

RESEARCH ARTICLE

White light reduces flight height of birds in low-density migration corridor

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Funding information

National Aeronautics and Space Administration, Grant/Award Number: 80NSSC21K0930

Abstract

Artificial light at night (ALAN) has been shown to influence the behavior of migratory birds, yet how different light spectra modulate these effects remains unclear. We conducted a field experiment for 31 nights at a remote site in northern Colorado, USA, using 2 800-W light-emitting diode (LED) floodlights with white, red, amber, and blue lighting treatments during fall migration in 2023 and 2024. Using a vertical-looking radar system, we quantified avian in-flight responses in migration traffic rate, flight height, and flight direction between paired control periods with no light and periods with lighting treatments. Although we found no effects of our treatments on migration traffic rate and weak effects on flight direction, we found that broad-spectrum white light with emissions across a 400–600 nm spectrum reduced mean avian flight height by an estimated 22.57 m (± 10.53 SE) compared to dark periods, and this response was stronger than red and blue lighting treatments. Our ability to detect behavior changes from a point source in a rural, low-density migration system supports the notion that the effects of artificial light at night on bird behavior may be more pervasive than is often recognized, and that this varies by ALAN spectra. Beyond providing insight into avian orientation and in-flight behavior, our results have implications for future research, the conservation management

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of artificial light at night, and lighting designs that minimize effects on migratory birds.

KEYWORDS

aeroecology, artificial light at night, bird migration, field experiment, light pollution, radar ornithology

For millions of years, animals have evolved with a light cycle that followed a predictable diurnal pattern (Hölker et al. 2010, Gaston et al. 2015). However, as human development has spread across much of the globe, illuminated landscapes have drastically altered this light cycle by emitting high levels of artificial light at night (ALAN), illuminating nocturnal airspace habitat that would otherwise be dark (Kyba et al. 2017, Seymoure et al. 2025). Given the recency of this development, we are only beginning to understand the full impacts on animal behavior and ramifications for wildlife conservation (McLaren et al. 2018, Grubisic and van Grunsven 2021). Furthermore, many studies have focused on brightly lit urban centers, creating a bias that may underestimate the biological effects of ALAN in rural, remote, and marine systems, which remain understudied (Gaston et al. 2021, Merckx et al. 2023). Taken together, the growing impact of ALAN is becoming an important focus within global change research (Davies and Smyth 2018).

The impact of ALAN on migratory birds is an area of study that has received particularly widespread attention. Yet, despite this, we still lack strong consensus around the proximate and ultimate mechanisms that drive bird responses to light (Adams et al. 2021). For instance, there is ample evidence that ALAN attracts birds at multiple spatial scales (Poot et al. 2008, McLaren et al. 2018, Van Doren et al. 2021) and often disorients their sense of direction (Gauthreaux 1982, Chernetsov 2016). However, it remains unclear if these effects are the consequence of disruptions to avian perceptions of photoperiods (Kumar et al. 2017), stellar compasses (Foster et al. 2018), magnetic compasses (Muheim et al. 2016), or another physiological or behavioral mechanism. Moreover, avian behavioral responses can be variable, including changes in flight height (May et al. 2017) or direction (Bruderer et al. 1999), and some lighting, such as flashing lights or lasers, can repel birds (Andelt et al. 1997, Goller et al. 2018, Clausen et al. 2019).

While it seems clear that ALAN can have profound effects on avian behavior, there are substantial gaps in our understanding of how and why these effects occur. Beyond the mere presence of light at night, the degree to which the characteristics of lighting modulate its effect is one such gap. A notable point of interest is the effects of different colors or, more specifically, spectral power distributions of light, on avian behavior. Early attempts to investigate this question along the Netherlands North Sea coastline suggested that birds were most disturbed by light with long wavelengths, such as red light, and less affected by short wavelengths, such as blue and green lights (Poot et al. 2008). However, recent studies that employed systematic, automated methods for quantifying bird responses suggest that shorter wavelengths of blue, green, and white lights are more attractive to migrating birds (Evans et al. 2007, Rebke et al. 2019, Zhao et al. 2020). There may also be taxonomic or age-based variation in behavioral responses, as suggested by Syposz et al. (2021), which found that breeding Manx shearwaters (*Puffinus puffinus*) were more strongly repelled by blue and green light than other colors. These findings have led some to suggest that avian vision is more sensitive to short-wavelength light and, thus, birds express stronger phototactic responses when exposed to it (Zhao et al. 2020). Indeed, there is some evidence that shorter wavelengths stimulate the cryptochrome proteins used for geomagnetic orientation and overlap more with songbird visual sensitivities (Nießner et al. 2014, Longcore 2023). Yet, there remains a high degree of uncertainty in our understanding of how birds respond to different spectra of light in different contexts. Beyond providing insights into basic, mechanistic animal biology, physiology, and behavior, filling these gaps could have wide-reaching conservation implications. Migratory bird collisions with anthropogenic structures are a major source of mortality (Loss et al. 2015), and it is strongly suspected that ALAN plays a role in drawing birds closer to structures and hinders their ability to navigate

(Parkins et al. 2015, Lao et al. 2020, Van Doren et al. 2021). The management of ALAN has emerged as an integral tool in migratory bird conservation (Burt et al. 2023), and identifying spectra-specific effects on bird behavior could inform more dynamic and effective management practices.

