

ARTICLE

Macrosystems Ecology

Seasonal associations with light pollution trends for nocturnally migrating bird populations

Frank A. La Sorte¹  | Kyle G. Horton²  | Alison Johnston¹  | Daniel Fink^{1,3}  | Tom Auer¹ 

¹Cornell Lab of Ornithology, Cornell University, Ithaca, New York, USA

²Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, Colorado, USA

³Centre for Research into Ecological and Environmental Modelling, Mathematics and Statistics, University of St Andrews, St Andrews, UK

Correspondence

Frank A. La Sorte
 Email: fal42@cornell.edu

Funding information

Amon G. Carter Foundation; Lyda Hill Philanthropies; National Science Foundation, Grant/Award Numbers: ABI sustaining DBI-1939187, GCR-2123405; The Leon Levy Foundation; The Wolf Creek Charitable Foundation; National Aeronautics and Space Administration, Grant/Award Number: 80NSSC21K1143

Handling Editor: Robert R. Parmenter

Abstract

Artificial light at night (ALAN) is adversely affecting natural systems worldwide, including the disorienting influence of ALAN on nocturnally migrating birds. Understanding how ALAN trends are developing across species' seasonal distributions will inform mitigation efforts, such as Lights Out programs. Here, we intersect ALAN annual trend estimates (1992–2013) with weekly estimates of relative abundance for 42 nocturnally migrating passerine bird species that breed in North America using observations from the eBird community science database for the combined period 2005–2020. We use a cluster analysis to identify species with similar weekly associations with ALAN trends. Our results identified three prominent clusters. Two contained species that occurred in northeastern and western North America during the breeding season. These species were associated with moderate ALAN levels and weak negative ALAN trends during the breeding season, and low ALAN levels and strong positive ALAN trends during the nonbreeding season. The difference between the breeding and nonbreeding seasons was lower for species that occurred in northern South America and greater for species that occurred in Central America during the nonbreeding season. For species that occurred in South America during the nonbreeding season, positive ALAN trends increased in strength as species migrated through Central America, especially in the spring. The third cluster contained species whose associations with positive ALAN trends remained high across the annual cycle, peaking during migration, especially in the spring. These species occurred in southeastern North America during the breeding season where they were associated with high ALAN levels, and in northern South America during the nonbreeding season where they were associated with low ALAN levels. Our findings suggest reversing ALAN trends in Central America during migration, especially in the spring, would benefit the most individuals of the greatest number of species. Reversing ALAN trends in southeastern North America during the breeding season and Central America during the nonbreeding season would generate the greatest benefits outside of migration.

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2022 The Authors. *Ecosphere* published by Wiley Periodicals LLC on behalf of The Ecological Society of America.

KEY WORDS

community science, eBird, light pollution, nocturnal migration, seasonal bird migration, Western Hemisphere

INTRODUCTION

Artificial light at night (ALAN) is adversely affecting natural systems worldwide (Rich & Longcore, 2013; Sanders et al., 2020). Organismal level responses to ALAN include changes in physiology and behavior, which can scale up to affect populations, communities, and ecosystems (Falcón et al., 2020; Gaston et al., 2015; Sanders & Gaston, 2018). A major consequence of ALAN for birds is its disorienting influence on nocturnal migration (Gauthreaux & Belser, 2006). At the individual level, nocturnally migrating birds are attracted to ALAN during migratory flight (Bruderer et al., 1999; Larkin & Frase, 1988; Van Doren et al., 2017). Populations of nocturnally migrating birds during stop-over have been shown to occur in closer proximity to ALAN (La Sorte et al., 2017; McLaren et al., 2018), and species numbers have been shown to be positively correlated with urban sources of ALAN (La Sorte & Horton, 2021). Encountering ALAN during nocturnal migration expands the cost of the migration journey in terms of time and energy expenditures, enhances the risk of mortality through collisions with illuminated structures (Lao et al., 2020; Loss et al., 2014; Van Doren et al., 2021), and impedes the selection of optimal stopover habitat (McLaren et al., 2018). ALAN can also adversely affect nocturnally migrating birds outside of seasonal migration. At the population level during the breeding and nonbreeding seasons, urban sources of ALAN are associated with lower abundance (La Sorte et al., 2017) and fewer nocturnally migrating species (La Sorte & Horton, 2021). At the individual level, ALAN can disrupt biological rhythm, behavior, and physiology for both migratory and resident species. Examples include adverse effects on body mass and reproductive success (Malek & Haim, 2019), disease tolerance (Kernbach et al., 2021; Malek & Haim, 2019), immunity and parasitism (Becker et al., 2020), intestinal microbiota (Jiang et al., 2020), breeding phenology (Dominoni et al., 2020; Kempenaers et al., 2010), migration phenology (Smith et al., 2021), foraging activity (Amichai & Kronfeld-Schor, 2019), and sleeping behavior (Aulsebrook et al., 2020; Sun et al., 2017).

Research examining the ecological implications of ALAN for migratory birds typically considers ALAN as a static source of environmental pollution. However, ALAN is a dynamic phenomenon driven by urban

growth and decay and changes in lighting technology (Falchi et al., 2016; Li et al., 2020). Migrating birds often occur across broad geographic regions during their annual life cycles and can encounter different forms and intensities of ALAN. To document the implications of ALAN therefore requires the application of a full annual cycle perspective (Marra et al., 2015). The spatial correspondence between the seasonal distributions of nocturnally migrating bird populations and ALAN trends, however, has not been explored. Our goal in this study is to document how associations with ALAN annual trends are defined across the full annual cycle for nocturnally migrating birds, with the objective of generating baseline information on the regions and seasons where mitigation efforts such as Lights Out programs (Horton et al., 2019) would generate the greatest benefits.

Here, we document how populations of nocturnally migrating bird species that breed in North America and migrate within the Western Hemisphere are associated with ALAN trends across the annual cycle. Specifically, we intersect weekly estimates of relative abundance (Fink et al., 2013; Fink, Auer, Johnston, Ruiz-Gutierrez, et al., 2020) for 42 nocturnally migrating passerine (NMP) bird species (Horton et al., 2019) generated using observations from the eBird community science program for the combined period 2005–2020 (Sullivan et al., 2014) with annual estimates of ALAN for the period 1992–2013 (Li et al., 2020). We use a hierarchical cluster analysis to identify species that share similar weekly associations with ALAN trends, and we map the combined seasonal distributions of species in each cluster. During the period from 1992 to 2013, urban growth has occurred throughout the Western Hemisphere with the exception of some regions in the northeastern United States that have experienced urban decay (United Nations, 2019). We therefore expect the 42 NMP species to be associated with positive ALAN trends across a large portion of their annual life cycles. Any exceptions should occur within the northeastern United States during migration and the breeding season as few NMP species winter at these higher latitudes. By testing these predictions, our objective is to inform ALAN mitigation efforts and advance our understanding of the ecological implications of different sources of environmental pollution for birds and other taxa.

