

High-intensity urban light installation dramatically alters nocturnal bird migration

Benjamin M. Van Doren^{a,b,1}, Kyle G. Horton^{a,c,d,1}, Adriaan M. Dokter^a, Holger Klinck^e, Susan B. Elbin^f, and Andrew Farnsworth^{a,2}

^aInformation Science Program, Cornell Lab of Ornithology, Ithaca, NY 14850; ^bEdward Grey Institute, Department of Zoology, University of Oxford, Oxford, OX1 3PS, United Kingdom; ^cDepartment of Biology, University of Oklahoma, Norman, OK 73019; ^dOklahoma Biological Survey, University of Oklahoma, Norman, OK 73019; ^eBioacoustics Research Program, Cornell Lab of Ornithology, Ithaca, NY 14850; and ^fNew York City Audubon, New York, NY 10010

Edited by James A. Estes, University of California, Santa Cruz, CA, and approved August 31, 2017 (received for review May 29, 2017)

Billions of nocturnally migrating birds move through increasingly photopolluted skies, relying on cues for navigation and orientation that artificial light at night (ALAN) can impair. However, no studies have quantified avian responses to powerful ground-based light sources in urban areas. We studied effects of ALAN on migrating birds by monitoring the beams of the National September 11 Memorial & Museum's "Tribute in Light" in New York, quantifying behavioral responses with radar and acoustic sensors and modeling disorientation and attraction with simulations. This single light source induced significant behavioral alterations in birds, even in good visibility conditions, in this heavily photopolluted environment, and to altitudes up to 4 km. We estimate that the installation influenced ≈ 1.1 million birds during our study period of 7 d over 7 y. When the installation was illuminated, birds aggregated in high densities, decreased flight speeds, followed circular flight paths, and vocalized frequently. Simulations revealed a high probability of disorientation and subsequent attraction for nearby birds, and bird densities near the installation exceeded magnitudes 20 times greater than surrounding baseline densities during each year's observations. However, behavioral disruptions disappeared when lights were extinguished, suggesting that selective removal of light during nights with substantial bird migration is a viable strategy for minimizing potentially fatal interactions among ALAN, structures, and birds. Our results also highlight the value of additional studies describing behavioral patterns of nocturnally migrating birds in powerful lights in urban areas as well as conservation implications for such lighting installations.

artificial light | nocturnal migration | remote sensing | radar ornithology | flight calls

The extent of artificial light at night (ALAN) at regional and global scales has increased 5–10% annually in portions of North America and Europe and exponentially in some other regions (1), resulting in sky glow that is often significantly brighter than luminance of the natural sky. ALAN may affect a diverse array of nocturnally active animals, and recent studies have highlighted the need for primary research into these potential impacts (2, 3). The biological effects of anthropogenic light pollution may be especially significant for nocturnally migrating birds (2–6).

Birds engage in seasonal migrations that are often global in distribution and span a broad range of spatial and temporal scales (7, 8). Avian migratory movements are often thought of as feats of endurance; some species undertake days-long, nonstop, transhemispheric flights, while others embark on complex, months-long journeys (9). Failed migration may have detrimental effects at individual and population scales (10, 11). Despite birds' primarily diurnal activity for the majority of the annual cycle, most migratory movements are nocturnal (7, 8), and the numbers of birds that migrate at night are enormous (12, 13). Numerous studies have offered perspectives on factors that govern nocturnal movements (14–18) and insights into adaptations necessary to orient and navigate at night (19, 20).

Visual cues are essential for navigation during migration (21), and ALAN may alter birds' abilities to orient and navigate (22, 23). The avian geomagnetic sense, which provides songbirds with

a compass to inform their spatial maps (19, 20, 24), may function with a dependency on frequencies of light, and ALAN may interfere with this dependency (25–28). Impediments to orientation and navigation senses may prove costly for avian migrants, creating new hazards during an already challenging and dynamic period of the annual cycle (29). Additionally, ALAN can alter the ways birds communicate (30) and avoid predation (31).

Accounts of birds' responses to light are numerous in literary and historical anecdotes, peer-reviewed journal articles, and popular media. Mortality at lighted structures has been documented across a wide geographic area and a broad range of species (4, 6, 32–44). It is likely that hundreds of millions of birds die annually from nocturnal collisions with buildings (29), representing a diverse array of migrant species (32, 33). Understanding the causes of these events is paramount; proposed explanations include that birds exhibit phototaxis and experience light-induced disorientation.

Generally, negative impacts of ALAN for birds in flight have been associated with conditions that are already poor for navigation and orientation, such as low cloud ceiling, fog, and stalled or weak frontal boundaries between air masses (34–39, 43, 45–48). Experimental field studies are generally rare (22, 26, 49–51) and offer limited evidence of the extent and intensity of ALAN's effects on nocturnally migrating birds, particularly with respect to

Significance

Artificial light at night is a novel stimulus in the evolutionary history of nocturnal animals. Light pollution can significantly alter these organisms' behaviors, from migration to foraging to vocal communication. Nocturnally migrating birds are particularly susceptible to artificial light because of adaptations and requirements for navigating and orienting in darkness. However, light's effects on in-flight behaviors have not been well quantified, especially in urbanized environments. Here we report that an iconic urban light installation dramatically altered multiple behaviors of nocturnally migrating birds—but these effects disappeared when lights were extinguished. We recommend selective removal of light pollution during nights with substantial bird migration to mitigate negative effects on birds, in particular collisions with lighted structures.

Author contributions: A.F. developed the study, collected visual observations and weather data, and wrote the paper; B.M.V.D. shaped the study, performed statistical analyses, and contributed to writing the paper; K.G.H. analyzed radar data and contributed to writing the paper; B.M.V.D. and K.G.H. generated figures and animations; A.M.D. developed simulations and produced associated figures and text; H.K. performed acoustic energy analysis; H.K. and A.F. analyzed acoustic data; S.B.E. provided bird mortality data, provided coordination, support, and access to the study site.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

Data deposition: All visual counts made at Tribute in Light are archived in the eBird database at ebird.org/ebird/hotspot/L1744278.

¹B.M.V.D. and K.G.H. contributed equally to this work.