We designed a field experiment with the explicit goal of understanding how in-flight bird behavior is impacted by different spectra of ALAN. Our experiment employed a lighting system with different lighting treatments and a portable radar to quantify avian in-flight behavior. Our specific objectives were to 1) determine if behavior was influenced by any of our color treatments relative to control periods when lights were off and 2) if the magnitude of those changes in behavior varied among treatments. Given previous support for the notion that avian vision is more sensitive to short wavelengths, we hypothesized that treatments containing short-wavelength light (white, blue) would attract more birds than longer wavelength lighting (red, amber), resulting in higher migration traffic rates, reduced flight heights, and greater deviations in flight direction.

STUDY AREA

We conducted an experiment in Pawnee National Grassland, a 780-km² remnant shortgrass prairie in Weld County, Colorado, USA, that is managed by the United States Forest Service. Weld County is in north-central Colorado and is part of the High Plains ecosystem, dominated by drought-tolerant, shortgrass prairie vegetation. Northern Colorado is a low-density migration traffic region relative to the eastern continental United States (Dokter et al. 2018) but serves as stopover habitat for birds along the North American Central Flyway and breeding habitat for many grassland species. Specifically, our study site was located within the eastern unit of Pawnee National Grassland (40.74° N, 104.03° W; Figure 1). The site was far from urban centers and direct sources of glare. While still impacted by skyglow, this site was 3 times darker than Sterling, Colorado, the closest city with a population >10,000 people, nearly 50 km away, and 13 times darker than the larger cities to the west, Fort Collins, Loveland, and Greeley, Colorado (Duriscoe et al. 2018). It is also

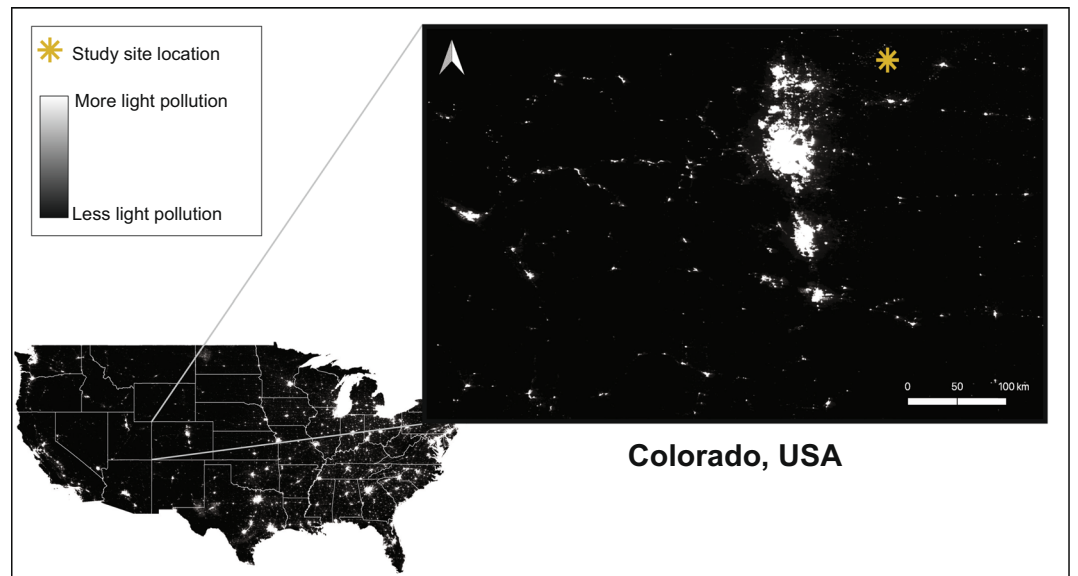


FIGURE 1 Study site location (yellow asterisk) and light pollution estimates from the National Oceanic and Atmospheric Administration's annual composite of artificial upward radiance (VNP46A4) in 2020 (Román et al. 2018).

approximately 16 km away from an isolated wind farm, which includes flashing red lighting. As one of the darkest locations in the region, this setting allowed us to conduct our study with minimal interference from external ALAN contamination.

METHODS

Lighting experiment design

We designed a field experiment with the explicit goal of understanding how in-flight bird behavior is impacted by different spectra of ALAN. We used 4 light-emitting diode (LED) floodlight color treatments (white, red, amber, and blue) to emit ALAN at a remote, dark landscape. Throughout our experiment, we recorded migratory bird flight behavior using a vertical-looking radar. These compact, radar systems have been leveraged to collect previously inaccessible data such as high-resolution variations in wingbeat frequency (Schmid et al. 2019) and vertical components of airspace habitat use by aerial insects (Simons et al. 2025).

We conducted the experiment from late August through late October of 2023 and 2024 to capture fall migration activity. We designed a lighting system that allowed us to manipulate the spectrum of a point ALAN source using 2 LED floodlights (Gopretty 800-W LED Flood Light; Gopretty, Chennai, India). We selected these floodlights for their commercial availability, representation of lighting commonly used in practice, and for producing the strongest output given the power limitations in our remote setup. We positioned floodlights approximately 2 m apart on the ground, and each floodlight produced a wide 140° beam angle. We used 5.5–6-mm-thick polyester film lighting gels to change the spectral emissions of our floodlights and produce broadband white, red, amber, and blue lighting treatments. We chose these treatments to represent a wide range of spectral emissions. Additionally, we used a handheld spectrometer and a dimmer (Impact D-1000 1,000-W AC Analog Dimmer Control; Gradus Group, New York, NY, USA) to standardize the irradiance of emissions within the 380–780-nm range to approximately 8 W/m², measured 1 m from the floodlights and aimed at the central point of their emission aperture (Figure 2). Previous work has documented the behavioral spectral sensitivities of 2 passerines (European starling [*Sturnus vulgaris*] and red-billed leiothrix [*Leiothrix lutea*]), with peaks near 500 nm (Figure 2; Longcore et al. 2023). While we recognize that both passerines are not native to the continental United States, data were unavailable for other relevant species, and we suspect these sensitivities provide some insight into potential ranges for other passerines. We provide additional characteristics of each treatment in our appendix (Supplemental Files A1–4), which were measured with a Sky Glow Spectrometer (Night Sky Metrics, Woodland Hills, CA, USA). We used a portable gas-powered generator to provide electricity for our experimental design (i.e., both the radar and lighting), which created some noise pollution, but this was consistent throughout our experiment.

