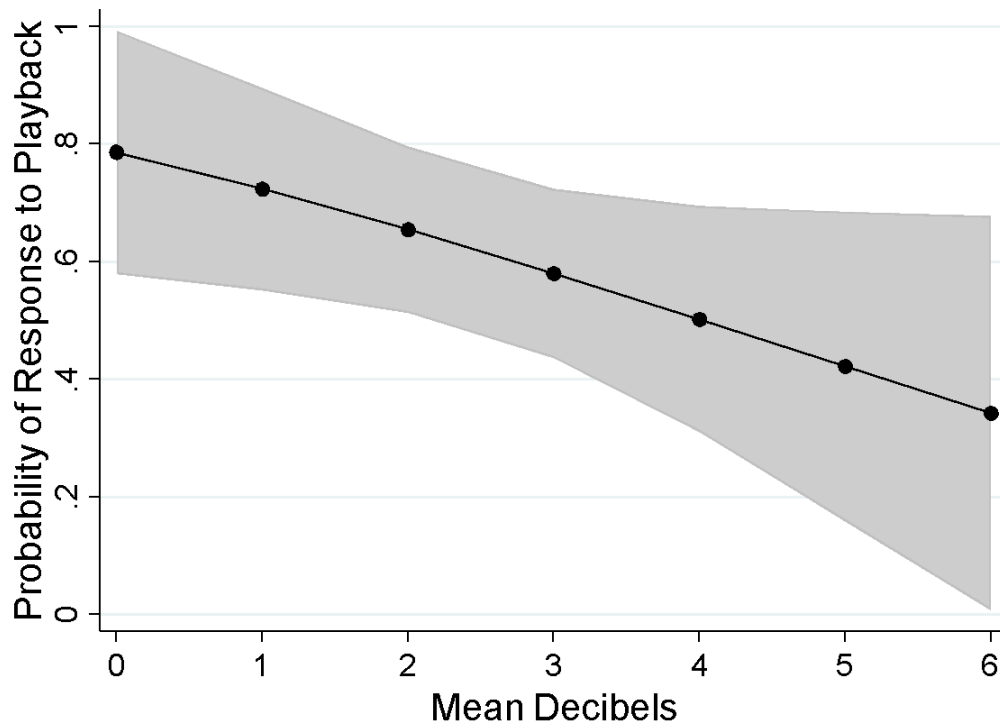

Figure 4. The mean background noise (*x*-axis; in decibels) versus probability of bird response to playback (*y*-axis).