²To whom correspondence should be addressed. Email: af27@cornell.edu.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1708574114/-DCSupplemental.

behaviors in clear sky conditions (but see ref. 48) and urbanized (e.g., heavily photopolluted) environments. Understanding the disruptive effects of short-term ALAN (e.g., lighting installations, sporting events) on nocturnal bird migration in urbanized and photopolluted areas and identifying the extents of these effects in clear sky conditions are important conservation priorities.

We took advantage of a unique opportunity to quantify birds' responses to ALAN by monitoring numbers, flight patterns, and vocalizations of birds aloft during alternating periods of illumination and darkness in the powerful light beams of the National September 11 Memorial & Museum's (NSMM's) "Tribute in Light" (TiL) in New York, NY (Fig. 1A). First, we quantified densities and flight speeds of aerial migrants near the light installation using data from the KOKX Brookhaven, NY WSR-88D radar station, revealing how numbers of birds and their rates of passage changed in the presence or absence of illumination. Second, we measured birds' vocal activity by recording their in-flight vocalizations, or flight calls, from the base of the installation. Increased flight calling activity in nocturnally migrating birds may indicate disorienting or confusing conditions (30, 52). If nocturnally migrating birds were attracted to and disoriented by the lights, we expected to observe higher densities of birds flying at slower flight speeds and vocalizing more frequently during periods of illumination. Finally, we used a flow model to simulate bird behaviors in ALAN conditions for comparison with observed radar data. These spatiotemporal distribution simulations investigated three important behavioral parameters to explain bird concentrations at the installation: the probability that the lights affected nearby birds, the distance over which the lights affected birds, and whether disoriented birds showed preferred flight directions toward the display. Together, these parameters determined how long birds remained in the illuminated area.

Results

We detected large aggregations of circling birds above the installation under clear sky conditions during periods of illumination (Figs. 1B and C and 2A, Movies S1–S3, and SI Appendix, Fig. S1). By summing the differences between bird numbers within 5 km of the installation and the number expected in that area given baseline densities, we estimate that ≈ 1.1 million birds (95% CI: 0.6–1.6 million) were affected by this single light source during our study period of seven nights over 7 y (SI Appendix, Fig. S2). The

numbers of birds affected varied by year, in part due to variation in the magnitude of migratory passage through the surrounding area on the study night (SI Appendix, Fig. S3), but all years showed strong increases in bird density with decreasing distance to the light source (Fig. 3 and SI Appendix, Fig. S4A). Under illumination, peak bird densities near the installation reached magnitudes 20 times greater than the surrounding baseline during all 7 y (SI Appendix, Fig. S5A), where we defined baseline as the mean density in the area 2–20 km from the site. Peak bird densities exceeded 60 times baseline in 5 of the 7 y and 150 times baseline in 3 y (2008, 2012, and 2013), but peak densities never exceeded 13 times baseline in the absence of illumination (SI Appendix, Fig. S5A). Vocal activity beneath the lights was intense during periods of aggregation (Fig. 2C and SI Appendix, Fig. S6). Bird densities, flight speeds, and vocal activities all varied closely with illumination (Fig. 2). Removal of illumination resulted in rapid changes in nocturnal migration behaviors, with birds dispersing, increasing flight speeds, decreasing calling activity, and moving away from the site in a matter of minutes (Fig. 3C and D).

We found a strong effect of illumination on the maximum standardized peak bird density and the maximum number of birds detected within 500 m of the installation during each period of darkness and adjacent periods of illumination. Considering the 0.5° radar elevation angle, maximum standardized bird densities were 14 times greater when the light display was illuminated ($t = 5.70$, $P < 0.0001$). Maximum bird numbers averaged 3.4 times greater during lit periods ($t = 3.89$, $P = 0.0003$). Remarkably, these effects were also present at high altitudes (1.5° radar elevation angle, sampling altitudes of 2.4–4.1 km): maximum standardized densities increased on average by 3.9 times ($t = 3.25$, $P = 0.002$) and maximum bird numbers by 3.3 times ($t = 2.34$, $P = 0.023$) during lit periods at high altitudes. We note that we did not detect many birds congregating in the beams during 2014; this year was not included in the above analyses because the lights were not shut down. We observed a strong effect of light on bird behavior during all other years (SI Appendix, Fig. S7).

Considering all radar observations, total numbers of birds within 500 m of the installation averaged 3.4 times higher during illuminated periods ($t = 9.34$, $P < 0.0001$). Standardized peak densities showed a similar pattern (factor = 6.4 times, $t = 3.72$, $P = 0.0003$), with the effect strengthened to 46 times higher during illuminated periods in 2015 ($t = 2.91$, $P = 0.004$). Again,

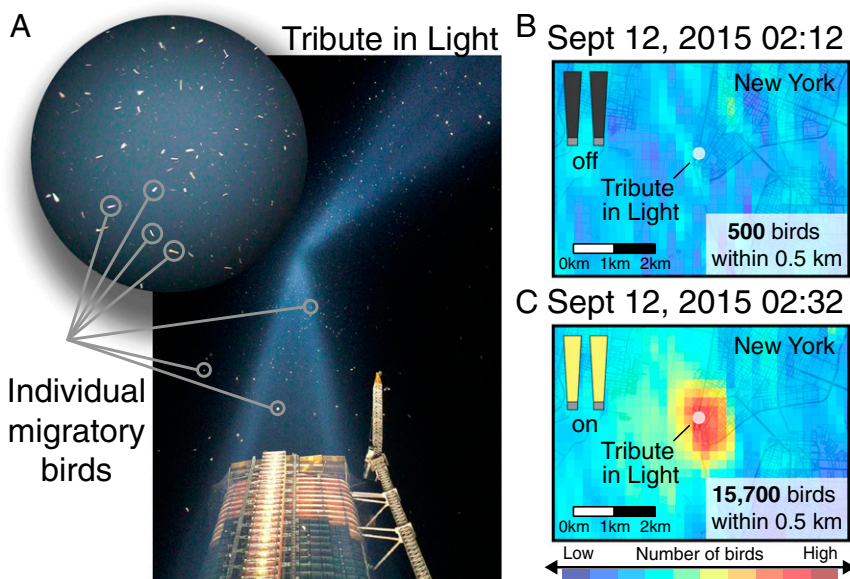


Fig. 1. Tribute in Light site. Observations (in Coordinated Universal Time) from the September 11–12 2015 Tribute in Light depicting altered behaviors of nocturnally migrating birds. (A) Direct visual observation. (B) Radar observation without TiL illumination and (C) with TiL illumination.