To minimize potential systematic bias from spatio-temporal factors and isolate the effect of ALAN spectrum, we employed a color block study design adapted from Rebke et al. (2019), randomizing the sequence of treatments by using a random number generator (Figure 3). We alternated between 15-minute control periods (LED floodlights were off) and 30-minute color treatment periods (both LED floodlights were on). Crucially, the 15-minute control periods allowed birds to pass the area before starting a new treatment and created a baseline comparison for each of our treatments. This paired design allowed us to quantify behavioral changes in response to lighting relative to the lights being off. Additionally, by focusing on those changes between control and treatment periods, we also aimed to partially control for natural variations in migration activity and behavior due to time of year, time of night, and environmental conditions. We considered a color block to be completed after all 4 treatments had been emitted and did not repeat a given treatment until starting a new color block. We started our experiment 15 minutes after the onset of civil twilight and continued until the onset of civil twilight the following morning, pausing during inclement weather.

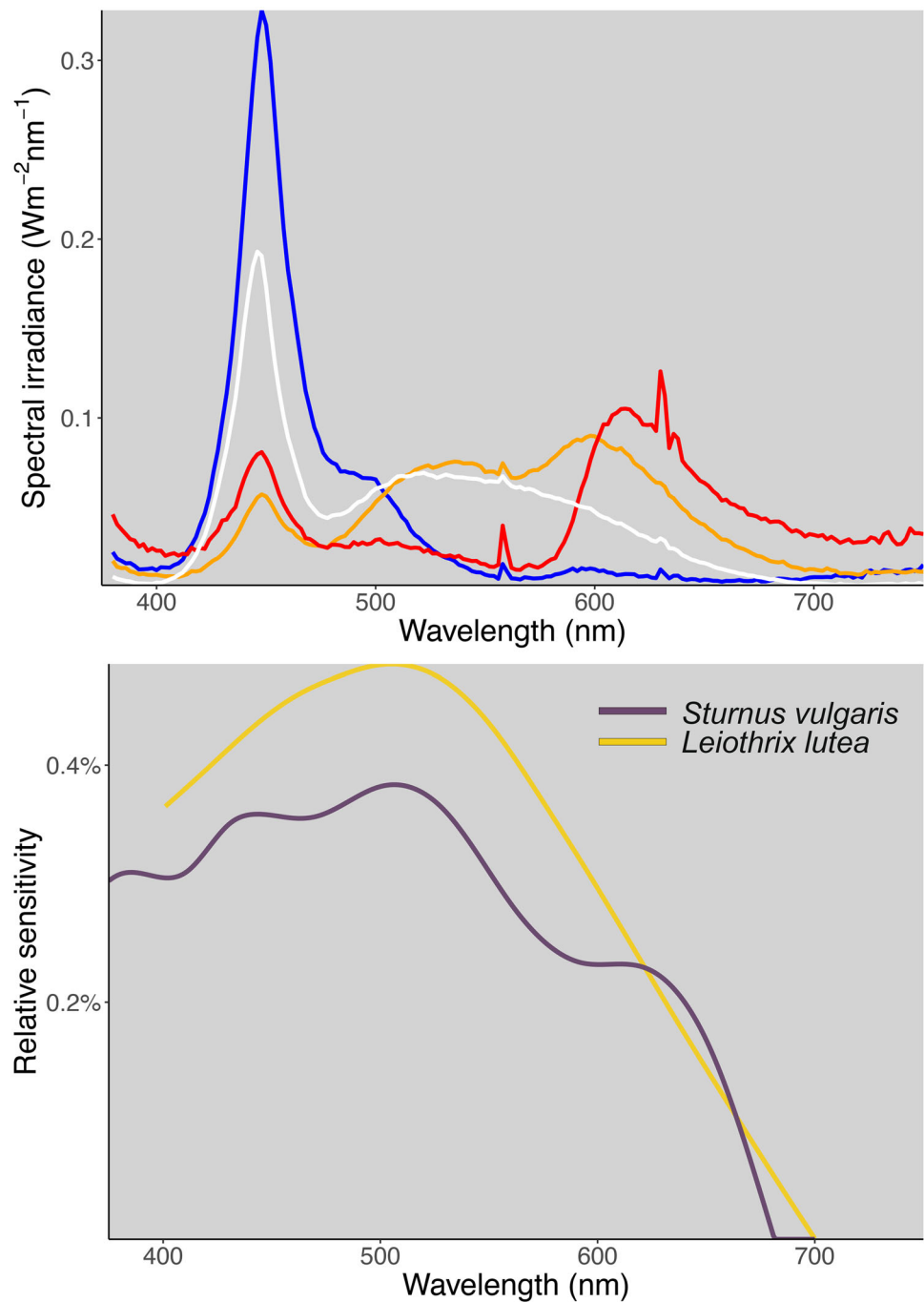


FIGURE 2 Summary of spectral irradiance (top) of the light source used as white, red, amber, and blue color treatments in a field experiment in Colorado, USA, 2023–2024. Spectral irradiance (y-axis) is plotted in $\text{W/m}^2/\text{nm}$ across wavelengths (x-axis) ranging from approximately 350 nm to 750 nm. The area under each curve sums to $8 \text{ W/m}^2/\text{nm}$, the standardized irradiance across all treatments. Relative behavioral spectral sensitivities (bottom) of 2 passerine species (European starling [*Sturnus vulgaris*] and red-billed leiothrix [*Leiothrix lutea*]), extracted from Longcore et al. (2023). We scaled the relative sensitivities by dividing the value at each wavelength by the sum across all wavelengths, such that the area under each curve equals one.

