Drivers of fatal bird collisions in an urban center

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Edited by James A. Estes, University of California, Santa Cruz, CA, and approved May 5, 2021 (received for review February 2, 2021)

Millions of nocturnally migrating birds die each year from collisions with built structures, especially brightly illuminated buildings and communication towers. Reducing this source of mortality requires knowledge of important behavioral, meteorological, and anthropogenic factors, yet we lack an understanding of the interacting roles of migration, artificial lighting, and weather conditions in causing fatal bird collisions. Using two decades of collision surveys and concurrent weather and migration measures, we model numbers of collisions occurring at a large urban building in Chicago. We find that the magnitude of nocturnal bird migration, building light output, and wind conditions are the most important predictors of fatal collisions. The greatest mortality occurred when the building was brightly lit during large nocturnal migration events and when winds concentrated birds along the Chicago lakeshore. We estimate that halving lighted window area decreases collision counts by 11× in spring and 6× in fall. Bird mortality could be reduced by ∼60% at this site by decreasing lighted window area to minimum levels historically recorded. Our study provides strong support for a relationship between nocturnal migration magnitude and urban bird mortality, mediated by light pollution and local atmospheric conditions. Although our research focuses on a single site, our findings have global implications for reducing or eliminating a critically important cause of bird mortality.

light pollution | conservation | bird migration | urban planning | mortality

North America has lost nearly one-third of its birdlife in the last half-century, with migratory species experiencing particularly acute declines (1). Fatal collisions with built structures represent a major source of direct, human-caused bird mortality across North America, second only to predation by domestic cats (2). Estimates indicate that between 365 million and 988 million birds die annually in collisions with buildings in the United States, with another 16 million to 42 million annual deaths in Canada (2, 3). Birds may collide with glass windows because they reflect the surrounding environment or allow birds to perceive a seemingly open pathway to the interior of the building (4). For the billions of birds that migrate at night, outdoor lighting (e.g., streetlights and floodlights) and interior lighting from buildings may be disorienting and draw birds into built-up areas, at high risk to collide with infrastructure (5–8). Light pollution not only alters nocturnal migratory behavior on a large scale (5, 7), but is also an acute conservation concern. Nocturnal collisions with well-lit communication towers alone are estimated to kill appreciable percentages of the populations of sensitive species (9).

Avian collisions with lighted structures have been documented in the scientific literature as early as the 19th century (10–12). In recent decades, this link between collisions and light pollution has been the subject of detailed investigation (8, 13–16). Observers of bird–building collisions and tower kills have long remarked on the apparent influence of meteorological factors such as cloud ceiling, fog, frontal passage, and abrupt changes in conditions, all of which have been associated with large mortality events (10, 13, 17–24). Steady-burning lights may be particularly hazardous (25). Due to high building density and intensity of artificial lighting, cities are of particular concern. Reports of mass collisions at lighted buildings in urban areas are frequent in both the popular and scientific press (13, 19–21, 26).

Understanding, predicting, and preventing collision mortality are areas of active scientific inquiry and priorities for policymakers (1, 13). Collisions occur more frequently during migration seasons and impact numerous species of migratory birds (29), and recent work suggests that nocturnal migratory movements can be useful for predicting bird–window collisions (30). Lights-out programs, which encourage the public to extinguish outdoor lighting to protect migratory birds, are receiving increasing attention (13). The act of extinguishing lighting allows birds to immediately return to normal, safe behavior (7) and reduces mortality at lighted buildings (13). Presently, advisories are generally issued for a given time period (e.g., peak migration periods) or on specific nights when weather conditions are favorable for large migratory movements [e.g., using migration forecasting, (31, 32)].