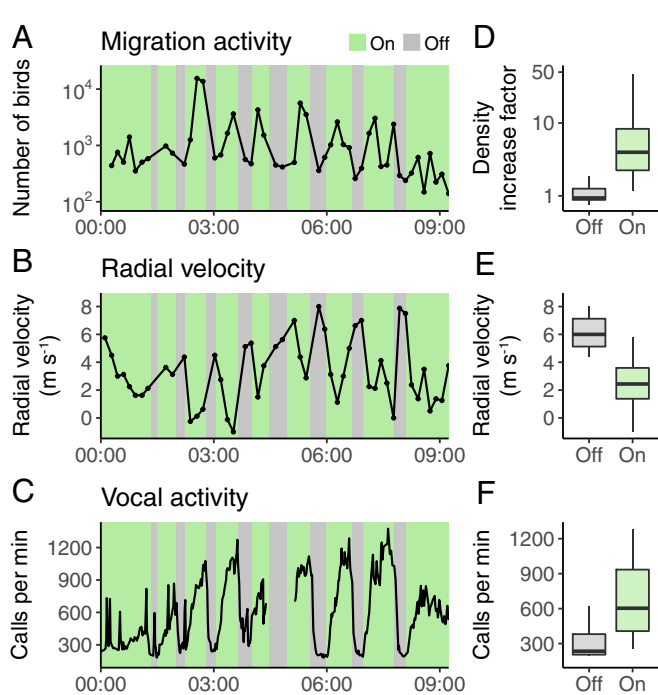


Fig. 2. Time series of radar and acoustic measures of Tribute in Light impact on migratory birds. Observations (in Coordinated Universal Time) from September 11–12, 2015 of (A) migration activity within 500 m of the installation, (B) radial velocity within 500 m of the installation, and (C) vocal activity during periods of TiL illumination. D–F show corresponding data with and without illumination. Density increase factor (D) is defined as the peak bird density near the installation divided by the mean density 2–20 km away.

these effects were also significant in the high altitude 1.5° radar data (total numbers: factor = 1.9 times, $t = 3.49$, $P = 0.0006$; standardized peak density: factor = 4 times, $t = 4.00$, $P < 0.0001$). Radial velocities were significantly lower during illuminated periods (main effect = -1.7 m s^{-1} , $t = -2.10$, $P = 0.037$), especially during 2012 (effect with interaction = -5.4 m/s , $t = -2.38$, $P = 0.02$) and 2015 (effect with interaction = -4.3 m/s , $t = -2.52$, $P = 0.01$). Flight call rates recorded beneath the installation were significantly higher during illuminated periods (main effect = 1.4 times, $t = 4.53$, $P < 0.0001$), especially in 2015 (factor with interaction = 2.9 times, $t = 6.88$, $P < 0.0001$); the effect was reduced in 2013 (factor with interaction = 1.1 times, $t = -2.30$, $P = 0.02$). Because our model of vocal activity included bird density as a predictor to account for variation in calling explained by the sheer quantity of birds, the significant increases in calling with illumination can be attributed primarily to behavioral differences.

Simulation results showed that birds were highly likely to become disoriented as they approached the installation (SI Appendix, Fig. S8). The model matching radar observations most closely (model 1; Fig. 4 and SI Appendix, Tables S1 and S2) had disorientation probability $a = 0.95$, indicating a very high likelihood of disorientation near ALAN, and the characteristic disorientation distance (σ) was 1,500 m. The concentrations of birds observed at the installation could only be explained by including directed flight toward ALAN for disoriented birds (concentration parameter $\kappa > 0$; best model $\kappa = 0.1$). In contrast, simulated birds diffused easily away from ALAN when assuming a non-directional random walk ($\kappa = 0$; model 3 in SI Appendix, Table S1). These results support our visual observations of birds circling around the installation and are indicative of light attraction.

The stabilization time to a steady-state increased with disorientation probability (a) and flight directionality toward ALAN (κ) (Fig. 4, Movies S4–S8, and SI Appendix, Table S1). The stabilization time provides information on the residence time of birds in the beam, as a steady state is only reached over time periods

longer than the average residence time. Our model 1, which is conservative in this regard, predicts a stabilization time of 34 min. We note that this is the result of average behavior for all birds contributing to the density pattern, and individual residence times may be considerably longer or shorter. Our simulation provides a theoretical framework for explaining our visual and remotely sensed observations, underscoring that the light installation attracted and entrained passage migrants.

Finally, direct visual observations showed that birds frequently circled the installation during periods of illumination and decreased speed on approach to the installation (SI Appendix). Such observations also highlighted a particular hazard that nocturnally migrating birds face in urbanized areas with ALAN: collisions with structures. Observers noted in 2015 and 2016 that many birds collided with the glass windows of a building under construction just north of the lights (50 West Street; Fig. 14). The full extent of mortality was not clear, primarily because of challenges surveying nearby sites, scaffolding preventing birds from falling to ground level, and removal of carcasses by scavengers and building staff. We therefore do not have sufficient data to analyze mortality with respect to illumination and migration intensity. However, existing data are archived in the New York City Audubon D-Bird database (<https://d-bird.org/>).

Discussion

This study quantifies ALAN-induced changes in multiple behaviors of nocturnally migrating birds. Our data show that the light installation strongly concentrates and disorients migrants flying over a heavily urbanized area, influencing ≈ 1.1 million birds during seven nights over 7 y.