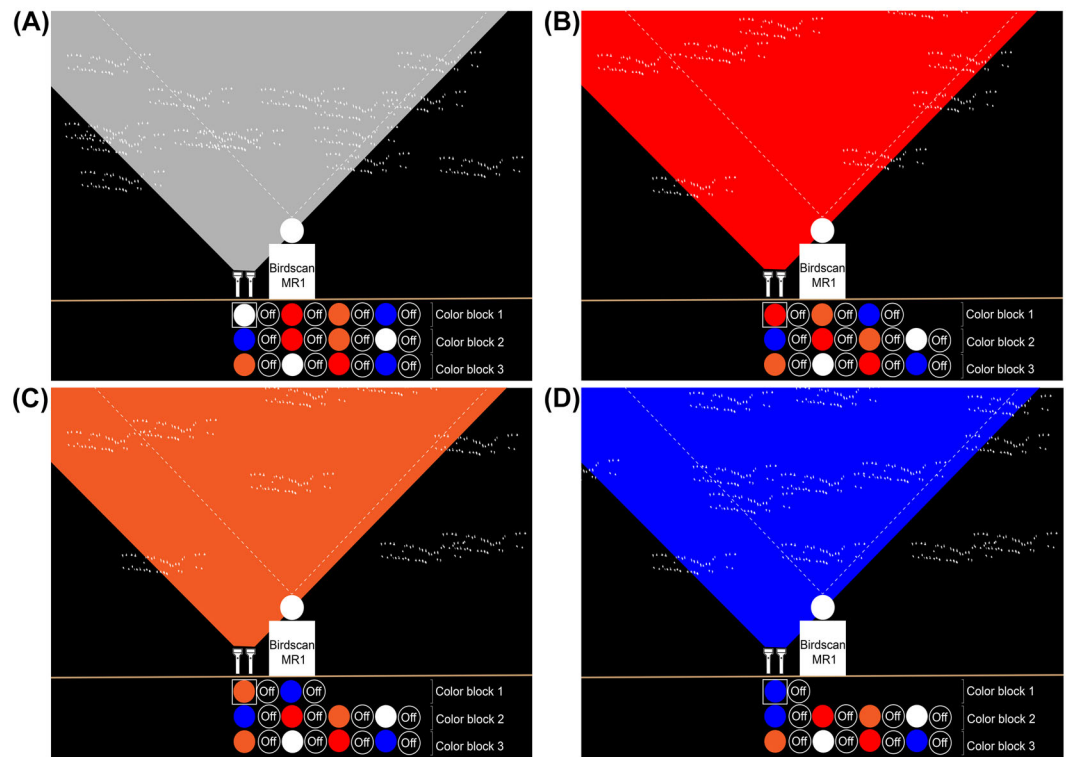


FIGURE 3 Experimental design for testing the effect of different spectra of artificial light at night on the in-flight behavior of nocturnally migrating birds in Colorado, USA, 2023–2024. Professional-grade spotlights emitted light into the sky and color treatments (white [A], red [B], amber [C], blue [D]) were cycled every 30 minutes, separated by 15-minute control periods when lights were turned off. The sequence of treatments was organized into color blocks, whereby colors were not repeated within a block and their order was randomized. We used a BirdScan MR1 radar to quantify activity in the atmosphere and collect bird behavior throughout the experiment.

Monitoring in-flight responses with BirdScan MR1

Throughout our experiment, we used a BirdScan MR1 to quantify in-flight bird behavior (Figure 3). This vertical-looking, mobile, 25-kW X-band (9.4 GHz, 3.2-cm wavelength) pulse radar system was explicitly designed to monitor and record animal movement in the lower atmosphere (Swiss Birdradar Solution 2023). This radar system uses a wide aperture angle to collect high-resolution data on the echoes produced by each individual object. The features from these echoes can be used to classify objects as insects, bats, and various taxonomic and functional groups of birds. We used the short-pulse, antenna-rotating setting, which emits electromagnetic pulses with a pulse length of 81 ns and a shot frequency of about 1,800 Hz, and allows for collection of information on flight speed and direction. These settings produce emitted pulses that reflect off objects in the airspace, creating backscatter from an altitudinal range of 50 m to approximately 1,000 m (Schmid et al. 2019, Weisshaupt et al. 2023). We deployed the BirdScan 3 m away from our spotlights with the intention of capturing in-flight bird behavior above and around our lighting setup.

