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. 1*A*). 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. 1 *B* and *C* and 2*A*, 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. S4*A*). Under illumination, peak bird densities near the installation reached magnitudes 20 times greater than the surrounding baseline during all 7 y (*SI Appendix*, Fig. S5*A*), 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. S5*A*). Vocal activity beneath the lights was intense during periods of aggregation (Fig. 2*C* 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. 3 *C* 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,

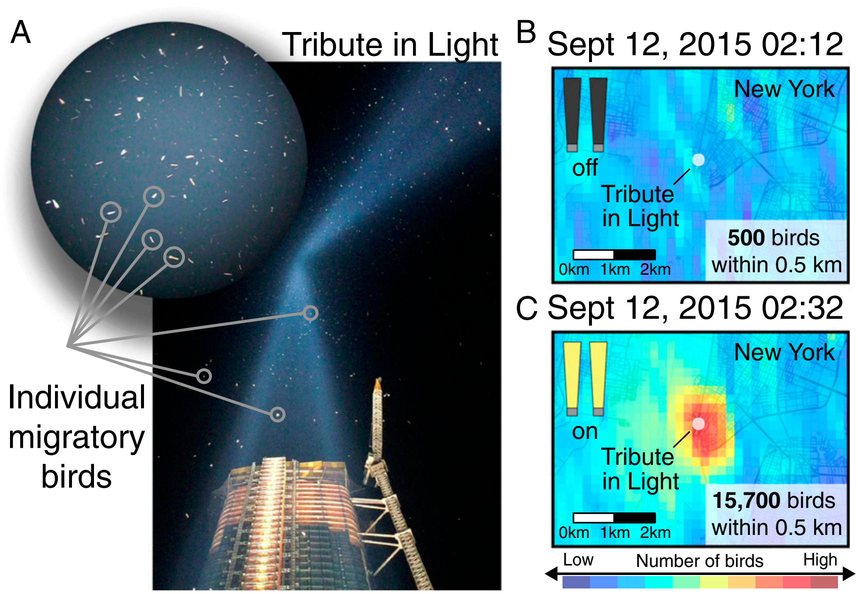

Fig. 1. Tribute in Light site. Observations (in Coordinated Universal Time) from the September 11–12 2015 Tribute in Light depicting altered behaviors of nocturnally migrating birds. (*A*) Direct visual observation. (*B*) Radar observation without TiL illumination and (*C*) with TiL illumination.