The generated aggression index of aggression was responsible for 70.52% of variance within occurrence of aggressive behaviors. Responses that factored higher on the aggression index featured a short response latency, a short approach distance to the speaker, a low number of chips, and a high number of songs, flip flops, and hops. High-ALAN cardinals used more aggressive responses while low-ALAN cardinals displayed weaker responses (Figure 5). Cardinals responding after nights of high moon luminosity used more aggressive responses (Figure 6; Table 3).
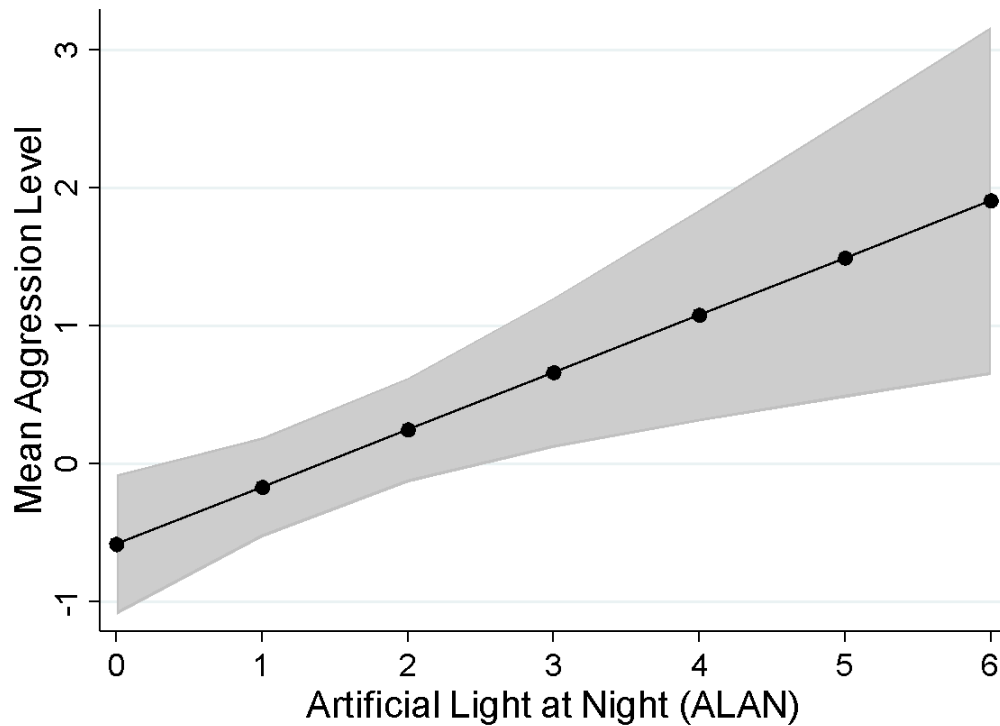
Figure 5. Artificial light at night (*x*-axis) versus the mean aggression index (*y*-axis).
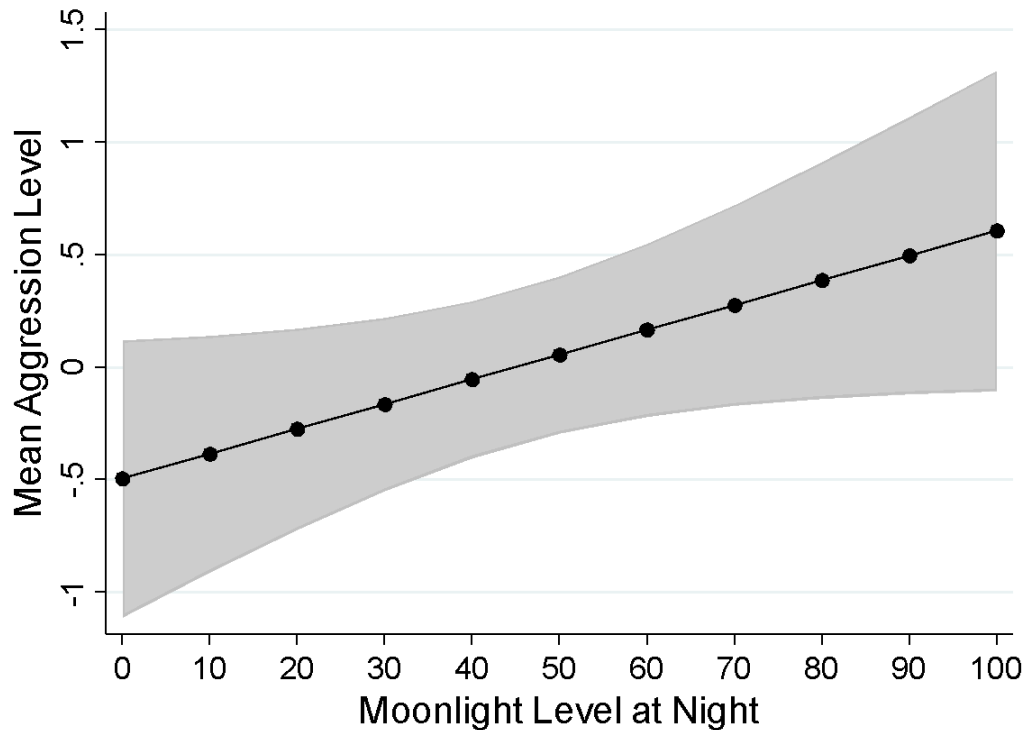
Figure 6. Moon luminosity at night (*x*-axis) versus the mean index of aggression (*y*-axis).