Calculating behavior metrics and environmental covariates

We used the birdscanR R package (Haest et al. 2023) to extract and process in-flight bird behavior data in R version 4.4 (R Core Team 2024). Specifically, we used a class selection filter to exclude insects, producing a dataset that

included only echoes identified as birds. Using these data, we characterized in-flight behavior in 3 response variable metrics: migration traffic rate, mean flight height, and mean flight direction. We defined migration traffic rate as the number of detected birds passing (at any height) a 1-km-wide horizontal line that is perpendicular to the direction of flight per hour (Swiss Birdradar Solution 2023), flight height as the mean altitude (m) of detected birds, and flight direction as the circular azimuthal mean (degrees) of detected birds. We calculated these metrics up to a maximum altitude of 800 m at a 5-minute temporal resolution for each of our control and treatment periods, removing the first 5 minutes from each color block to account for variability attributed to adjustment phases. We calculated the mean of each behavioral response variable for each control and color treatment period.

Several environmental conditions, such as moon illumination (Rodríguez and Rodríguez 2009) and cloud cover (Ronconi et al. 2015), may influence how birds respond to ALAN. Although understanding those interactions was not an explicit focus of our study, we included these variables in our models to control for their influence on avian flight behavior. We used the `calculateMoonlightIntensity` function in the `moonlit` R package (Śmielak 2023) to estimate the hourly moon illumination. This function predicts the intensity of moon illumination (lux) relative to an average full moon, while accounting for the elevation angle of the moon at a given ground location. We downloaded total cloud cover data from the National Centers for Environmental Prediction's North American Regional Reanalysis (NARR) for the grid cell containing our study site (Mesinger et al. 2006). These data reflect the fraction of the sky covered by clouds at all altitudinal levels, expressed as a percentage, estimated at a 3-hour temporal resolution and 32-km spatial resolution. We selected the cell with the closest center to our study site. Although they likely influence flight behavior, we chose not to include any landscape variables given that our data were all collected at the same site.

Model-building and assessment

We conducted 2 analyses to address our 2 complementary research objectives. First, we analyzed whether bird behavior changed in response to each lighting color treatment relative to control periods, using behavioral metrics (migration traffic rate, flight height, and flight direction) as response variables. Second, we compared the magnitude of these changes among color treatments, using changes in behavioral metrics relative to the preceding control treatments as response variables. For both, we chose to fit generalized additive mixed models (GAMMs) with the `gam` function in the `mgcv` package (Wood 2017) in an effort to capture non-linear seasonal and time-of-night relationships with flight behavior. We also log-transformed migration traffic rate to address violations of normality and homoscedasticity assumptions, as the data exhibited a highly asymmetric distribution with a long right tail, characterized by frequent periods of low migration traffic and fewer periods of extremely high activity. We estimated models using restricted maximum likelihood (REML) and assumed a Gaussian error distribution with an identity link.

For our first objective, we modeled each color treatment separately, subsetting the dataset to color blocks and the preceding control period. For example, to understand how red light affected bird behavior, we included all red treatments and the preceding control periods. Using these subsets, we fit GAMMs for each of our 3 response variables. We included time after sunset (minutes) as a smooth term predictor using a default thin-plate spline smooth, whether the light was on or off as a categorical predictor (with lights off as the reference level), cloud cover and moon illumination as continuous linear predictors, and a smooth term to fit date using a random effect basis. The resulting models allowed us to determine if bird behavior was statistically different during treatment than control periods and estimate an effect size that accounted for variation explained by environmental covariates.

For our second objective, we compared the relative changes in behavioral responses among color treatments (white, red, amber, and blue), using white treatments as the reference level. We subtracted the value for a behavioral metric during each control period from the value in its subsequent color block. We treated this calculated difference as the response variable in this set of GAMMs and set the white color treatment as the reference

level. We reasoned that white light is a natural comparison point, given that it was our treatment without a filter and, more broadly, is often the default choice for residential, commercial, and municipal lighting. We, again, used time after sunset, cloud cover, and moon illumination as predictors, treating each with the same model specifications as the previous models. These models allowed us to determine changes in avian behavioral responses following transitions between color treatments and quantify the effects of environmental conditions on those responses. Finally, to further characterize how lighting treatment affected the vertical distribution of flight heights, we fit models with these same predictors and model structure but used the difference between the 25th percentile of flight height in the treatment versus control period as the response variable. We did not feel that this percentile approach was appropriate for migration traffic rate, as it is an aggregate metric that cannot be further subset within-period quantile decomposition, nor flight direction because it is a circular variable for which quantile metrics lack meaningful interpretation without an arbitrary reference point.

We used the `gam.check` function in the `mgcv` R package to check fit diagnostics and ensure convergence (Wood 2017). We selected basis dimensions (k) by incrementally increasing k until the k -index was >1.0 and the P -value was <0.05 , indicating sufficient basis complexity. Using these criteria, we confirmed that additional increases did not meaningfully change the estimated smooth. We used root mean square generalized cross-validation scores to assess convergence and visually inspected diagnostic plots to check for major violations of model assumptions.

RESULTS

We conducted our experiment on 31 nights across the 2 fall migration seasons. We collected data for 312 paired control and color treatment periods ($n_{\text{white}} = 84$, $n_{\text{red}} = 72$, $n_{\text{amber}} = 77$, $n_{\text{blue}} = 79$), recording 78,243 bird echoes. Across the 31 nights, the mean migration traffic rate was 1,263 birds/hour. However, the distribution of migration traffic across 5-minute periods was heavily right-skewed, with many periods having low mean migration traffic rates (min. = 22 birds/km/hour) and few color blocks having high mean migration traffic rates (max. = 9,610 birds/km/hour; Figure S1).