MATERIALS AND METHODS

Avian relative abundance

We acquired weekly estimates of relative abundance for NMP species within the Western Hemisphere from Adaptive Spatio-Temporal Exploratory Models (AdaSTEM) (Fink et al., 2013; Fink, Auer, Johnston, Ruiz-Gutierrez, et al., 2020) based on diurnal bird observations from the eBird community science program (Sullivan et al., 2014). We used the R package *ebirdst* (version 0.2.0) to obtain AdaSTEM weekly estimates of relative abundance, and we used the variable abundance_median in our analysis (Auer et al., 2020). eBird is a semi-structured “big data” resource where the sampling scheme and level of search effort are determined by each eBird participant. AdaSTEM mitigates the effects of spatial bias in the density of bird observations by conducting spatial subsampling of the eBird data, thus reducing the impact of spatially uneven data densities on model uncertainty. The AdaSTEM procedure selects eBird observations for analysis where survey time, date, and location are reported and the number of individuals of all bird species detected and identified during the survey period is recorded. Observations in AdaSTEM are restricted to those collected using the “stationary,” “traveling,” or “area search” protocols from the period 1 January 2005 through 10 April 2020. Area surveys were restricted to those covering $<56\text{ km}^2$, and traveling surveys were restricted to those of $\leq 15\text{ km}$. AdaSTEM uses these covariates to describe heterogeneity in the observation process to control for variation in detectability associated with search effort. The AdaSTEM predictions for relative abundance are standardized by estimating the expected relative abundance on a search conducted for a fixed time period and distance at the optimal time of day for the detection of that species by a skilled birdwatcher.

The AdaSTEM weekly estimates of relative abundance were available for 807 species at a $2.96 \times 2.96\text{-km}$ spatial resolution estimated for the year 2019 (Fink, Auer, Johnston, Strimas-Mackey, et al., 2020). From the 169 NMP species that occur in North America (Horton et al., 2019), estimates of relative abundance were available for 168 NMP species. From these, we retained 153 NMP species for analysis that had estimates of relative abundance for at least 50 weeks of the year. We included this step to remove species whose estimates of relative abundance did not encompass the majority of the annual cycle. Using range map data from Ridgely et al. (2007), we then selected species whose breeding and nonbreeding range polygons did not intersect and whose breeding range centroids occurred within the subtropics and northern temperate zone (north of 24°N latitude)

and whose nonbreeding range centroids occurred within the tropics (south of 24°N latitude). This resulted in a total of 42 species for analysis (see Appendix S1: Table S1). We included this final step to enhance the strength of the migration signal in our analysis by providing regions of passage where the species only occurred during migration.

To delineate seasons to support our interpretation, we estimated the four seasons of the annual cycle (nonbreeding, spring migration, breeding, and autumn migration) for the 42 NMP species using the following approach (see Figure 1). We first calculated each species’ population-level migration speed by measuring the great-circle distance (shortest distance between two points on the surface of the earth) between species’ weekly geographic centroids where weekly estimates of relative abundance were used as a weighting factor. We estimated great-circle distance using the Vincenty (ellipsoid) method (Hijmans, 2021) applied to the coordinates of the centers of the $2.96 \times 2.96\text{-km}$ cells. We used a generalized additive mixed model (GAMM) (Wood, 2017) to generate estimates of migration speed with great-circle distance as the response and week as the predictor. We

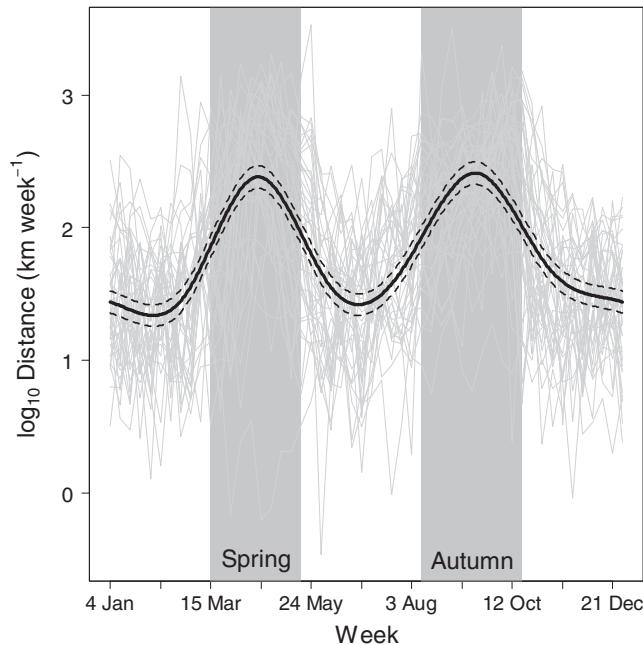


FIGURE 1 The great-circle (geodesic) distance between weekly centroids of occurrence weighted by relative abundance for 42 nocturnally migrating passerine bird species (see Appendix S1: Table S1). The fitted black line and 95% confidence band are from a generalized additive mixed model (GAMM) with species included as a random effect. The vertical polygons demarcate spring migration (15 March–17 May) and autumn migration (10 August–19 October) as delineated by the inflection points in the fitted GAMM line

included the intercept for species as a random effect, and we used a cyclic penalized cubic regression spline to smoothly join the first week and last week of each year (Wood, 2017). We estimated seasonal migration phenology across the 42 species by extracting the daily predicted values of population-level migration speed from the GAMM fit. We defined spring migration as the period bounded by the two inflection points that occurred between 1 January and 29 June when the slope of the instantaneous rate of change in the daily predicted values reached zero (Figure 1). We defined autumn migration as the period bounded by the two inflection points that occurred between 29 June and 31 December when the slope of the instantaneous rate of change in the daily predicted values reached zero (Figure 1). We defined the breeding and nonbreeding seasons as the boreal summer and boreal winter, respectively, that occurred between the two migration periods.

Artificial light at night

Large-scale measures of ALAN are coordinated through two primary remote sensing platforms. The first is the Defense Meteorological Satellite Program (DMSP)—Operational Linescan System (OLS). The second is the Visible Infrared Imaging Radiometer Suite (VIIRS) onboard the Suomi National Polar-orbiting Partnership (Suomi NPP) satellite (Miller et al., 2012; Miller et al., 2013). Currently, DMSP provides the most extensive temporal record of ALAN, spanning 1992 to 2013, with near-global coverage (Li & Zhou, 2017a). While DMSP provides more extensive temporal coverage than VIIRS (2013–present), DMSP lacks cross-sensor calibration (i.e., measures originate from as many as six DMSP satellite sensors, which are not directly comparable across the time series). Due to the lack of calibration, DMSP does not report values as radiance, but in digital number (DN). Post hoc calibration techniques are therefore required to standardize the DMSP values and generate temporally consistent measures for quantifying ALAN trends (Li et al., 2020; Li & Zhou, 2017b).

Here, we used the harmonized global nighttime light dataset (Li et al., 2020) standardized using stepwise calibration (Li & Zhou, 2017a) to estimate ALAN by year for the period 1992–2013 within the Western Hemisphere (see Figure 2). Values in the harmonized dataset are based on the 6-bit DMSP DN (range = 0–63) and are gridded at a 30-arcsecond spatial resolution (ca. 1 km at the equator). The DN values map to a linear scale of radiance (Hsu et al., 2015). To support our analysis, we generated two ALAN summaries. First, we averaged the ALAN time series across years (Figure 2a) to provide a

spatial ALAN summary. Second, we estimated trends in the ALAN time series across years using ordinary least-squares regression applied to each 30-arcsecond cell (Figure 2b). We reprojected and resampled the two ALAN summaries to match the AdaSTEM sinusoidal equal-area projection and 2.96 × 2.96-km spatial resolution.

The harmonized dataset uses DMSP data for the period 1992–2013, which we included in our analysis, and VIIRS data for the period 2014–2018, which we excluded from our analysis. We chose not to include VIIRS data because of the poor quality of the ALAN estimates at higher latitudes (Li et al., 2020) and the use of 2016 VIIRS data as one of the 79 environmental descriptors in AdaSTEM (Fink, Auer, Johnston, Ruiz-Gutierrez, et al., 2020). The correlation between the 2016 VIIRS data and our ALAN trend estimates based on DMSP data for the 42 NMP species was consistently low ($\rho < 0.1178$; see Appendix S2: Figure S1), indicating that our ALAN trend estimates were independent of the AdaSTEM estimates of relative abundance.