Here, we integrate meteorological, migration-intensity, and window-radiance data to understand how these factors interact to cause bird collisions. We use a 21-y dataset of fatal collisions recorded at a single large building (McCormick Place Lakeside Center) in Chicago, IL (Fig. 1), to understand the behavioral, environmental, and anthropogenic drivers of these mortality events. Chicago poses the greatest potential risk from light pollution to migrating birds of all cities in the United States

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Significance

Collisions with built structures are an important source of bird mortality, killing hundreds of millions of birds annually in North America alone. Nocturnally migrating birds are attracted to and disoriented by artificial lighting, making light pollution an important factor in collision mortality, and there is growing interest in mitigating the impacts of light to protect migrating birds. We use two decades of data to show that migration magnitude, light output, and wind conditions are important predictors of collisions at a large building in Chicago and that decreasing lighted window area could reduce bird mortality by ∼60%. Our finding that extinguishing lights can reduce bird death has global implications for conservation action campaigns aimed at eliminating an important cause of bird mortality.

Author contributions: B.M.V.D., D.E.W., M.H., K.G.H., A.F., and B.M.W. designed research; B.M.V.D., D.E.W., and M.H. performed research; B.M.V.D., E.F.S., and D.S. analyzed data; and B.M.V.D., D.E.W., M.H., K.G.H., E.F.S., D.S., A.H.S., J.W., A.F., and B.M.W. wrote the paper.

The authors declare no competing interest.

This article is a PNAS Direct Submission.

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This article contains supporting information online at https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2101666118/-/DCSupplemental.

Published June 7, 2021.

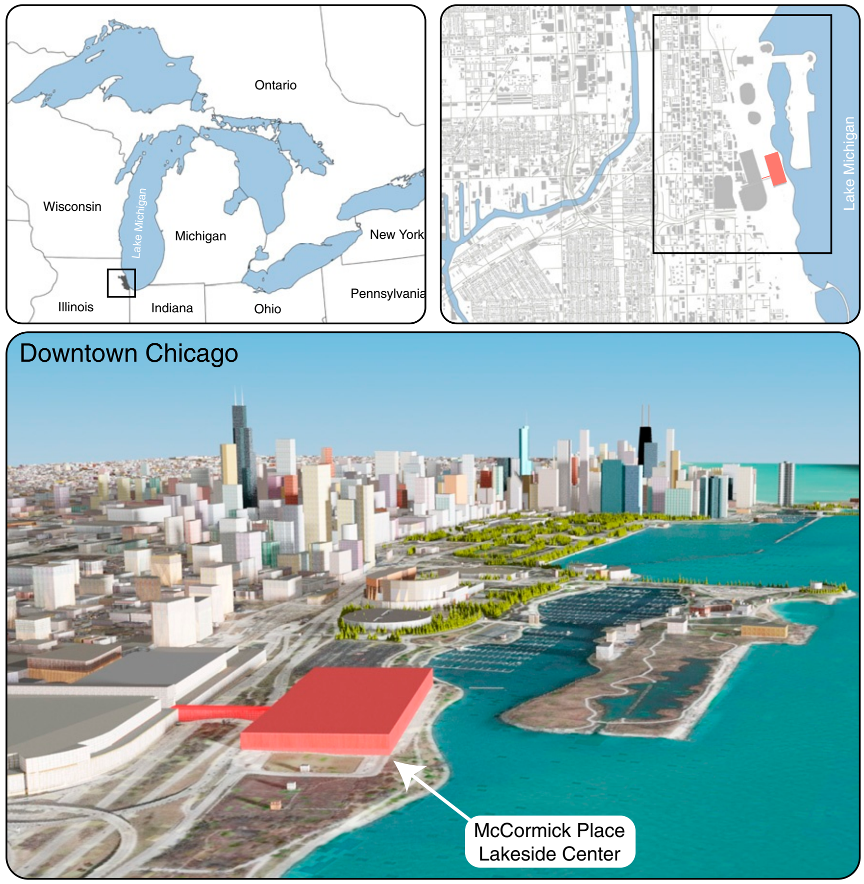

Fig. 1. Location of McCormick Place along the Chicago lakefront. The Lakeside Center building monitored in this study is highlighted in red in a three-dimensional rendering.