Existing published accounts report attraction to lights almost exclusively under poor-visibility conditions (45, 53), but our results show alterations to migrants' behaviors in clear and mostly clear

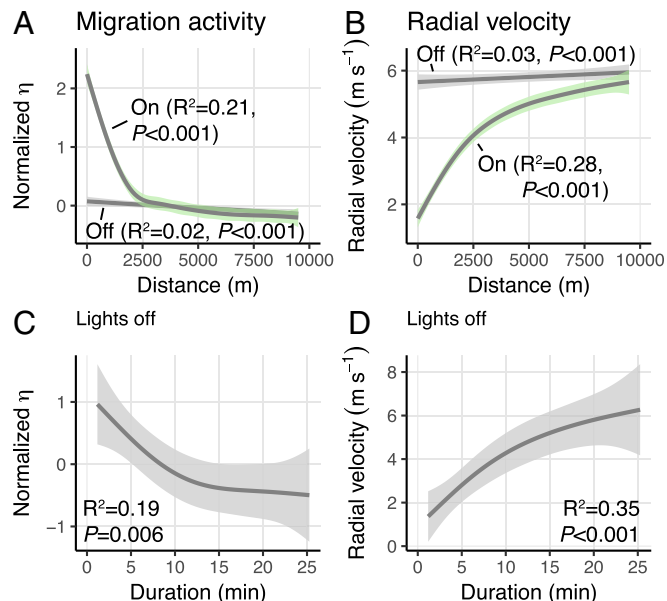


Fig. 3. Spatial and temporal influence of Tribute in Light on migratory birds. Migration activity (Left column) and radial velocity (Right column) at the installation pooled across years by distance from the study site (A and B) and activity as a function of time since TiL shutdown (C and D). To account for year-to-year variation, migration activity was normalized across years using a z-score standardization (values minus the nightly mean, divided by the nightly SD). Illumination represented by green and periods without illumination by gray. C and D include only measures ≤ 500 m from the installation. Data fit with generalized additive models (A and B: bs = “cs,” $m = 2$, $k = 10$; C and D: bs = “ds,” $m = 2$, $k = 5$) and weighted by migration activity for radial velocity models. Shading represents 95% confidence intervals.

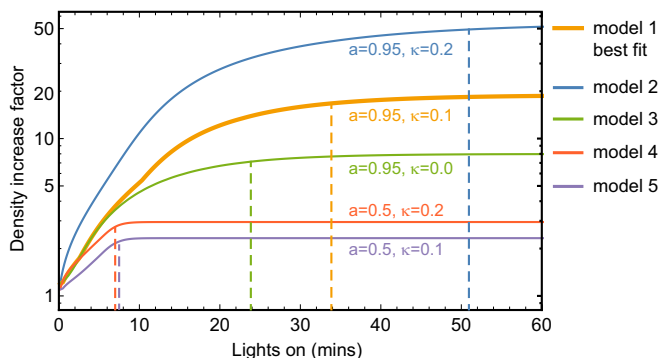


Fig. 4. Simulated bird concentrations over time at an ALAN source (solid lines). Vertical dashed lines indicate time to steady-state stabilization. Model parameters a and κ are described in [SI Appendix, Eqs. S1 and S2](#), with parameter σ fixed at 1,500 m ([SI Appendix, Table S1](#)). Model 1 represents the best fit to the observed patterns at the installation, but this model is still conservative in that higher-than-predicted concentrations of birds occurred in certain periods. In general, bird concentrations at the installation could only be explained by including directed flight toward ALAN for disoriented birds ($\kappa > 0$). These results support our observations that birds were disoriented by and attracted to the installation.

sky conditions (e.g., after ref. 48). Furthermore, to the best of our knowledge, no previous studies have reported attractive effects of ground-based lights to extend far above the ground, although nocturnally migrating birds will attempt to escape from direct illumination by a searchlight (54). In our study, we found behavioral responses to the installation up to ≈ 4 km above the ground. The vertical orientation of the light beams may be partly responsible for their high-altitude effects, as illuminated atmospheric moisture, dust, insects, or potentially other birds may attract migrants. We also demonstrated that short-term removal of ALAN eliminated its disruptive effects almost instantaneously. Our ground-truthed, direct visual observations of decreases in flight speed and increases in circling behaviors corroborate previous findings that birds shift direction and fly more slowly and erratically in the presence of ALAN (22, 23, 32, 33, 39, 44, 48, 49, 55). Furthermore, the increase in vocal activity that we describe agrees with other studies' findings, highlighting disorientation due to artificial lighting (23, 30). Finally, although each year exhibited a unique array of atmospheric conditions, we documented a strong concentrating effect of light in all but one of the 7 study years ([SI Appendix, Fig. S7](#)). We conclude that high intensity lights have the ability to greatly impact avian migratory behavior under a wide range of conditions. The fact that we did not document a strong effect during 1 y (2014) highlights a need for further research on how differing ambient conditions influence birds' attraction to light sources at night.

Light-induced alterations to nocturnal migration behaviors may represent significant energetic expenditures for migrating birds, but the effects of such alterations have not been quantified (56). Our visual observations indicate that bright lights alone can induce unnecessary ascent and descent, long periods of circling, and other types of complex and irregular maneuvering in birds close to the ground (22); these flight patterns are undoubtedly more energetically expensive than typical straight-path migratory flights. Specific hazards resulting from altered flight behavior may include susceptibility to predation (31), collisions with man-made structures (29), and changes to stopover ecology (57). Importantly, birds entrained for hours (39, 41, 42, 55, 58) by artificial lighting expend energy to remain airborne but do not make forward progress. Those that do not die from complications of exhaustion (59) may be delayed for days, as it takes time for lean migrants to regain fat stores during migratory stopover (60). Although our best model's stabilization time of 34 min suggests that most birds do not remain at the installation for hours, this model could not explain the largest concentrations we observed; other methods will

be necessary to better understand variation in individual birds' behavior over time in the lights.

Further controlled experiments in field and laboratory settings would help determine the causes of attraction and disorientation at local and landscape scales. Studies that varied light intensity locally found that birds respond more strongly with more intense light (61–63). Sampling bird migration at and near light installations of varying intensities may provide additional opportunities to study attraction and disorientation. There are few vertically pointing light installations of comparable intensity in the United States (e.g., Luxor, Las Vegas, NV), but many structures use similarly powerful horizontal lights (e.g., sports stadia, construction sites, offshore oil rigs). Studies at such locations have not used multimodal remote sensing to quantify disruptions but have noted behavioral changes similar to those that we observed (e.g., aggregation, circling, and increased vocal activity) (57, 64).