Analysis

We documented how the 42 NMP species are associated with ALAN trends across the annual cycle using the following approach. We first calculated the weighted average ALAN trend for each species and week across the 2.96 × 2.96-km cells using species' weekly estimates of relative abundance as a weighting factor. We applied a hierarchical cluster analysis to the 42 vectors of average ALAN trends (vector length = 52 weeks) to identify groups of species that shared similar ALAN trends across the annual cycle. We used the Euclidean distance between the 42 vectors and the complete linkage method in the hierarchical cluster analysis. We estimated nodal support using multiscale bootstrap resampling (Shimodaira, 2002, 2004). The bootstrap procedure used 10,000 bootstrap samples with 1,000 bootstrap samples applied to each of 10 scaling constants (Suzuki et al., 2019). We reported both the approximately unbiased p -values and the bootstrap probability p -values. We identified prominent clusters of species using an adaptive branch pruning technique, which detects clusters based on the structure of the branches within the dendrogram and is a more flexible approach compared to the constant or static height method (Langfelder et al., 2008). We used the “dynamic hybrid” method and applied a range of minimum cluster sizes from one to 20 species (Langfelder et al., 2016). We selected a minimum cluster size for analysis that captured the prominent features of the dendrogram where the selected clusters occurred in whole or in

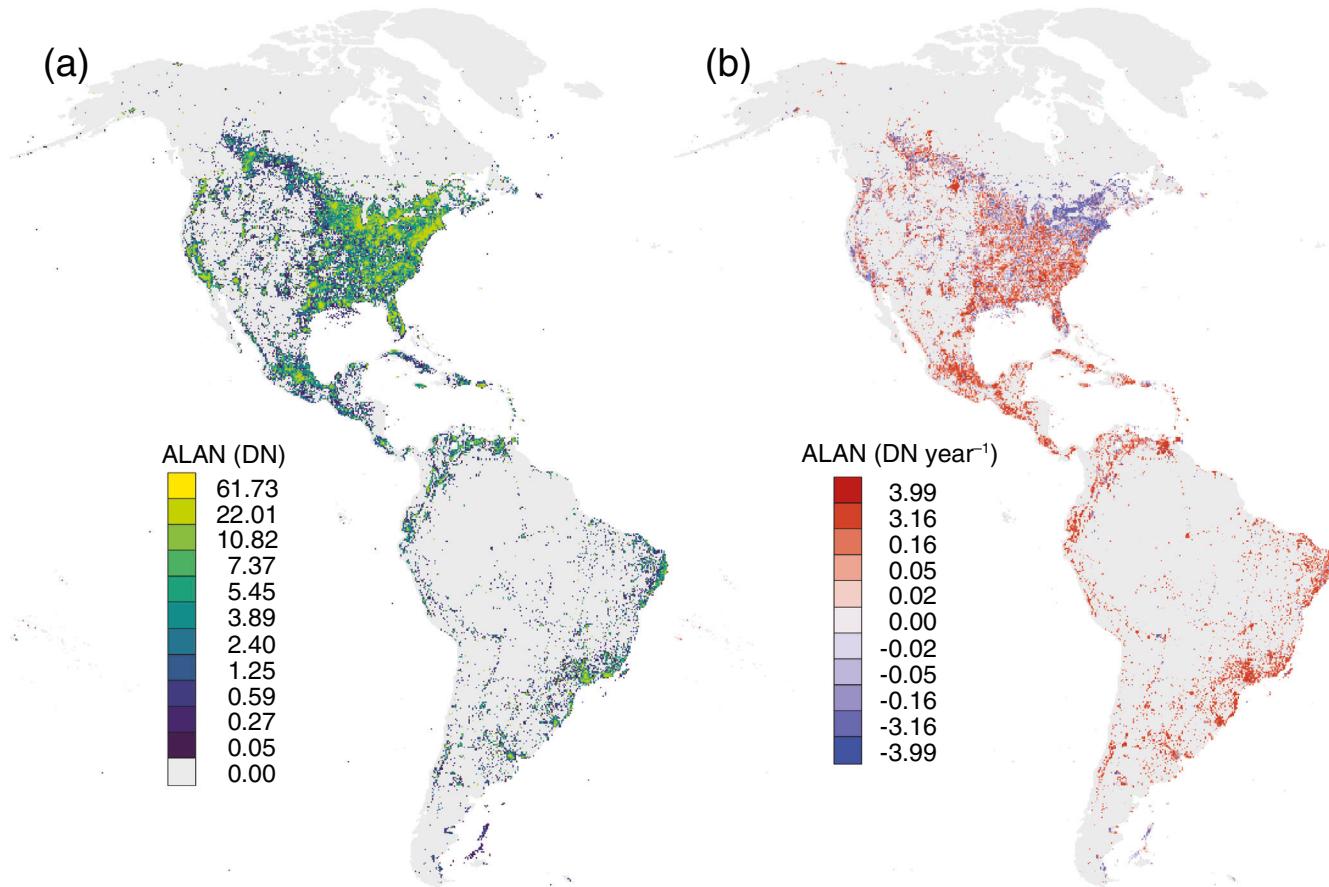


FIGURE 2 (a) Average artificial light at night (ALAN) and (b) the trend in ALAN during the period 1992–2013 within the Western Hemisphere. The ALAN data are gridded at a 30-arcsecond spatial resolution (ca. 1 km at the equator), and the units are digital numbers (DNs; range = 0–63). The trend analysis was implemented using ordinary least-squares regression. The data are displayed using a Mollweide equal-area projection

part across the range of minimum cluster sizes. We summarized the results of the cluster analysis by averaging the ALAN trend estimates by week across the species in each cluster. We applied the same procedure to the average ALAN values to provide a summary of species' baseline associations with ALAN. To provide a spatial summary of where species in each cluster occurred during each season, we first calculated the proportion of days during each season species occurred in the 2.96 × 2.96-km cells. We then averaged these proportions across species in each cluster.

All analyses were conducted using the R software for statistical computing and graphics, version 4.0.2 (R Development Core Team, 2021). We calculated great-circle distance using the `distVincentyEllipsoid` function in the R package `geosphere` (Hijmans, 2021). We implemented the hierarchical cluster analysis using the `hclust` function in the R package `stats` and the multiscale bootstrap resampling procedure using the `pvclust` function in the R package `pvclust` (Suzuki et al., 2019). We implemented the adaptive branch pruning technique

using the R package `dynamicTreeCut` with the `deepSplit` option set to zero (Langfelder et al., 2016). We implemented the GAMM analysis using the R package `gamm4` (Wood & Scheipl, 2020), and we estimated first derivatives using the R package `features` (Varadhan, 2015).

RESULTS

Within the Western Hemisphere, the highest ALAN levels occurred in the eastern and southern portions of North America, along the Pacific coast of the United States, and within the northern and southeastern portions of South America (Figure 2a). During the period from 1992 to 2013, approximately 77.3% of the Western Hemisphere experienced no change in ALAN, approximately 15.9% experienced positive ALAN trends, and approximately 6.8% experienced negative ALAN trends (Figure 2b). Positive ALAN trends occurred within southeastern North America (Figure 2b), and within regions in Central America and South America that contained high ALAN levels

(Figure 2a,b). Negative ALAN trends occurred primarily in northeastern North America (Figure 2b).