**Table 3.** Generalized linear model results for the effects of treatments on response aggression.

Treatment	t-value	P value
Moon luminosity	2.08	0.056
ALAN	3.37	0.005 *
Noise	-1.31	0.212

Playback Trial Results

Vocal activity varied throughout the ARU sampling trials (n = 298 five-minute clips). Audio samples recorded in dark areas (n = 175) had a mean of 5.95 chips (standard deviation = 29.47). Audio samples recorded in bright areas (n = 123) had a mean of 8.02 chips (standard deviation = 42.82). The number of chips per 5-minute sample varied enough that statistical analyses were inconclusive. However, graphical examination of the number of chips produced, alongside ALAN and moon brightness (Figures 7 and 8), suggests that lunar illumination can influence nighttime activity.
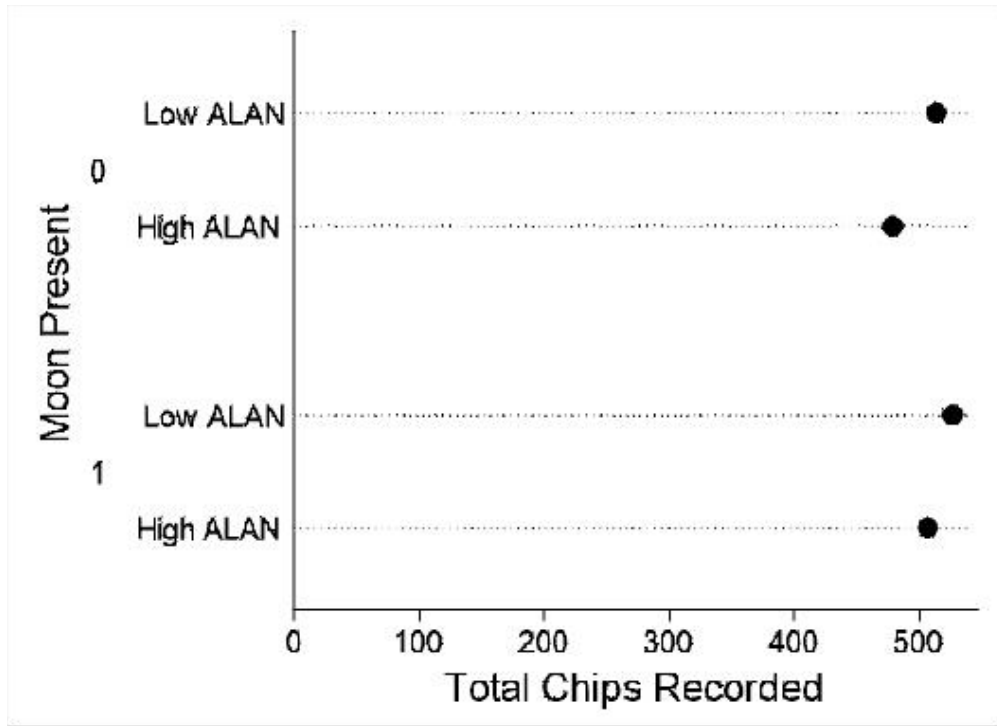
Figure 7. The number of total chips recorded across all samples (*x*-axis) divided according to moon presence and ALAN level (*y*-axis).
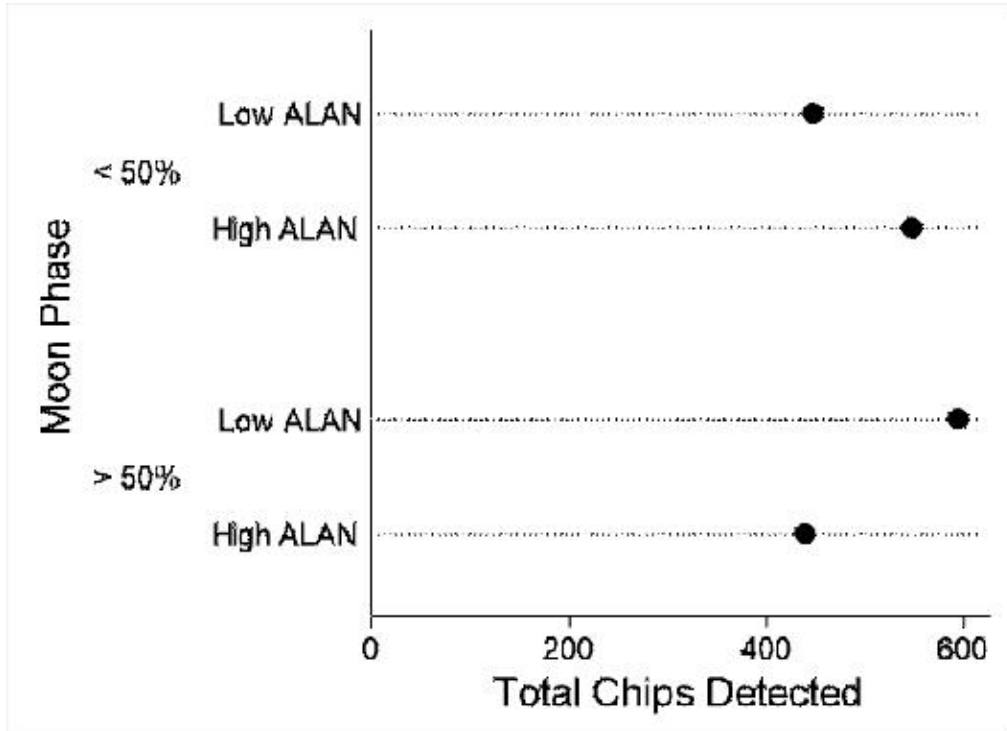
Figure 8. The number of total chips recorded across all samples (*x*-axis) divided according to moon luminosity and ALAN level (*y*-axis).