Studies of ALAN are revealing large-scale effects on bird behavior that range from flight alterations to changes in stopover habitat use. There is mounting evidence that migratory bird populations are more likely to occur in urban areas during migration, especially in the autumn (65). Light pollution may explain this relationship, as recent research suggests that birds associate with higher levels of ALAN during migration (66). Given alarming declines in migratory bird populations (67, 68), these studies highlight a need to understand ALAN's implications for migratory bird populations.

Finally, our study highlights a model relationship for collaboration among diverse stakeholders. A hallmark of this project was frequent and public cooperation among the NSMM, the Municipal Arts Society, New York City Audubon, the Cornell Lab of Ornithology, and stakeholders with direct interest and responsibility for this event, all of whom acknowledged its potential to negatively impact birds. All parties agreed to keep the display illuminated unless potentially hazardous conditions for birds necessitated a short-term shutdown of the lights. Whereas discontinuing the display would be best for nocturnally migrating birds, such a scenario may not be possible at this time. TiL is arguably one of the world's most iconic and emotional displays of light. The fact that the event's organizers and participants were willing to periodically shut down the lights for the benefit of migratory birds is an encouraging acknowledgment of the importance of bird conservation. Moreover, despite occasional confusion and frustration among the tribute's viewers, media coverage often highlighted a unified message from stakeholders about balancing potential hazards to migrating birds with the intent and spirit of the display.

Methods

During our 7-y study period, the tribute lights were shut down a total of 22 times, for ≈ 20 min each. This allowed us to directly contrast birds' behaviors during adjacent dark and illuminated periods. We note that this study was opportunistic and not a controlled experiment. Furthermore, we note that such an opportunistic approach results in some inevitable challenges in interpretation, for example because we were unable to control for additional factors that could influence the degree to which birds congregate at light sources. Such factors likely include wind speed, wind direction, temperature, cloud cover, and ground-based sources of light and sound. However, because ambient conditions were generally similar within each night, we can still readily measure the additive effect of illumination on bird behavior, given each year's suite of conditions.

Study Site and Scope. TiL is an event held annually since 2002 on September 11th to memorialize lives lost during the terrorist attacks of September 11th, 2001 (www.911memorial.org/tribute-light). NSMM currently operates the light installation atop a parking garage near the site of the former World Trade Center in New York City (NYC, NY) at the southern end of Manhattan Island (40.707°, -74.015°).

Massive nocturnal migratory movements of birds regularly occur over our study area during mid-September (12, 13, 69, 70). However, since the timing of these movements depends on local and regional weather and wind conditions (71–74), the magnitude of migratory passage on the single night of September 11th varies greatly among years. An agreement between New

York City Audubon (NYCA) and NSMM govern when to initiate the shutdown procedures: when numbers of birds circling in the beams exceed 1,000 individuals, based on visual observations, NYCA requests that lights be extinguished for ≈ 20 min. These requests originate from observers on site that are directly monitoring birds and their behaviors in the beams.

We examined September 11th nights from 2008 to 2016. High-resolution radar imagery did not exist before 2008, which limited our temporal scope. We excluded 2009 and 2011 because of the presence of precipitation, which interferes with analysis of radar data containing bird migration information. Of the remaining 7 y, migration conditions varied from marginal to favorable, assessed based on prevailing atmospheric conditions. Of these 7 y, the lights were shut down at least once during 5 of them; as a result, many of our analyses are restricted to these 5 y (2010, 2012, 2013, 2015, and 2016). Of the remaining 2 y, the first (2008) occurred before stakeholders could reach a consensus on a protocol for shutting down the light installation when birds were present and in danger. Organizers did not shut down the installation in 2014 because few birds were present in the lights.

Local Weather Conditions. We downloaded hourly local climatic data (LCD) for September 11 and 12, 2008–2016 (excluding 2009 and 2011 as described above) from the closest official National Weather Service station to the installation between evening and morning civil twilight (sun angle 6° below the horizon): WBAN 94728, Central Park, New York, NY at 40.789° , -73.967° ; and meteorological terminal aviation routine weather reports (METARs) from Newark Liberty International Airport, the closest such station at 40.690° , -74.174° . Based on a review and summary of these data, we classified all nights during our study as clear (*SI Appendix, Tables S3 and S4*).

Weather Surveillance Radar Data. We gathered radar data from the Brookhaven, NY WSR-88D radar (KOKX; 40.866° , -72.864°) to quantify migrants' flight behaviors and extracted georeferenced measures of reflectivity (z ; $\text{cm}^2 \text{ km}^{-3}$) and radial velocity (w ; ms^{-1}) from the $\approx 0.5^\circ$ and $\approx 1.5^\circ$ elevation angles (12, 13, 70, 75, 76). We measured between civil twilight periods within a 20-km radius surrounding the installation (98.5 km from the radar, azimuth 260°) and consolidated analyses into 500-m height annuli bins. We dealiased velocities when necessary following refs. 76 and 77. We restricted our analyses to data points within 90 min of a shutdown period except when described.

We studied the effect of light stimuli on migratory birds using several metrics. First, we used the radar sweep with the lowest elevation angle ($\approx 0.5^\circ$) to estimate the number of birds present in a cylinder centered on the installation with a radius along the ground of 500 m and a height of 1.7 km, the approximate width of the radar beam above the site (78). We calculated total effective scattering area per unit volume ($\text{cm}^2 \text{ km}^{-3}$) of birds in this cylinder using bird density measures from the 0–500-m bin. Then, we converted to numbers of birds using an estimated value of one bird = 8.1 cm^2 , which is the measured cross-sectional area on S-band radar of a small passerine songbird (common chaffinch, *Phylloscopus collybita*) (79). We chose a relatively small cross-section value because visual observations indicated that birds in the lights were predominantly small songbirds. The radar beam set to the 0.5° elevation angle passes above the installation at an altitude of $\approx 1.5 \text{ km}$ (50% power range, 0.7–2.4 km), which is higher than the altitudes at which the greatest migratory activity during this season in this region generally occurs (80). Therefore, we used an analysis of the entire radar scan to estimate the proportion of migration occurring beneath (or above) the radar beam at the installation, out of sight of the radar. We then adjusted our estimates to account for these undetected birds by multiplying by the necessary correction factor (*SI Appendix, Fig. S10*). This approach assumes that the light beams did not greatly alter the altitudinal distribution of birds near the installation. The validity of this assumption is supported by direct visual observations at the site, where observers noted descent only by the lowest-flying individuals, which would not be detected by radar. Furthermore, any unaccounted-for descent at higher altitudes would render our estimates conservative, because a greater proportion of birds flying below the radar beam than expected would yield a lower estimate of total bird numbers.