Cluster analysis

The 42 NMP species presented associations with ALAN annual trends that varied across weeks and among species (Figure 3). The hierarchical cluster analysis based on a minimum cluster size of eight species identified three prominent clusters containing 19, 15, and eight species, respectively (Figure 4, Appendix S2: Figures S2–S3). During the nonbreeding season, species in Clusters 1 and 3 were associated on average with low ALAN levels and positive ALAN trends, whereas species in Cluster 2 were associated on average with slightly higher ALAN levels and stronger positive ALAN trends (Figure 5, Appendix S2: Figure S4). During the breeding season, species in Clusters 1 and 2 were associated on average with low ALAN levels and negative ALAN trends that were close to zero, whereas species in Cluster 3 were associated on average with higher ALAN levels and strong positive ALAN trends (Figure 5, Appendix S2: Figure S4). During spring migration, ALAN levels were high on average across the three clusters, positive ALAN trends increased above nonbreeding season levels on average for species in Clusters 1 and 3 and differed little on average from

nonbreeding season levels for species in Cluster 2 (Figure 5, Appendix S2: Figure S4). During autumn migration, ALAN levels were high on average across the three clusters, positive ALAN trends increased substantially on average above breeding season levels for species in Clusters 1 and 2 and increased to a lesser degree on average for species in Cluster 3 (Figure 5, Appendix S2: Figure S4). ALAN trends reached similar positive levels on average during spring and autumn migration for species in Clusters 1 and 2, and positive ALAN trends were higher on average during spring migration for species in Cluster 3 (Figure 5).

Seasonal distributions

Species in the three clusters presented contrasting seasonal distributions within the Western Hemisphere (Figure 6). Species in Cluster 1 occurred in Central America and northern South America during the nonbreeding season, and in western and eastern North America during the breeding season (Figure 6). These species occurred across North America, Central America, and

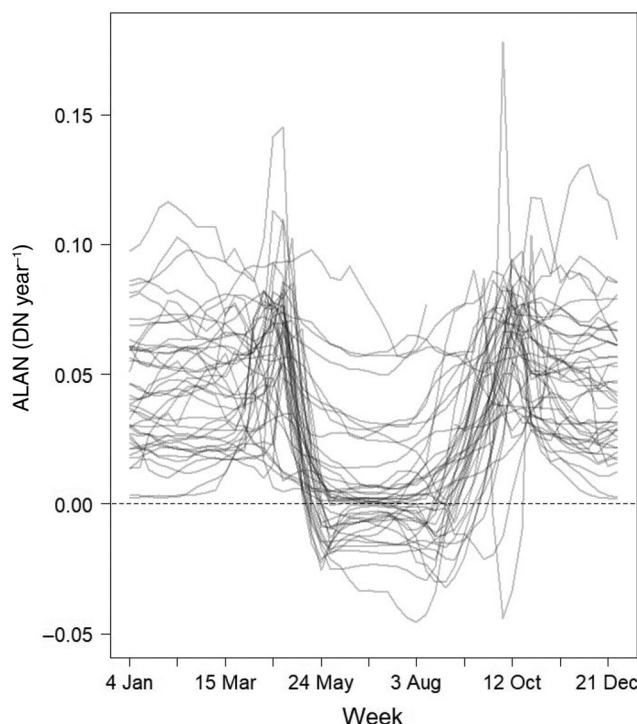


FIGURE 3 Weekly associations with trends in artificial light at night (ALAN) during the period 1992–2013 for 42 nocturnally migrating passerine bird species (see Appendix S1: Table S1)

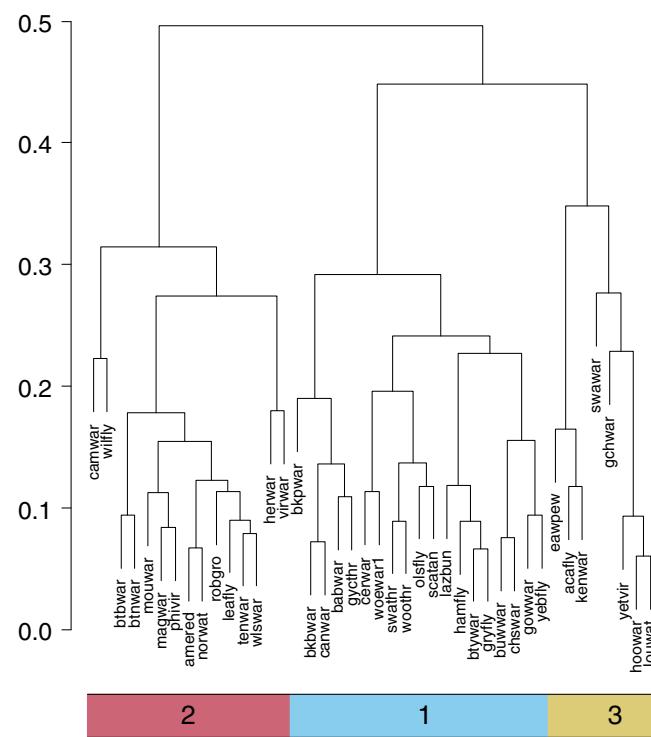


FIGURE 4 Dendrogram from a hierarchical cluster analysis of weekly associations with trends in artificial light at night for 42 nocturnally migrating passerine (NMP) bird species. The dendrogram labels are the common name alpha codes for the 42 NMP species (see Appendix S1: Table S1). The colored annotations below the dendrogram identify species grouped into three clusters using an adaptive branch pruning technique

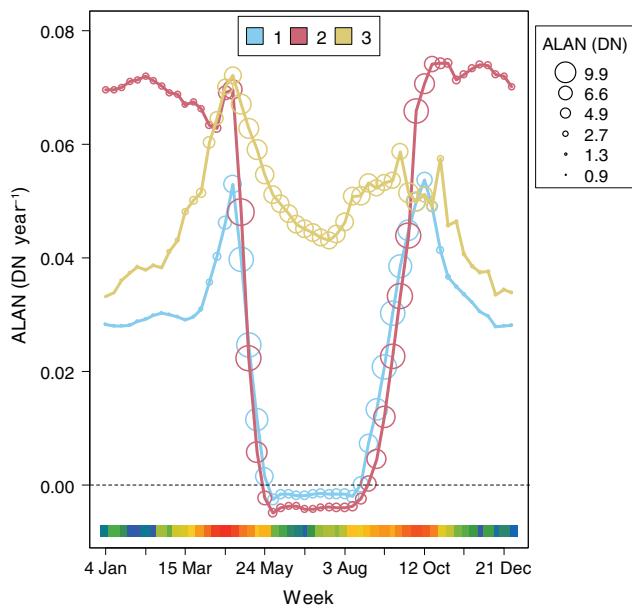


FIGURE 5 Weekly associations with trends in artificial light at night (ALAN) averaged across 42 nocturnally migrating passerine (NMP) bird species in three clusters (see Figure 4). The size of the circles corresponds to average ALAN. The sample sizes are 19, 15, and eight species, respectively. The color ramp is migration speed (see Figure 1) averaged across the 42 NMP species (blue = slow, green = intermediate, and red = fast). The ALAN units are digital numbers (DNs; range = 0–63)

northern South America during spring and autumn migration (Figure 6). Species in Cluster 2 were concentrated in Central America during the nonbreeding season and in western North America and northeastern North America during the breeding season (Figure 6). These species occurred across North America, Central America, and northern South America during spring and autumn migration (Figure 6). Species in Cluster 3 occurred in northwestern South America during the nonbreeding season, and in southeastern North America during the breeding season (Figure 6). These species occurred across southeastern North America, Central America, and northwestern South America during spring and autumn migration (Figure 6).