(33), and over 40,000 dead birds have been recovered from McCormick Place alone since 1978 (Figs. 2 and 3). Since 2000, we have recorded the number of birds and the lighting status of each window bay during dawn collision monitoring. Nocturnal lighting at McCormick Place correlates positively with bird collisions in many songbird species (34), but this association has not been quantified in the context of other important factors, including migration intensity and weather conditions. We estimate the effect of window lighting on collision counts and assess how the intensity of nocturnal bird migration mediates this relationship. We also test whether wind and weather conditions may magnify these associations. Finally, we investigate the spatiotemporal scales at which weather and migration data best explain collision mortality, identifying the times of night and areas of airspace associated with these events.

Results

Of 11,567 fatal collisions recorded between 2000 and 2020, 64.8% occurred in fall. In both spring and fall, nearly half of all documented collisions occurred on 25% percent of nights with the largest migration events (fall: 49.6%; spring: 49.4%).

Spatiotemporal Scales of Collision Predictors. We monitored nocturnal bird migration and atmospheric conditions using Doppler weather radar (WSR-88D) and weather observations from nearby Chicago Midway Airport, and we used Bayesian latent indicator scale selection (BLISS) (36) to choose the spatial and temporal scales of these predictors that best explained bird collisions. From radar data, we derived a regional measure of nocturnal bird migration, as well as localized measures from the immediate Chicago airspace. Birds migrating over the Great Lakes are known to reorient toward the coastline at dawn (37–39), but the extent to which collisions at McCormick Place may represent individuals over water attempting to reach land is unknown. We found that radar returns from the airspace over Lake Michigan explained collisions better than returns from over land (*SI Appendix*, Fig. S1); in spring, overwater airspace across a 4-km radius received the most support, whereas a 32-km scale was favored in fall. The analysis selected the middle third of the night, when birds are in active migration, over the beginning or end of the night as the period that best explained collision counts (*SI Appendix*, Fig. S1).

Drivers of Daily Fatal Collisions. Migration and lighted window area were consistently the strongest predictors of fatal collisions (Figs. 3 and 4; *SI Appendix*, Figs. S2, S3, and S4 and Tables S1 and S2). We defined lighted window area as the proportion of total window-bay area emitting light from within the building. The estimated exponentiated effect of lighted window area on collisions was a 1.95× (95% CI [1.77, 2.15]) increase in spring and a 1.52× (95% CI [1.42, 1.63]) increase in fall for a one-SD increase in lighted window area. These estimated effects correspond to a predicted 10.7-fold increase in collision counts between 50% and 100% lighted window area in spring and a corresponding 6.3-fold increase in fall. These predictions are estimated at the average values of all other predictors and high-visibility conditions. Two lines of evidence support a causal interpretation of this effect: First, these estimates were virtually identical in models that excluded the local migration predictor (spring: 1.95× vs. 1.94×; fall:

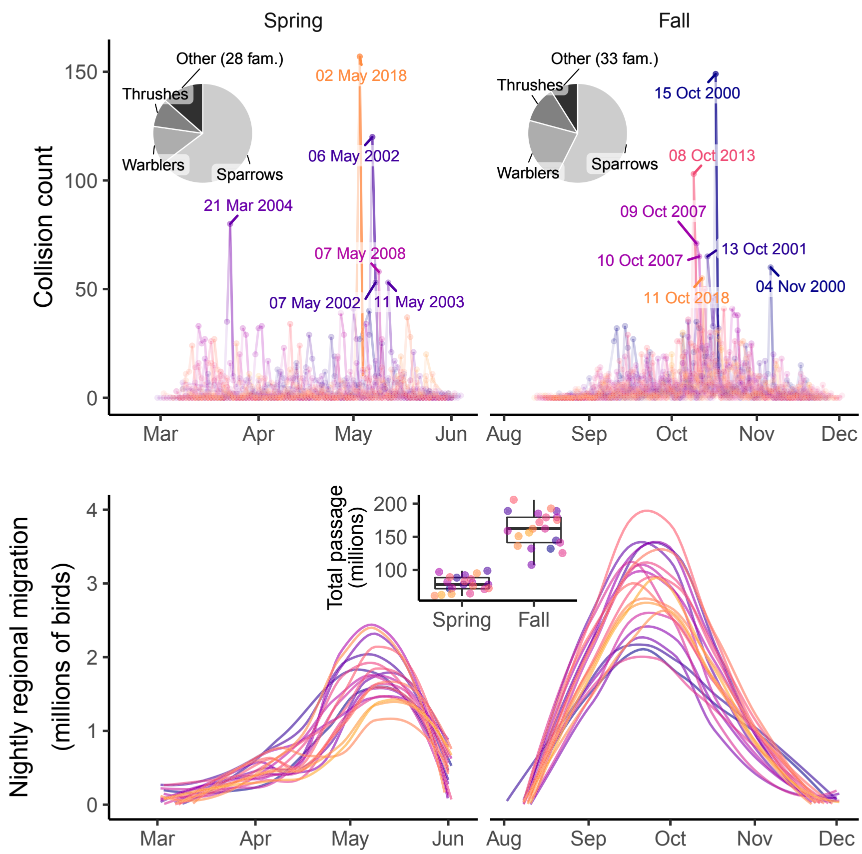

Fig. 2. Summary of collisions recorded at McCormick Place and regional bird migration between 2000 and 2020. (*Upper*) Individual years are drawn in different colors. Dates are given for mortality events totaling more than 50 birds. Pie charts show the family (fam.) composition of collected birds, with families representing less than 5% of total collisions merged into a single "other" category. (*Lower*) Summed annual migration passage at the KLOT radar in estimated number of individual birds (years colored). (*Lower*, *Inset*) Summed seasonal passage totals in estimated number of birds crossing a 75-km transect, with each point representing a year. Estimates are based on methods from ref. 35.

1.52× vs. 1.52×), the only variable we identified as a possible confounding factor (*SI Appendix*, Fig. S5), and, second, a strong causal effect of window lighting was supported by multivariate matching analysis (*SI Appendix*, Fig. S6 and Table S3).

Local weather phenomena may be important in creating conditions conducive to fatal bird collisions (10, 18–20). This may be especially evident in the context of local topography in the Chicago region, where migrating birds frequently concentrate along the shore of Lake Michigan (24, 37–39). Furthermore, there is evidence that dense cloud and low visibility may increase collision counts, especially in the presence of light pollution (10, 18–20). Regional migration intensity and westerly winds showed strong positive associations with collision counts (Fig. 4). In spring, southerly winds, lower visibilities, less moon illumination, and higher local migration intensities were also associated with increases in fatalities (*SI Appendix*, Fig. S3 and Table S1). Cloud ceiling interacted with lighted window area: When fewer window bays were lighted, cloud ceiling was only weakly predictive of collisions; however, when many bays were lighted, lower cloud ceilings strongly increased collision counts. Fall demonstrated similar patterns to spring (*SI Appendix*, Fig. S4 and Table S2), but we detected no strong association with cloud ceiling, visibility, or moon illumination.

Our collision model successfully predicted observed data (*SI Appendix*, Fig. S7). Cross-validation revealed that most years showed consistently low prediction error calculated by using mean absolute error (MAE). Annual mean MAE was 2.66 ± 0.76 SD in spring and 2.98 ± 0.83 SD in fall, and models performed similarly well during years with below- and above-average lighting levels (*SI Appendix*, Fig. S8). Due to the COVID-19 pandemic, few entertainment or conference events occurred at McCormick Place in 2020, leading to low lighting during the entire year. Model performance for this atypical year was comparable to performance during other years, lending confidence that our model can accurately explain collision counts across a range of lighting conditions.