Color treatment effects relative to control periods

The white light treatment reduced the mean flight height relative to control periods (estimated difference = $-22.57 \text{ m} \pm 10.53 \text{ SE}$, $t = -2.14$, $P = 0.03$; Figure S2). We did not find an effect of other color treatments on flight height or an effect of any color treatment on migration traffic rate or flight direction relative to control periods (Table 1). We include residual diagnostic plots for our model showing the effect of white light treatment on flight height in the Appendix (Figure S2).

Regarding covariates for our first set of models, date was consistently a significant ($P < 0.05$) predictor variable, suggesting a non-linear, seasonal pattern to all our flight behavior responses. For flight direction, time after sunset was also consistently a significant non-linear predictor ($P < 0.05$) across all treatments (Table S1).

Comparison between color treatment responses

Mean bird flight height was lower in response to white light treatments compared with responses to other color treatments (estimated difference = $-19.83 \text{ m} \pm 9.39 \text{ SE}$, $t = -2.11$, $P = 0.04$). This effect was statistically significant for red (estimated difference = $25.77 \text{ m} \pm 12.75 \text{ SE}$, $t = 2.02$, $P = 0.04$) and blue (estimated difference = $29.02 \text{ m} \pm 12.44 \text{ SE}$, $t = 2.33$, $P = 0.02$) color blocks relative to white color blocks (Table S2). All these relationships held true but were stronger for models that used the 25th percentile of flight height as the response variable

TABLE 1 Summary of parametric coefficients from generalized additive mixed models evaluating the effects of color on bird migration traffic rate (log-transformed), mean flight height, and mean flight direction in Colorado, USA, 2023–2024. Each model includes a linear (parametric) term for the color treatment. We modeled sampling and environmental covariates (not included in this table) such as time after sunset and date using smooth terms (thin-plate splines and random effects). We included moonlight and total cloud cover as linear covariates. Estimates ($\pm$ SE) represent the effect size (in the unit shown) of each color category on the response variable. The t -values and corresponding P -values indicate the significance of these effects. Significant effects ($P < 0.05$) are denoted with an asterisk (*).

	Color	Estimate ($\pm$ SE)	t	P
Migration traffic rate (birds/km/hour)				
	White	0.05 $\pm$ 0.09	0.55	0.58
	Red	−0.04 $\pm$ 0.12	−0.35	0.73
	Amber	0.03 $\pm$ 0.10	0.35	0.73
	Blue	−0.11 $\pm$ 0.10	−1.01	0.31
Flight height (m)				
	White	−22.57 $\pm$ 10.53	−2.14	0.03*
	Red	5.22 $\pm$ 13.54	0.39	0.70
	Amber	−1.82 $\pm$ 1.18	−0.15	0.88
	Blue	−0.23 $\pm$ 13.74	−0.02	0.98
Flight direction (°)				
	White	−5.07 $\pm$ 9.29	−0.55	0.59
	Red	−13.91 $\pm$ 12.30	−1.13	0.26
	Amber	−9.27 $\pm$ 12.51	−0.74	0.46
	Blue	22.89 $\pm$ 12.18	1.88	0.06

(white: estimated difference = $-23.57 \text{ m} \pm 10.91 \text{ SE}$, $t = -2.16$, $P = 0.03$; red: estimated difference = $30.24 \text{ m} \pm 14.71 \text{ SE}$, $t = 2.06$, $P = 0.04$; blue: estimated difference = $33.55 \text{ m} \pm 14.34 \text{ SE}$, $t = 2.34$, $P = 0.02$). This was supported by data visualizations and residual inspection, which revealed that these differences were largely driven by long tails, with flight height responses centered on zero (Figure 4; Figure S3). Blue light altered flight direction relative to our white light treatment (estimated difference = $29.02^\circ \pm 13.00 \text{ SE}$, $t = 2.30$, $P = 0.02$). However, we did not find an effect between color treatments with respect to migration traffic rate (Figure S1).

Regarding covariates for our second set of models, none of our fixed effects or smooth terms were significant ($P > 0.05$), suggesting that the effect of light treatments on flight behavior did not depend on time since sunset or environmental conditions (Table S2). Further, our time after sunset variable was functionally linear (effective degrees of freedom = 1.00).

DISCUSSION

We conducted a field experiment to understand avian in-flight behavioral responses to different spectra of ALAN. Our results show that white light reduced the flight height of migrating birds relative to periods of no lighting. We also found some evidence of differential responses between lighting treatments, with white light reducing flight