DISCUSSION

Our analysis identified three prominent clusters of NMP species whose weekly patterns of relative abundance within the Western Hemisphere generated contrasting associations with ALAN trends. Two clusters contained species that occurred in western and northeastern North America during the breeding season. Species in these clusters were associated with moderate ALAN levels and slightly negative

ALAN trends. During the nonbreeding season, species in these clusters were associated with low ALAN levels and positive ALAN trends. The difference between the two seasons was less pronounced for species that wintered in northern South America and more pronounced for species that wintered in Central America. For species that wintered in South America, the magnitude of the positive ALAN trends increased as these species migrated through Central America, especially in the spring. We identified a third cluster of species whose associations with positive ALAN trends remained strong across the annual cycle, peaking during migration, especially in the spring. This cluster occurred in southeastern North America during the breeding season where they were associated with high ALAN levels and wintered in northern South America where they were associated with low ALAN levels.

During the breeding season, associations with the highest ALAN levels occurred in southeastern North America. For species that occurred outside this region during the breeding season in western and northeastern North America, associations with ALAN levels and ALAN trends were close to zero. During migration, species presented associations with high ALAN levels and positive ALAN trends within Central America, especially during spring migration for species that occurred in southeastern North America during the breeding season. Species that wintered in Central America were associated with the strongest ALAN trends. For species that wintered in South America, associations with positive ALAN trends were approximately half as strong.

Our findings identified Central America as a region where NMP species encounter high ALAN levels and positive ALAN trends during migration and the nonbreeding season. The unique geography of Central America dictates broad-scale migration strategies within the region (La Sorte et al., 2016). Our findings suggest that the geographic constriction in Central America is associated with higher ALAN levels and stronger ALAN trends. Some migrating species that occur in eastern North America during the breeding season avoid this region by migrating over the Gulf of Mexico, a strategy that tends to be more widespread during autumn migration (La Sorte et al., 2016). The use of this trans-gulf strategy is evident in our findings where species that occur in southeastern North America during the breeding season are associated with ALAN levels that decrease from spring to autumn migration.

Our findings identified southeastern North America as the region containing the highest ALAN levels and strongest positive ALAN trends during the breeding season, and Central America as containing the highest ALAN levels and strongest positive ALAN trends during the nonbreeding season. Birds that occur in these regions during these seasons would encounter high ALAN levels

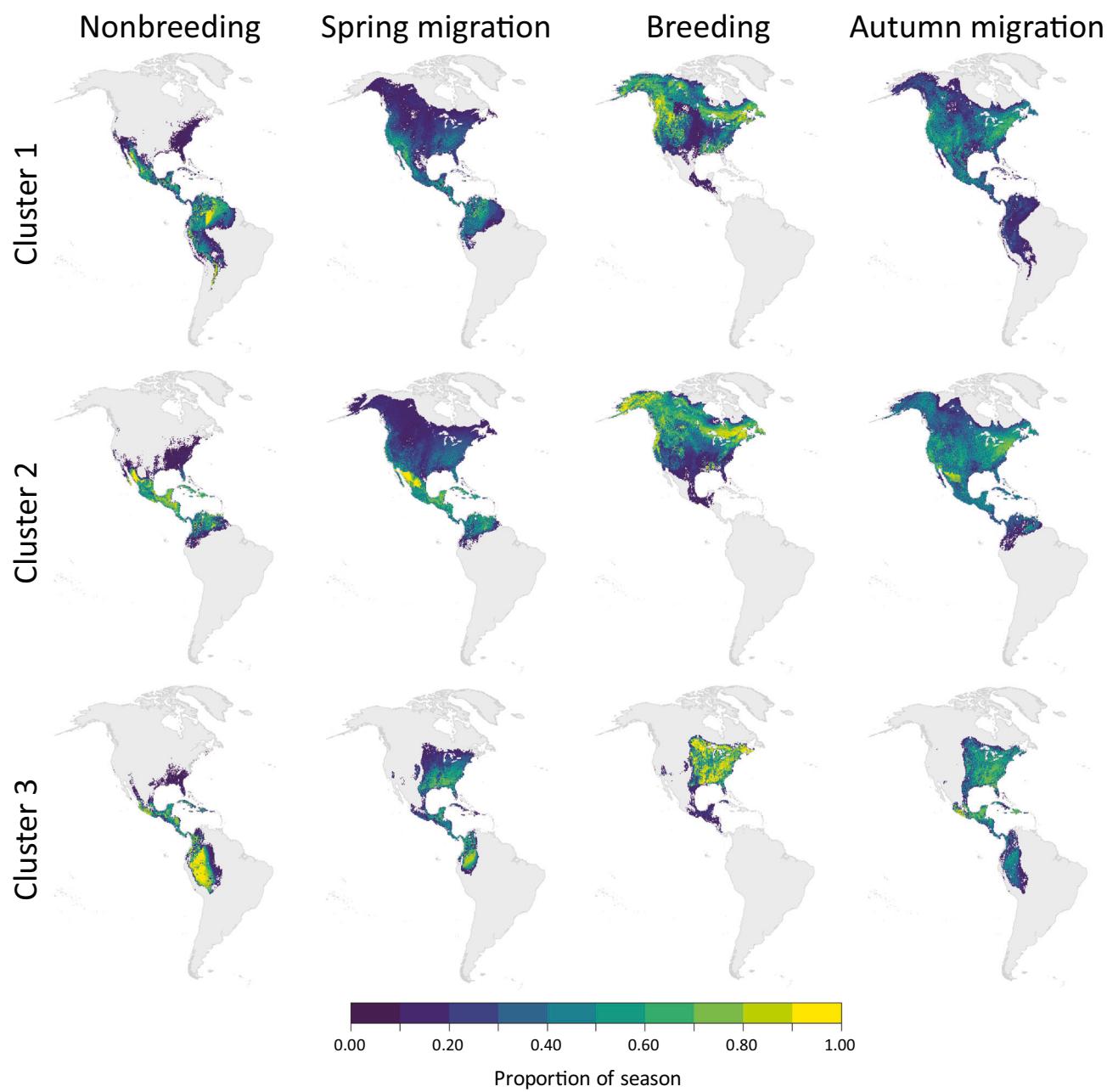


FIGURE 6 The seasonal distributions within the Western Hemisphere of 42 nocturnally migrating passerine bird species (Appendix S1; Table S1) grouped into three clusters ($n = 19, 15$, and 8 , respectively) based on their weekly associations with trends in artificial light at night (see Figure 3). The maps show the proportion of each season species occur in the grid cells averaged across species in each cluster. The data are displayed using a Mollweide equal-area projection

that are increasing, enhancing the potential for ALAN to negatively affect survival and fecundity.

ALAN dynamics have historically been driven by changes in lighting technology. This is currently based on the transition to light-emitting diodes (LED) technology (Nair & Dhoble, 2015), which has resulted in higher ALAN emissions and changes in ALAN spectral composition in some regions (Kyba, 2018; Kyba et al., 2017). Depending on the situation, the transition to LED technology can

exacerbate or reduce the adverse effects of ALAN on birds (Falcón et al., 2020). Unlike previous lighting technology, LED provides greater flexibility in the choice of spectral composition, creating opportunities to reduce the adverse effects of ALAN. For example, different ALAN spectral compositions can affect the level of disorientation and attraction that occurs during nocturnal migration (Poot et al., 2008; Rebke et al., 2019; Zhao et al., 2020). Different ALAN spectral compositions can also affect lay date

(de Jong et al., 2015), the level of daily activity patterns (de Jong et al., 2017), and energy expenditures (Welbers et al., 2017). It would be valuable to assess how the ALAN trends documented in this study are being affected by LED technology, which has accelerated after 2013, and the implications for the region's nocturnally migrating bird species.

