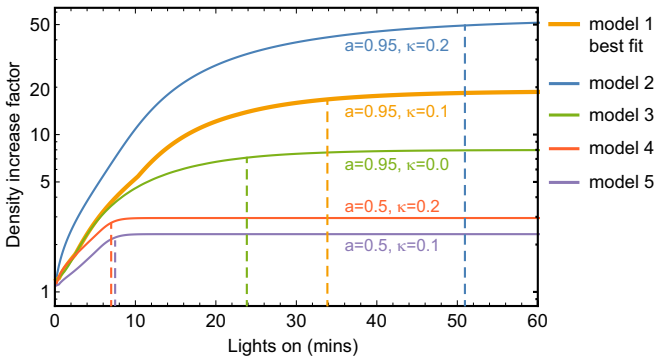

Fig. 4. Simulated bird concentrations over time at an ALAN source (solid lines). Vertical dashed lines indicate time to steady-state stabilization. Model parameters a and κ are described in *SI Appendix*, Eqs. **S1** and **S2**, with parameter σ fixed at 1,500 m (*SI Appendix*, Table S1). Model 1 represents 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