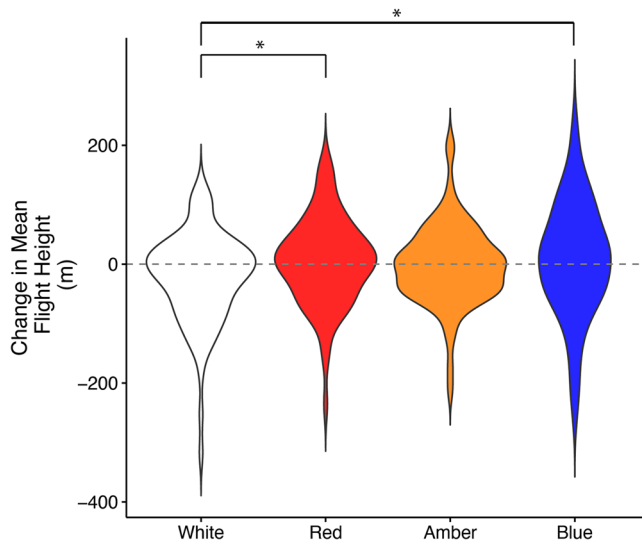


FIGURE 4 Violin plots showing the distribution of the changes in mean flight height of nocturnally migrating birds compared to controls for each light color treatment in Colorado, USA, 2023–2024. The x-axis represents the color treatment groups. Each violin plot illustrates the kernel density estimation of the data within each group, with the area scaled to reflect the sample size ($n_{\text{white}} = 84$, $n_{\text{red}} = 72$, $n_{\text{amber}} = 77$, $n_{\text{blue}} = 79$). An asterisk denotes statistical evidence for a difference between pairs of treatment responses ($P < 0.05$).

heights more than red and blue treatments, and blue and white lighting having different effects on flight direction, though we did not find strong evidence that either color affected flight direction when compared to control periods. Our research both provides support for previous findings and adds nuance to our understanding of how birds respond to ALAN. Further, our ability to demonstrate subtle avian behavioral responses in a low-density migration corridor highlights how the effects of ALAN may extend beyond brightly lit, high-density migration areas.

Overall, our results suggest that our white light treatment, which was composed of a broad spectral distribution with peaks in short wavelengths in the range of 430–450 nm (~6,440–6,740 kelvin), reduced bird flight height. Analysis of birds at the 25th percentile of flight height revealed that these changes were larger for, and likely driven by, low-flying birds. Our use of a vertical-looking radar allowed us to monitor specific flight behavior and capture subtle flight height responses that may be overlooked through other monitoring techniques. Studies on the effects of ALAN on birds often employ visual and acoustic monitoring (Evans et al. 2007), netting rates (Zhao et al. 2020), and thermal imagery (Rebke et al. 2019) to assess avian responses and have largely focused on increases in local abundance or density rather than behavioral responses that may not be reflected in count data. That is, we did not see an increase in migration traffic rates in response to any of our treatments, and the responses we did observe were subtle and would be difficult to quantify through other survey techniques. To our knowledge, the only other studies with comparable methods were May et al. (2017), which found that violet lighting reduced flight height by 7 m, and the dissertation of d'Entremont (2015), which used X-band radar to determine that short-wavelength lighting reduced flight height around wind turbines in northeastern British Columbia, Canada. We find it encouraging that our results complement these findings and believe additional research that captures fine-scale flight behavior changes will be useful.

The absence of evidence for effects of other colors of light on migratory bird flight behavior may be partially explained by birds' heightened sensitivity to shorter (bluer) wavelengths. Mechanistically, there is some evidence that avian vision is sensitive to short-wavelength light (Nießner et al. 2014, Longcore 2023) and that this overlap may cause stronger phototaxis through orientation disruption (Zhao et al. 2020). Within this context, our results

suggest that the white treatment probably appeared brighter to most birds than the red or amber treatments. Birds flying lower in response to our white treatment than our red treatment may support a growing literature suggesting that nocturnally migratory birds are less affected by ALAN sources dominated by longer wavelengths (Evans et al. 2007, Rebke et al. 2019, Zhao et al. 2020). However, the absence of response to blue light and the finding that birds flew lower in response to white light than in response to the blue treatment cannot be explained by birds' spectral sensitivities because most bird species for which this has been quantified are equally sensitive to both treatments (Figure 2). Seymoure et al. (2019) document the overlap of spectral peaks of various lighting treatments with model avian visual systems, finding photoreceptors are stimulated differently depending upon light type. Given the steep drop in spectral power of our blue treatment after 500 nm, it may be possible the white broadband signal was more stimulating to birds in flight. These findings highlight the importance of taking the full spectral distribution of ALAN sources into account, beyond their peak.

To that end, we stress the importance of detailed reporting of lighting characteristics, including spectral power distributions, in ALAN studies and suggest that a standardized protocol for doing so could help refine differential behavioral responses and mechanistic drivers. Further tests of LEDs marketed as white with different spectral power distributions would further inform our understanding of bird response to ALAN and guide mitigation measures. This may be particularly relevant when considering taxonomic variation in responses to different ALAN spectra. Like much of the literature on the effect of ALAN on birds (Adams et al. 2021), the majority of our targets were likely passerines. Yet there may be variable responses for aquatic species, such as seabirds (Heswall et al. 2022). Indeed, even amongst passerines, there appear to be variable responses to ALAN (Osterhaus et al. 2025). Detailed spectral data will be helpful as we continue to explore taxa-specific responses.

We were somewhat surprised that we failed to detect an effect of any of our treatments on migration traffic rate. Many historical and high-profile examples of ALAN influencing avian behavior are strongly based on the presumption or evidence of increased traffic rates (Saunders 1930, Van Doren et al. 2017). In combination with our findings on flight height, we suggest that these results may demonstrate a highly localized effect of ALAN on flight behavior. That is, we suspect that the range of our radar data collection exceeded the effective range of our lighting treatments. Thus, although the overall traffic did not change within the sampling area, birds within a smaller range of exposure flew lower when passing over our white lighting treatment. This may have practical relevance as, again, such a result would emphasize the subtle effects of ALAN on migratory behavior (Gaston et al. 2021). Alternatively, our limited sample size (72–84 replicates per color treatment) and low density of migration in our study region (Dokter et al. 2018) may have contributed to our inability to detect effects of our treatments on migration traffic rate and flight direction. Other studies have found increased density of nocturnally migrating birds around white, blue, and green light sources (Evans et al. 2007, Rebke et al. 2019, Zhao et al. 2020). Our findings do not necessarily indicate that ALAN does not increase migratory bird density in our study area but could instead suggest that any effect that exists was too small to find with our study design.