One limitation of our analysis is that the time period for the ALAN trend estimates (1992–2013) did not align with the time period of the eBird data (2005–2020), or the year relative abundance estimates were rendered (2019). In this study, we summarized range-wide associations with ALAN trends by week across the annual cycle for multiple species. At this scale, it is unlikely a temporal mismatch would systematically bias our results. Nevertheless, as the temporal breadth and detail of these data sources increase, the ecological consequences of ALAN trends can be explored in a more detail. Another potential limitation of our analysis is the presence of spatial heterogeneity in the density of bird observations used to estimate relative abundance. AdaSTEM accounts for variation in data density at regional scales using model ensembles whose spatial extents are adaptively sized based on data density (Fink et al., 2013; Fink, Auer, Johnston, Ruiz-Gutierrez, et al., 2020). This procedure results in a similar level of uncertainty across the study area, and likely similar levels of uncertainty across our weekly range-wide summaries. However, exploring species-specific, local-scale associations with ALAN trends within data-poor regions could be problematic. Efforts to expand the coverage of eBird data within poorly sampled regions of the globe would be valuable in refining the spatial quality of these kinds of analyses.

The risks associated with avian migration (Klaassen et al., 2014; Lok et al., 2015; Loonstra et al., 2019; Sergio et al., 2019) are likely to be exacerbated as global change progresses (Zurell et al., 2018). This includes increasing levels of ALAN and changes in ALAN spectral compositions, which is especially relevant given the high levels of ALAN within regions of passage for the world's nocturnally migrating birds (Cabrera-Cruz et al., 2018). Our findings identify the regions and seasons where ALAN mitigation efforts would likely generate the greatest benefits within the Western Hemisphere. Our findings also provide the basis to explore the role of ALAN in recent populations' declines of North America's birds (Rosenberg et al., 2019). Our assessment identified Central America as a critical region during migration where reversing ALAN trends would likely benefit the most individuals of the greatest number of species, especially during spring migration. Our findings also identified southeastern North America during the breeding season and Central America during the nonbreeding season where reversing ALAN trends would likely have the

greatest benefits outside of migration. The challenges created by ALAN for birds and other taxa will continue to expand through urban growth and changes in lighting technology, emphasizing the importance of documenting ALAN associations and their implications at the individual and population levels across regions and seasons.

ACKNOWLEDGMENTS

This research would not be possible without the contributions of the eBird participants, expert reviewers, and the many other individuals whose work and engagement make the eBird project successful. We thank M. Strimas-Mackey for assistance with data acquisition. We thank S. Gillings and an anonymous reviewer for constructive suggestions on an earlier draft. This project was supported by The Leon Levy Foundation, The Wolf Creek Charitable Foundation, Lyda Hill Philanthropies, Amon G. Carter Foundation, National Aeronautics and Space Administration (80NSSC21K1143), and National Science Foundation (ABI sustaining DBI-1939187, GCR-2123405). Computing support was provided by the National Science Foundation (CNS-1059284 and CCF-1522054), and the Extreme Science and Engineering Discovery Environment (XSEDE; National Science Foundation, ACI-1548562) through allocation TG-DEB200010 run on Bridges at the Pittsburgh Supercomputing Center.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Frank A. La Sorte: Conceptualization (equal), formal analysis (lead), writing—original draft (lead). Kyle G. Horton: Conceptualization (equal), writing—review and editing (supporting). Alison Johnston: Methodology (supporting), software (supporting), writing—review and editing (supporting). Daniel Fink: Methodology (lead), software (lead). Tom Auer: Methodology (supporting), software (supporting), data curation (lead).

DATA AVAILABILITY STATEMENT

The bird data used in this study are available from the Cornell Lab of Ornithology: <https://ebird.org/data/download> (queried from the eBird Reference Dataset for the period 1 January 2005 through 10 April 2020). The nighttime light data used in this study are available from Li et al. (2020).

ORCID

Frank A. La Sorte  <https://orcid.org/0000-0001-8521-2501>

Kyle G. Horton  <https://orcid.org/0000-0003-3243-3081>

Alison Johnston  <https://orcid.org/0000-0001-8221-013X>

Daniel Fink  <https://orcid.org/0000-0002-8368-1248>
 Tom Auer  <https://orcid.org/0001-8619-7147>

REFERENCES

Amichai, E., and N. Kronfeld-Schor. 2019. "Artificial Light at Night Promotes Activity throughout the Night in Nesting Common Swifts (*Apus apus*)."
Scientific Reports 9: 11052.

Auer, T., D. Fink, and M. Strimas-Mackey. 2020. "ebirdst: Tools for Loading, Plotting, Mapping and Analysis of eBird Status and Trends Data Products." R Package Version 0.2.0. <https://cornelllabofornithology.github.io/ebirdst/>.

Aulsebrook, A. E., F. Connelly, R. D. Johnsson, T. M. Jones, R. A. Mulder, M. L. Hall, A. L. Vyssotski, and J. A. Lesku. 2020. "White and Amber Light at Night Disrupt Sleep Physiology in Birds."
Current Biology 30: 3657–63.

Becker, D. J., D. Singh, Q. Pan, J. D. Montoue, K. M. Talbott, S. M. Wanamaker, and E. D. Ketterson. 2020. "Artificial Light at Night Amplifies Seasonal Relapse of Haemosporidian Parasites in a Widespread Songbird."
Proceedings of the Royal Society B: Biological Sciences 287: 20201831.

Bruderer, B., D. Peter, and T. Steuri. 1999. "Behaviour of Migrating Birds Exposed to X-Band Radar and a Bright Light Beam."
Journal of Experimental Biology 202: 1015–22.

Cabrera-Cruz, S. A., J. A. Smolinsky, and J. J. Buler. 2018. "Light Pollution Is Greatest within Migration Passage Areas for Nocturnally Migrating Birds around the World."
Scientific Reports 8: 3261.

de Jong, M., S. P. Caro, P. Gienapp, K. Spoelstra, and M. E. Visser. 2017. "Early Birds by Light at Night: Effects of Light Color and Intensity on Daily Activity Patterns in Blue Tits."
Journal of Biological Rhythms 32: 323–33.

de Jong, M., J. Q. Ouyang, A. Da Silva, R. H. van Grunsven, B. Kempenaers, M. E. Visser, and K. Spoelstra. 2015. "Effects of Nocturnal Illumination on Life-History Decisions and Fitness in Two Wild Songbird Species."
Philosophical Transactions of the Royal Society B: Biological Sciences 370: 20140128.

Dominoni, D. M., J. Kjellberg Jensen, M. de Jong, M. E. Visser, and K. Spoelstra. 2020. "Artificial Light at Night, in Interaction with Spring Temperature, Modulates Timing of Reproduction in a Passerine Bird."
Ecological Applications 30: e02062.

Falchi, F., P. Cinzano, D. Duriscoe, C. C. M. Kyba, C. D. Elvidge, K. Baugh, B. A. Portnov, N. A. Rybnikova, and R. Furgoni. 2016. "The New World Atlas of Artificial Night Sky Brightness."
Science Advances 2: e1600377.