To complement estimates of the total number of birds in proximity to the installation, we also calculated the extent to which birds were concentrated at high densities in the airspace near the installation, relative to the baseline

value in the surrounding airspace. To produce this baseline, we calculated the mean and SD of density values between 2 and 20 km from the installation. We then found the peak bird density value within 500 m of the installation, and we subtracted the baseline mean density from this peak density and divided the difference by the baseline SD (again, 2–20 km from the installation). The resulting value, referred to as “standardized peak density,” represents the number of SDs the peak density falls above the baseline density.

Acoustic Data. We collected continuous acoustic data at 32-kHz sampling rates and 16-bit sample sizes during each year's event with a pressure zone microphone (Old Bird 21c; Old Bird, Inc.) specifically designed for monitoring avian flight calls, connected to (i) a Nagra ARES-BB+ (2010 and 2013) or (ii) a custom-built passive acoustic recording system (2015 and 2016), comprising a Raspberry Pi 2 Model B (Raspberry Pi Foundation) with a Cirrus Logic Raspberry Pi audio card (Cirrus Logic). We focused analysis on the 6- to 9-kHz frequency band to minimize interference from anthropogenic, geophonic, and nonavian biophonic noise and because many of the migrating birds in the New York City area emit flight calls in this frequency band (81). The microphone sensitivity in the relevant frequency band for this study (6–9 kHz) was $-33 \text{ dB re } 1 \text{ V Pa}^{-1}$ ($\pm 2 \text{ dB}$).

Visual Observations. We complemented remote sensing data that characterized behaviors of nocturnally migrating birds above the installation with visual observations. Numerous observers, including one of us (A.F.) and volunteers from NYCA and the local birdwatching community, made visual counts of nocturnally migrating birds at the installation during the period between civil twilight dusk and dawn. All visual counts are archived in the eBird reference database (ref. 82; ebird.org/ebird/hotspot/L1744278).

Statistics. We used generalized additive models (R package mgcv) (83) to quantify the effects of TiL illumination on birds' behaviors (*SI Appendix*). We tested the categorical factors of light (on/off) and year on four metrics: standardized peak density, the total number of birds present within 500 m of the installation, the radial velocities of birds above the installation, and the number of flight calls recorded beneath the site. For models of time series, we also included smooth terms that accounted for overall variation in densities and behavior through the night. We confirmed that there was negligible temporal autocorrelation of residuals using the acf function in R for all analyses involving time series (*SI Appendix*). We log-transformed response variables when necessary to reduce residual skewness; for models with log-transformed response variables, we express effect size as a multiplicative factor, found by exponentiating the coefficient. Finally, to determine whether the light effects we present in the study are representative of those observed across years, we compared standardized peak densities across the lighted periods of all 7 y, including the 2 during which no light shutdowns occurred.

Simulations. To understand the dynamic patterns of bird density at the installation, we formulated a spatiotemporal flow model to simulate behavioral changes resulting from exposure to light. In our simulation, birds could transition between two behavioral states: an undisturbed migratory state and a disoriented state induced by ALAN. Detailed methodology of our simulations is in *SI Appendix*.

ACKNOWLEDGMENTS. We thank Eli Bridge, Wesley Hochachka, Steve Kelling, Jeff Kelly, Frank La Sorte, Felix Liechti, Michael Patten, and Brian Sullivan for review of manuscript drafts; anonymous reviewers provided invaluable comment and criticism. Matt Robbins, Raymond Mack, Christopher Tessaglia-Hymes, and Bioacoustics Research Program staff assisted with development, deployment, and operation of autonomous acoustic recording units. Graham Taylor provided information about flight energetics. John Rowden and Debra Kriensky coordinated volunteers for New York City Audubon. Special thanks to Michael Ahern, Jared Abramson, Jennifer Hellman, Massimo Moratti, Dorian Cynajko, and Olivia Egger for TiL logistical support. Support was provided by National Science Foundation Grant IIS-1125098 (to A.F. and B.M.V.D.), National Science Foundation Grant EF-1340921 (to K.G.H.), the Leon Levy Foundation (A.F. and S.B.E.), the Marshall Aid Commemoration Commission (B.M.V.D.), and a Cornell Lab of Ornithology Edward W. Rose Postdoctoral Fellowship and NASA Grant NNX14AC41G (to A.M.D.).

1. Falchi F, et al. (2016) The new world atlas of artificial night sky brightness. *Sci Adv* 2: e1600377.
2. Gaston KJ, Bennie J, Davies TW, Hopkins J (2013) The ecological impacts of nighttime light pollution: A mechanistic appraisal. *Biol Rev Camb Philos Soc* 88: 912–927.
3. Gaston KJ, Visser ME, Holker F (2015) The biological impacts of artificial light at night: The research challenge. *Philos Trans R Soc Lond B Biol Sci* 370:20140133.

4. Rich C, Longcore T (2005) *Ecological Consequences of Artificial Night Lighting* (Island Press, Washington, DC), p 458.
5. Spoelstra K, Visser ME (2013) The impact of artificial light on avian ecology. *Avian Urban Ecol* 4:21–28.
6. Gauthreaux SA, Jr, Belser CG, Rich C, Longcore T (2006) Effects of artificial night lighting on migrating birds. *Ecological Consequences of Artificial Night Lighting*, eds Rich C, Longcore T (Island Press, Washington, DC), pp 67–93.