Similarly, while the use of 2 portable light sources in the absence of other disturbances allowed us to isolate the effects of each light treatment, the isolation of the effects of ALAN limits the study's relevance to the effects of multiple ALAN sources in combination with other stressors. In practice, ALAN is typically composed of a mix of sources ranging in spectrum, intensity, and shielding, amongst other characteristics. The combination of and interactions between ALAN sources and other environmental pollutants likely complicates bird responses. For example, Cabrera-Cruz et al. (2019) used weather surveillance radar to determine that, contrary to their predictions, avian flight height increased when birds flew over urban areas in the eastern United States, potentially as a result of urban heat island effects. Some studies have found that birds are more attracted to light when moon illumination is low (Rodríguez and Rodríguez 2009, Bolshakov et al. 2013). We were also surprised that we failed to detect effects of moon illumination or cloud cover, although this too may be partially driven by a limited sample size. Nonetheless, given the growing evidence that avian responses to ALAN are complex and may be altered or masked by other environmental features, future work that explicitly explores such interactions could be valuable.

Taken together, the relatively weak effect we observed on flight height may actually support the notion that ALAN's effects on wildlife behavior could be more widespread and pervasive than previously assumed (Gaston et al. 2021) but remain undetected in studies using more typical behavior metrics (e.g., number of individuals or flight calls). Our models estimated a 22.57 m (± 10.52 SE) decrease in flight height relative to an observed mean flight height of 412 m ($SD \pm 100$ m). This is a subtle behavioral change that would have been difficult to observe without a high-resolution radar system. However, we submit that this effect may be biologically meaningful if it effectively pulls birds into airspace where they are more likely to collide with tall anthropogenic structures such as buildings or communication towers or into atmospheric conditions that are energetically costly. Artificial light at night is also often discussed within the context of brightly lit urban centers. Yet our ability to demonstrate an effect of a relatively small point source of ALAN could be indicative of isolated ALAN sources having widespread and important biological influences. Birds likely encounter hundreds or thousands of isolated light sources as they migrate across continents. In this regard, our findings support Gaston et al. (2021) in calling for a more holistic consideration of how remote or mobile point sources of ALAN may be impacting wildlife distributions and behavior.

RESEARCH IMPLICATIONS

Our study contributes to the growing body of evidence that ALAN influences avian behavior, demonstrating that even small, isolated light sources can impact bird behavior and suggesting broader implications for ALAN management beyond urban centers. There were several aspects of our study that may be useful for future research that seeks to understand the role of ALAN spectral characteristics on avian in-flight behavior. As noted above, we suspect that the low density of migration activity in our study system at least partially influenced our ability to estimate relationships by limiting statistical power. Additional experimental research that leverages the emerging portable radar equipment to collect high-resolution behavioral data within dense migration corridors could elucidate stronger support or crucial nuances that we failed to detect here. Further, given increasing evidence that short-wavelength lighting may influence bird behavior more strongly than long-wavelength lighting, future work that explores variation in responses to color temperatures within commonly used, commercially available white lighting could be highly valuable. Finally, our experimental design and inclusion of control variables allowed us to partially control for environmental drivers of flight behavior. However, particularly in migration systems that offer stronger statistical power, research on potential interactions between lighting and atmospheric conditions could offer key insights into dynamic lighting guidelines.

ACKNOWLEDGMENTS

M. F. Jimenez acknowledges that this experiment took place on the Indigenous lands of the Arapahoe, Pawnee, Cheyenne, and Kiowa peoples. This project was supported by the NASA New (Early Career) Investigator Program in Earth Science (Grant #80NSSC21K0930). We thank Dr. Kristen Ruegg, Dr. David Koons, and Dr. Veronica Yovovich for their comments on the first version of this manuscript. We also thank the reviewers for their time spent reviewing and in helping to improve our manuscript. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

CONFLICT OF INTEREST STATEMENT

None of the authors have a conflict of interest to disclose.

ETHICS STATEMENT

All experimental procedures involving animals were approved by the Institutional Animal Care and Use Committee (IACUC) of Colorado State University (Protocol #4501, "Assessing the impacts of different spectrums of anthropogenic light at night on nocturnally migrating birds") and were conducted in accordance with institutional and federal guidelines for the care and use of laboratory animals.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Code for White Light Reduces Flight Height of Birds in Low-D at <https://github.com/Migfjim1/lightsspectrum>.

All data and code used for our analyses are available through our publicly accessible GitHub page (<https://github.com/Migfjim1/lightsspectrum>).

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Associate Editor: Courtney Duchardt.

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How to cite this article: Jimenez, M. F., C. A. Adams, C. S. Burt, B. D. Gerber, J. White, R. Zinn, and K. G. Horton. 2026. White light reduces flight height of birds in low-density migration corridor. *Journal of Wildlife Management* e70279. <https://doi.org/10.1002/jwmg.70279>