Falcón, J., A. Torriglia, D. Attia, F. Viénot, C. Gronfier, F. Behar-Cohen, C. Martinsons, and D. Hicks. 2020. "Exposure to Artificial Light at Night and the Consequences for Flora, Fauna, and Ecosystems."
Frontiers in Neuroscience 14: 1183.

Fink, D., T. Auer, A. Johnston, V. Ruiz-Gutierrez, W. M. Hochachka, and S. Kelling. 2020. "Modeling Avian Full Annual Cycle Distribution and Population Trends with Citizen Science Data."
Ecological Applications 30: e02056.

Fink, D., T. Auer, A. Johnston, M. Strimas-Mackey, O. Robinson, S. Ligocki, B. Petersen, et al. 2020. *eBird Status and Trends, Data Version: 2018*. Released: 2020. Ithaca, NY: Cornell Lab of Ornithology. <https://doi.org/10.2173/ebirdst.2018>

Fink, D., T. Damoulas, and J. Dave. 2013. "Adaptive Spatio-Temporal Exploratory Models: Hemisphere-Wide Species Distributions from Massively Crowdsourced eBird Data." In *Twenty-Seventh AAAI Conference on Artificial Intelligence (AAAI-13)*, Bellevue, WA.

Gaston, K. J., M. E. Visser, and F. Hölker. 2015. "The Biological Impacts of Artificial Light at Night: The Research Challenge."
Philosophical Transactions of the Royal Society B: Biological Sciences 370: 20140133.

Gauthreaux, S. A., Jr., and C. G. Belser. 2006. "Effects of Artificial Night Lighting on Migrating Birds." In *Ecological Consequences of Artificial Night Lighting*, edited by C. Rich and T. Longcore, 67–93. Washington, DC: Island Press.

Hijmans, R. J. 2021. "geosphere: Spherical Trigonometry." R Package Version 1.5-14. <http://CRAN.R-project.org/package=geosphere>.

Horton, K. G., C. Nilsson, B. M. Van Doren, F. A. La Sorte, A. M. Dokter, and A. Farnsworth. 2019. "Bright Lights in the Big Cities: Migratory Birds' Exposure to Artificial Light."
Frontiers in Ecology and the Environment 17: 209–14.

Hsu, F.-C., K. E. Baugh, T. Ghosh, M. Zhizhin, and C. D. Elvidge. 2015. "DMSP-OLS Radiance Calibrated Nighttime Lights Time Series with Intercalibration."
Remote Sensing 7: 1855–76.

Jiang, J., Y. He, H. Kou, Z. Ju, X. Gao, and H. Zhao. 2020. "The Effects of Artificial Light at Night on Eurasian Tree Sparrow (*Passer montanus*): Behavioral Rhythm Disruption, Melatonin Suppression and Intestinal Microbiota Alterations."
Ecological Indicators 108: 105702.

Kempenaers, B., P. Borgström, P. Loës, E. Schlicht, and M. Valcu. 2010. "Artificial Night Lighting Affects Dawn Song, Extra-Pair Siring Success, and Lay Date in Songbirds."
Current Biology 20: 1735–9.

Kernbach, M. E., L. B. Martin, T. R. Unnasch, R. J. Hall, R. H. Y. Jiang, and C. D. Francis. 2021. "Light Pollution Affects West Nile Virus Exposure Risk across Florida."
Proceedings of the Royal Society B: Biological Sciences 288: 20210253.

Klaassen, R. H. G., M. Hake, R. Strandberg, B. J. Koks, C. Trierweiler, K.-M. Exo, F. Bairlein, and T. Ålerstam. 2014. "When and where Does Mortality Occur in Migratory Birds? Direct Evidence from Long-Term Satellite Tracking of Raptors."
Journal of Animal Ecology 83: 176–84.

Kyba, C. C. M. 2018. "Is Light Pollution Getting Better or Worse?"
Nature Astronomy 2: 267–9.

Kyba, C. C. M., T. Kuester, A. Sánchez de Miguel, K. Baugh, A. Jechow, F. Hölker, J. Bennie, C. D. Elvidge, K. J. Gaston, and L. Guanter. 2017. "Artificially Lit Surface of Earth at Night Increasing in Radiance and Extent."
Science Advances 3: e1701528.

La Sorte, F. A., D. Fink, J. J. Buler, A. Farnsworth, and S. A. Cabrera-Cruz. 2017. "Seasonal Associations with Urban Light Pollution for Nocturnally Migrating Bird Populations."
Global Change Biology 23: 4609–19.

La Sorte, F. A., D. Fink, W. M. Hochachka, and S. Kelling. 2016. "Convergence of Broad-Scale Migration Strategies in Terrestrial Birds."
Proceedings of the Royal Society B: Biological Sciences 283: 20152588.

La Sorte, F. A., and K. G. Horton. 2021. "Seasonal Variation in the Effects of Artificial Light at Night on the Occurrence of Nocturnally Migrating Birds in Urban Areas."
Environmental Pollution 270: 116085.

Langfelder, P., B. Zhang, and S. Horvath. 2008. "Defining Clusters from a Hierarchical Cluster Tree: The Dynamic Tree Cut Package for R." *Bioinformatics* 24: 719–20.

Langfelder, P., B. Zhang, and S. Horvath. 2016. "dynamicTreeCut: Methods for Detection of Clusters in Hierarchical Clustering Dendograms." R Package Version 1.63-1. <https://CRAN.R-project.org/package=dynamicTreeCut>.

Lao, S., B. A. Robertson, A. W. Anderson, R. B. Blair, J. W. Eckles, R. J. Turner, and S. R. Loss. 2020. "The Influence of Artificial Light at Night and Polarized Light on Bird-Building Collisions." *Biological Conservation* 241: 108358.

Larkin, R. P., and B. A. Frase. 1988. "Circular Paths of Birds Flying near a Broadcasting Tower in Cloud." *Journal of Comparative Psychology* 102: 90–3.

Li, X., and Y. Zhou. 2017a. "A Stepwise Calibration of Global DMSP/OLS Stable Nighttime Light Data (1992–2013)." *Remote Sensing* 9: 637.

Li, X., and Y. Zhou. 2017b. "Urban Mapping Using DMSP/OLS Stable Night-Time Light: A Review." *International Journal of Remote Sensing* 38: 6030–46.

Li, X., Y. Zhou, M. Zhao, and X. Zhao. 2020. "A Harmonized Global Nighttime Light Dataset 1992–2018." *Scientific Data* 7: 168.

Lok, T., O. Overdijk, and T. Piersma. 2015. "The Cost of Migration: Spoonbills Suffer Higher Mortality during Trans-Saharan Spring Migrations Only." *Biology Letters* 11: 20140944.

Loonstra, A. H. J., M. A. Verhoeven, N. R. Senner, C. Both, and T. Piersma. 2019. "Adverse Wind Conditions during Northward Sahara Crossings Increase the in-Flight Mortality of Black-Tailed Godwits." *Ecology Letters* 22: 2060–6.

Loss, S. R., T. Will, S. S. Loss, and P. P. Marra. 2014. "Bird-Building Collisions in the United States: Estimates of Annual Mortality and Species Vulnerability." *The Condor* 116: 8–23.

Malek, I., and A. Haim. 2019. "Bright Artificial Light at Night Is Associated with Increased Body Mass, Poor Reproductive Success and Compromised Disease Tolerance in Australian Budgerigars (*Melopsittacus undulatus*).". *Integrative Zoology* 14: 589–603.