Discussion

Contrary to the original hypothesis that ALAN would decrease aggressive responses, cardinal aggression was higher with both high ALAN and brighter moon phases. The amount of both artificial and natural lighting at night could influence factors that control aggression in birds' morning responses. ALAN and moon luminosity had similar effects on morning aggression, indicating that extended periods of ALAN might trigger the same behavioral cues as brightly moonlit nights. Individual birds displaying stronger responses to perceived territory threats might have increased testosterone, short-term stress levels, or energy budgets to utilize. ALAN has advanced the timing of testosterone (Dominoni et al., 2013) and increased corticosterone in some species of songbirds. Longer periods of photostimulation have been reported to increase testosterone levels and physical activity in male birds (Wikelski et al., 1999). Increased ALAN might not be impacting sleep so much as it might be amplifying chemical contributors to behavioral aggression.

ALAN could contribute to observed differences in vocal activity at night. Cardinals chip when foraging, for territory defense, to warn against predators, or to communicate between mates (Lemon, 1968), so the number of chips during the night indicates activity. Previous study suggests avian species prefer roosting in higher ALAN levels (Gorenzel & Salmon, 1995). Birds with different dispositions might prefer different ALAN levels; anxious birds might be less stressed in high ALAN areas because they can scan for predators. Cardinals, in fact, prefer areas with high visibility to guard their nests (Mitchell et al., 1996). The total number of chips detected was lower during high-ALAN trials, indicating those cardinals were less active during the night perhaps due to the increased security described above. When combined with moon luminosity levels, the difference in chipping between ALAN levels was even greater, suggesting the presence of both natural and artificial light strengthened impacts on nighttime avian behavior; however, the amount of data collected insufficient to determine the strength of this relationship. Lunar illumination has not been accounted for in similar previous studies but has profound effects on avian physiology (Portugal et al., 2019), and results demonstrate that the true effects of ALAN may not be determined without attention to lunar illumination's influence.

ALAN might not be disruptive to all avian species and might even provide a benefit based on species or disposition. Previous studies have asserted obvious negative effects, such as

nighttime window collisions in migratory birds (Lao et al., 2020), but few have studied how ALAN affects non-migratory birds that do not rely on nighttime travel. ALAN could better equip cardinals for increased morning aggression. If cardinals can use more aggressive responses, they can better defend their territories and might have increased reproductive success (Conner et al., 1986). Urban settings will only continue to expand, bringing increased ALAN to natural landscapes, so understanding how ALAN affects different species both migratory and non-migratory is key. Knowledge of these effects can inform future management practices and regulations involving light pollution. While *C. cardinalis* populations are not declining, the methods used in this study could be used to determine ALAN influence on other avian species that claim territories and respond to playbacks.

Future study could broaden understanding of cardinal behavior beyond these observations. Examination of chemical contributors to aggression could reveal precisely which physiological factors ALAN influences. Capturing and identifying individual cardinals roosting in bright and dark ALAN, testing their corticosterone and testosterone levels, and observing their behavior could reveal if any stress or hormonal changes influence their behavior. Stress levels could also be compared using heart rate monitors on individual birds and could indicate energy expenditure or comfort when roosting. Examination of safety (such as predator surveying and nest predation rates) and reproductive success in high and low ALAN areas could reveal if cardinal nests are safer between the two conditions, which could provide evidence for the indirect effects of ALAN discussed above.

Acknowledgements

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