7. Newton I (2008) *The Migration Ecology of Birds* (Elsevier/Academic, Amsterdam), 1st Ed.
8. Alerstam T (1990) *Bird Migration* (Cambridge Univ Press, Cambridge, UK).
9. Conklin JR, Senner NR, Battley PF, Piersma T (2017) Extreme migration and the individual quality spectrum. *J Avian Biol* 48:19–36.
10. Hewson CM, Thorup K, Pearce-Higgins JV, Atkinson PW (2016) Population decline is linked to migration route in the common cuckoo. *Nat Commun* 7:12296.
11. Cohen EB, et al. (2017) How do en route events around the Gulf of Mexico influence migratory landbird populations? *Condor* 119:327–343.
12. Horton KG, Van Doren BM, Stepanian PM, Farnsworth A, Kelly JF (2016) Where in the air? Aerial habitat use of nocturnally migrating birds. *Biol Lett* 12:20160591.
13. Farnsworth A, et al. (2016) A characterization of autumn nocturnal migration detected by weather surveillance radars in the northeastern USA. *Ecol Appl* 26:752–770.
14. Richardson WJ (1990) Wind and orientation of migrating birds: A review. *Experientia* 46:416–425.
15. Kelly JF, et al. (2016) Novel measures of continental-scale avian migration phenology related to proximate environmental cues. *Ecosphere* 7:e01434.
16. Marra PP, Francis CM, Mulvihill RS, Moore FR (2005) The influence of climate on the timing and rate of spring bird migration. *Oecologia* 142:307–315.
17. Liechti F (2006) Birds: Blowin' by the wind? *J Ornithol* 147:202–211.
18. Alerstam T, Lindström Å (1990) Optimal bird migration: The relative importance of time, energy, and safety. *Bird Migration: Physiology and Ecophysiology*, ed Gwinner E (Springer, Berlin), pp 331–351.
19. Mouritsen H, Heyers D, Güntürkün O (2016) The neural basis of long-distance navigation in birds. *Annu Rev Physiol* 78:133–154.
20. Hiscock HG, et al. (2016) The quantum needle of the avian magnetic compass. *Proc Natl Acad Sci USA* 113:4634–4639.
21. Vincze O, Vágási CI, Pap PL, Osváth G, Möller AP (2015) Brain regions associated with visual cues are important for bird migration. *Biol Lett* 11:20150678.
22. Day RH, Rose JR, Prichard AK, Streever B (2015) Effects of gas flaring on the behavior of night-migrating birds at an artificial oil-production island, Arctic Alaska. *Arctic* 68:367–379.
23. Cochran WW, Graber RR (1958) Attraction of nocturnal migrants by lights on a television tower. *Wilson Bull* 70:378–380.
24. Kishkinev D, Chernetsov N, Pakhomov A, Heyers D, Mouritsen H (2015) Eurasian reed warblers compensate for virtual magnetic displacement. *Curr Biol* 25:R822–R824.
25. Wiltschko W, Munro U, Ford H, Wiltschko R (1993) Red light disrupts magnetic orientation of migratory birds. *Nature* 364:525–527.
26. Poot H, et al. (2008) Green light for nocturnally migrating birds. *Ecol Soc* 13:47.
27. Muheim R, Sjöberg S, Pinzon-Rodriguez A (2016) Polarized light modulates light-dependent magnetic compass orientation in birds. *Proc Natl Acad Sci USA* 113: 1654–1659.
28. Wiltschko R, Stappert K, Thalau P, Wiltschko W (2010) Directional orientation of birds by the magnetic field under different light conditions. *J R Soc Interface* 7(Suppl 2): S163–S177.
29. Loss SR, Will T, Marra P (2015) Direct mortality of birds from anthropogenic causes. *Annu Rev Ecol Evol Syst* 46:99–120.
30. Watson MJ, Wilson DR, Mennill DJ (2016) Anthropogenic light is associated with increased vocal activity by nocturnally migrating birds. *Condor* 118:338–344.
31. DeCandido R, Allen D (2006) Nocturnal hunting by peregrine falcons at the Empire State Building, New York City. *Wilson J Ornithol* 118:53–58.
32. Avery M, Springer PF, Cassel JF (1976) The effects of a tall tower on nocturnal bird migration: A portable ceilometer study. *Auk* 93:281–291.
33. Jones J, Francis CM (2003) The effects of light characteristics on avian mortality at lighthouses. *J Avian Biol* 34:328–333.
34. Saunders W (1930) The destruction of birds at long point light-house, Ontario, on four nights in 1929. *Auk* 47:507–511.
35. Berenstein N (2015) Deathtraps in the flyways: Electricity, glass and bird collisions in urban North America, 1887–2014. *Cosmopolitan Animals* (Springer, Berlin), pp 79–92.
36. Spofford WR (1949) Mortality of birds at the ceilometer of the Nashville airport. *Wilson Bull* 61:86–90.
37. Kerlinger P, et al. (2010) Night migrant fatalities and obstruction lighting at wind turbines in North America. *Wilson J Ornithol* 122:744–754.
38. James P (1956) Destruction of warblers on Padre Island, Texas, in May, 1951. *Wilson Bull* 68:224–227.
39. Larkin R (2000) Investigating the behavioral mechanisms of tower kills. *Transcripts of Proceedings of the Workshop on Avian Mortality at Communications Towers, August 11, 1999* (Cornell University, Ithaca, NY).
40. Hüppop O, Hüppop K, Dierschke J, Hill R (2016) Bird collisions at an offshore platform in the North Sea. *Bird Study* 63:73–82.
41. Gätke H (1895) *Heligoland as an Ornithological Observatory: The Result of Fifty Years' Experience* (Edinburgh Univ Press, Edinburgh).
42. Drewitt AL, Langston RH (2008) Collision effects of wind-power generators and other obstacles on birds. *Ann N Y Acad Sci* 1134:233–266.
43. Verheijen F (1981) Bird kills at tall lighted structures in the USA in the period 1935–1973 and kills at a Dutch lighthouse in the period 1924–1928 show similar lunar periodicity. *Ardea* 69:199–203.
44. Gehring J, Kerlinger P, Manville AM, 2nd (2009) Communication towers, lights, and birds: Successful methods of reducing the frequency of avian collisions. *Ecol Appl* 19:505–514.
45. Johnston DW (1955) Mass bird mortality in Georgia, October, 1954. *Oriole* 20:17–26.
46. Crawford RL, Engstrom RT (2001) Characteristics of avian mortality at a north Florida television tower: A 29-year study. *J Field Ornithol* 72:380–388.