Marra, P. P., E. B. Cohen, S. R. Loss, J. E. Rutter, and C. M. Tonra. 2015. "A Call for Full Annual Cycle Research in Animal Ecology." *Biology Letters* 11: 20150552.

McLaren, J. D., J. J. Buler, T. Schreckengost, J. A. Smolinsky, M. Boone, E. Emiel van Loon, D. K. Dawson, and E. L. Walters. 2018. "Artificial Light at Night Confounds Broad-Scale Habitat Use by Migrating Birds." *Ecology Letters* 21: 356–64.

Miller, S. D., S. P. Mills, C. D. Elvidge, D. T. Lindsey, T. F. Lee, and J. D. Hawkins. 2012. "Suomi Satellite Brings to Light a Unique Frontier of Nighttime Environmental Sensing Capabilities." *Proceedings of the National Academy of Sciences of the United States of America* 109: 15706–11.

Miller, S. D., W. Straka, III, S. P. Mills, C. D. Elvidge, T. F. Lee, J. Solbrig, A. Walther, A. K. Heidinger, and S. C. Weiss. 2013. "Illuminating the Capabilities of the Suomi National Polar-Orbiting Partnership (NPP) Visible Infrared Imaging Radiometer Suite (VIIRS) Day/Night Band." *Remote Sensing* 5: 6717–66.

Nair, G. B., and S. J. Dhoble. 2015. "A Perspective Perception on the Applications of Light-Emitting Diodes." *Luminescence* 30: 1167–75.

Poot, H., B. J. Ens, H. de Vries, M. A. H. Donners, M. R. Wernand, and J. M. Marquenie. 2008. "Green Light for Nocturnally Migrating Birds." *Ecology and Society* 13: 47.

R Development Core Team. 2021. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. <https://www.R-project.org/>

Rebke, M., V. Dierschke, C. N. Weiner, R. Aumüller, K. Hill, and R. Hill. 2019. "Attraction of Nocturnally Migrating Birds to Artificial Light: The Influence of Colour, Intensity and Blinking Mode under Different Cloud Cover Conditions." *Biological Conservation* 233: 220–7.

Rich, C., and T. Longcore. 2013. *Ecological Consequences of Artificial Night Lighting*. Washington, DC: Island Press.

Ridgely, R. S., T. F. Allnutt, T. Brooks, D. K. McNicol, D. W. Mehlman, B. E. Young, and J. R. Zook. 2007. *Digital Distribution Maps of the Birds of the Western Hemisphere, Version 3.0*. Arlington, VA: NatureServe.

Rosenberg, K. V., A. M. Dokter, P. J. Blancher, J. R. Sauer, A. C. Smith, P. A. Smith, J. C. Stanton, et al. 2019. "Decline of the North American Avifauna." *Science* 366: 120–4.

Sanders, D., E. Frago, R. Kehoe, C. Patterson, and K. J. Gaston. 2020. "A Meta-Analysis of Biological Impacts of Artificial Light at Night." *Nature Ecology & Evolution* 5: 74–81.

Sanders, D., and K. J. Gaston. 2018. "How Ecological Communities Respond to Artificial Light at Night." *Journal of Experimental Zoology Part A: Ecological and Integrative Physiology* 329: 394–400.

Sergio, F., G. Tavecchia, A. Tanferna, J. Blas, G. Blanco, and F. Hiraldo. 2019. "When and Where Mortality Occurs throughout the Annual Cycle Changes with Age in a Migratory Bird: Individual vs Population Implications." *Scientific Reports* 9: 17352.

Shimodaira, H. 2002. "An Approximately Unbiased Test of Phylogenetic Tree Selection." *Systematic Biology* 51: 492–508.

Shimodaira, H. 2004. "Approximately Unbiased Tests of Regions Using Multistep-Multiscale Bootstrap Resampling." *Annals of Statistics* 32: 2616–41.

Smith, R. A., M. Gagné, and K. C. Fraser. 2021. "Pre-Migration Artificial Light at Night Advances the Spring Migration Timing of a Trans-Hemispheric Migratory Songbird." *Environmental Pollution* 269: 116136.

Sullivan, B. L., J. L. Aycrigg, J. H. Barry, R. E. Bonney, N. Bruns, C. B. Cooper, T. Damoulas, et al. 2014. "The eBird Enterprise: An Integrated Approach to Development and Application of Citizen Science." *Biological Conservation* 169: 31–40.

Sun, J., T. Raap, R. Pinxten, and M. Eens. 2017. "Artificial Light at Night Affects Sleep Behaviour Differently in Two Closely Related Songbird Species." *Environmental Pollution* 231: 882–9.

Suzuki, R., Y. Terada, and H. Shimodaira. 2019. "pvclust: Hierarchical Clustering with P-Values via Multiscale Bootstrap Resampling." R Package Version 2.2-0. <https://CRAN.R-project.org/package=pvclust>.

United Nations. 2019. *World Urbanization Prospects: The 2018 Revision (ST/ESA/SER.A/420)*. New York: Department of Economic and Social Affairs, Population Division, United Nations.

Van Doren, B. M., K. G. Horton, A. M. Dokter, H. Klinck, S. B. Elbin, and A. Farnsworth. 2017. "High-Intensity Urban Light Installation Dramatically Alters Nocturnal Bird Migration."

Proceedings of the National Academy of Sciences of the United States of America 114: 11175–80.

Van Doren, B. M., D. E. Willard, M. Hennen, K. G. Horton, E. F. Stuber, D. Sheldon, A. H. Sivakumar, J. Wang, A. Farnsworth, and B. M. Winger. 2021. “Drivers of Fatal Bird Collisions in an Urban Center.” *Proceedings of the National Academy of Sciences of the United States of America* 118: e2101666118.

Varadhan, R. 2015. “features: Feature Extraction for Discretely-Sampled Functional Data.” Johns Hopkins University and MKG Subramaniam and AT&T Research Labs. R Package Version 2015.12-1. <https://CRAN.R-project.org/package=features>.

Welbers, A. A. M. H., N. E. van Dis, A. M. Kolvoort, J. Ouyang, M. E. Visser, K. Spoelstra, and D. M. Dominoni. 2017. “Artificial Light at Night Reduces Daily Energy Expenditure in Breeding Great Tits (*Parus major*).” *Frontiers in Ecology and Evolution* 5: 55.

Wood, S. N. 2017. *Generalized Additive Models: An Introduction with R*, 2nd ed. Boca Raton, FL: Chapman & Hall/CRC.

Wood, S. N., and F. Scheipl. 2020. “gamm4: Generalized Additive Mixed Models Using Mgev and Lme4.” R Package Version 0.2-6. <https://CRAN.R-project.org/package=gamm4>.

Zhao, X., M. Zhang, X. Che, and F. Zou. 2020. “Blue Light Attracts Nocturnally Migrating Birds.” *The Condor* 122: 1–12.

Zurell, D., C. H. Graham, L. Gallien, W. Thuiller, and N. E. Zimmermann. 2018. “Long-Distance Migratory Birds Threatened by Multiple Independent Risks from Global Change.” *Nature Climate Change* 8: 992–6.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher’s website.

How to cite this article: La Sorte, Frank A., Kyle G. Horton, Alison Johnston, Daniel Fink, and Tom Auer. 2022. “Seasonal Associations with Light Pollution Trends for Nocturnally Migrating Bird Populations.” *Ecosphere* 13(3): e3994. <https://doi.org/10.1002/ecs2.3994>