47. Clark AR, Bell CE, Morris SR (2005) Comparison of daily avian mortality characteristics at two television towers in western New York, 1970–1999. *Wilson Bull* 117:35–43.
48. Avery M, Springer PF, Cassel JF (1977) Weather influences on nocturnal bird mortality at a North Dakota tower. *Wilson Bull* 89:291–299.
49. Bruderer B, Peter D, Steuri T (1999) Behaviour of migrating birds exposed to X-band radar and a bright light beam. *J Exp Biol* 202:1015–1022.
50. Evans WR, Akashi Y, Altman N, Manville A (2007) Response of night-migrating songbirds in cloud to colored and flashing light. *North Am Birds* 60:476–488.
51. Bolshakov CV, Bulyuk VN, Sinelschikova AY, Vorotkov MV (2013) Influence of the vertical light beam on numbers and flight trajectories of night-migrating songbirds. *Avian Ecol Behav* 24:35–49.
52. Farnsworth A (2005) Flight calls and their value for future ornithological studies and conservation research. *Auk* 122:733.
53. Lundstrom LA, Horn DJ, Capparella AP (2013) The effects of tower structure and weather conditions on avian mortality at three television towers in central Illinois. *Trans Ill State Acad Sci* 106:9–12.
54. Larkin RP, Torre-Bueno JR, Griffin DR, Walcott C (1975) Reactions of migrating birds to lights and aircraft. *Proc Natl Acad Sci USA* 72:1994–1996.
55. Larkin RP, Frase BA (1988) Circular paths of birds flying near a broadcasting tower in cloud. *J Comp Psychol* 102:90–93.
56. Lennox RJ, et al. (2016) Conservation physiology of animal migration. *Conserv Physiol* 4:co072.
57. Lebbin DJ, Harvey MG, Lenz TC, Andersen MJ, Ellis JM (2007) Nocturnal migrants foraging at night by artificial light. *Wilson J Ornithol* 119:506–508.
58. Casement M (1984) Landbirds from ships at sea 1983. *Sea Swallow* 33:22–35.
59. Ramirez P, Dickerson K, Lindstrom J, Meteyer CU, Darrah S (2015) Lapland longspur mortality at an oil well drilling rig site, Laramie County, Wyoming. *Wildl Soc Bull* 39:165–168.
60. Seewagen CL, Guglielmo CG (2010) Effects of fat and lean body mass on migratory landbird stopover duration. *Wilson J Ornithol* 122:82–87.
61. Verheijen FJ (1985) Photopollution: Artificial light optic spatial control systems fail to cope with. Incidents, causation, remedies. *Exp Biol* 44:1–18.
62. Martin G (1990) The visual problems of nocturnal migration. *Bird Migration: Physiology and Ecophysiology*, ed Gwinner E (Springer, Berlin), pp 185–197.
63. Verheijen FJ (1960) The mechanisms of the trapping effect of artificial light sources upon animals. *Arch Neerl Zool* 13:1–107.
64. Rodriguez A, et al. (2017) Seabird mortality induced by land-based artificial lights. *Conserv Biol* 10.1111/cobi.12900.
65. Zuckerberg B, Fink D, La Sorte FA, Hochachka WM, Kelling S (2016) Novel seasonal land cover associations for eastern North American forest birds identified through dynamic species distribution modelling. *Divers Distrib* 22:717–730.
66. La Sorte FA, Fink D, Buler JJ, Farnsworth A, Cabrera-Cruz SA (2017) Seasonal associations with urban light pollution for nocturnally migrating bird populations. *Glob Change Biol* 10.1111/gcb.13792.
67. Robbins CS, Sauer JR, Greenberg RS, Droege S (1989) Population declines in North American birds that migrate to the neotropics. *Proc Natl Acad Sci USA* 86:7658–7662.
68. North American Bird Conservation Initiative (2016) *The State of North America's Birds 2016* (Environment and Climate Change Canada, Ottawa).
69. Van Doren BM, Sheldon D, Geevarghese J, Hochachka WM, Farnsworth A (2015) Autumn morning flights of migrant songbirds in the northeastern United States are linked to nocturnal migration and winds aloft. *Auk* 132:105–118.
70. Horton KG, Van Doren BM, Stepanian PM, Farnsworth A, Kelly JF (2016) Seasonal differences in landbird migration strategies. *Auk* 133:761–769.
71. Kemp MU, et al. (2013) The influence of weather on the flight altitude of nocturnal migrants in mid-latitudes. *Ibis* 155:734–749.
72. La Sorte FA, et al. (2015) Migration timing and its determinants for nocturnal migratory birds during autumn migration. *J Anim Ecol* 84:1202–1212.
73. Richardson WJ (1978) Timing and amount of bird migration in relation to weather: A review. *Oikos* 30:224–272.
74. Van Belle J, Shamoun-Baranes J, Van Loon E, Bouten W (2007) An operational model predicting autumn bird migration intensities for flight safety. *J Appl Ecol* 44:864–874.
75. Stepanian PM, Horton KG (2015) Extracting migrant flight orientation profiles using polarimetric radar. *IEEE Trans Geosci Remote Sens* 53:6518–6528.
76. Sheldon DR, et al. (2013) Approximate Bayesian inference for reconstructing velocities of migrating birds from weather radar. *Proceedings of the Twenty-Seventh AAAI Conference on Artificial Intelligence*, eds desJardins M, Littman ML (Bellevue, Washington), pp 1334–1340.
77. Sheldon D (2015) WSRlib: MATLAB toolbox for weather surveillance radar. Available at <https://bitbucket.org/dsheldon/wsrlib>. Accessed September 16, 2017.
78. Doviak RJ, Zrnic DS (1993) *Doppler Radar and Weather Observations* (Academic, San Diego), 2nd Ed.
79. Eastwood E (1967) *Radar Ornithology* (Methuen, London).
80. La Sorte FA, et al. (2015) Seasonal changes in the altitudinal distribution of nocturnally migrating birds during autumn migration. *R Soc Open Sci* 2:150347.
81. Evans W, O'Brien M (2002) *Flight Calls of Migratory Birds: Eastern North American Landbirds [CD-ROM]* (Oldbird, Ithaca, NY).
82. Sullivan BL, et al. (2014) The eBird enterprise: An integrated approach to development and application of citizen science. *Biol Conserv* 169:31–40.
83. Wood SN (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *J R Stat Soc Series B Stat Methodol* 73:3–36.