Drivers of Collisions at Individual Window Bays. Lighting of individual window bays was a key driver of mortality at those window bays. In spring, the predicted collision count at a window bay was 4.1× higher when that bay was illuminated at night. When taking individual window lighting into account, total lighted window area was less important (Fig. 5*A*; *SI Appendix*, Table S4). This pattern was similar in fall (Fig. 5*B*; *SI Appendix*, Table S5) and supported by multivariate matching analysis (*SI Appendix*, Fig. S6 and Table S3). Overall, these results suggest that fatal collisions are driven primarily by lighting at the level of the individual window bay, although surrounding lighting still elevates collision counts. The direction each window bay faced significantly influenced collision count (Fig. 5*C*). The sides of the building facing north and east showed the highest predicted collision count in both seasons, a pattern likely related to idiosyncratic features of our study site (*Discussion*). Wind direction influenced which sides of the building were most prone to collisions in different seasons (*SI Appendix*, Fig. S9).

https://doi.org/10.1073/pnas.2101666118

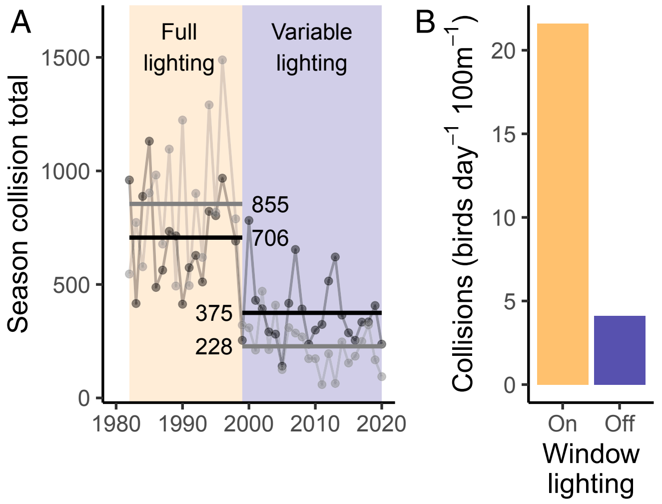

Fig. 3. Recorded collisions by year and window lighting. (*A*) Collisions recorded at McCormick Place between 1982 and 2020 for spring (light gray) and fall (dark gray) seasons. Horizontal lines with numeric labels show average seasonal collision totals before and after the window-lighting regime changed from fully lighted to partially lighted in 1999. The year 1997 is not shown because construction limited access to the site during that year. (*B*) Mean recorded daily collisions by window-lighting status from 2000 to 2020.

Predicted Efficacy of a Lights-Out Program. We predicted how collision counts might have differed under different lighting scenarios. In spring, we expect a 59% (95% CI [52, 65]) decrease in collisions if lighting had been reduced every night to the minimum levels historically recorded (∼50% lighted window area). In fall, the predicted decrease was 53% (95% CI [47, 59]). Likewise, if all building windows had been emitting light every night, we expect that total mortality would have been higher by 116% (95% CI [97, 136]) and 47% (95% CI [40, 54]) in spring and fall, respectively. It may not be feasible to extinguish lighting every single night, so we quantified the predicted decrease in mortality if lighted window area had been reduced only on the nights with the largest 25% of migration events. In this scenario, we expect a decrease of 32% (95% CI [26, 38]) in collisions in spring and 27% (95% CI [22, 31]) in fall.

Our model results illustrate that collision risk is dependent not only on migration intensity, but also atmospheric conditions, so we identified the 25% of nights with the highest predicted risk of collisions, taking into account both migration intensity and weather conditions (and assuming constant lighted window area). Then, we quantified the predicted decrease in mortality if lighting had been reduced on these high-risk nights. In this scenario, we expect that taking action on high-risk nights would have decreased total seasonal collisions by 44% (95% CI [38, 50]) in spring and 31% (95% CI [27, 36]) in fall.

These differing scenarios highlight that, although many nights with large migration events are high risk, other nights may also pose high collision risk due to weather conditions, despite lower migration intensities (*SI Appendix*, Fig. S10). In both spring and fall, only about half of high-risk nights were also nights in the top 25% of migration events (spring: 52%; fall: 60%).

Discussion

Bird mortality from collisions represents hundreds of millions of deaths annually in the United States alone (2). Attraction to artificial light at night contributes greatly to these collisions, and there is growing interest among community, municipal, and conservation stakeholders in mitigating the impacts of light on nocturnally migrating birds. Our data show that nightly bird mortality at an urban convention center is strongly related to migration traffic, lighted window area, and local weather conditions. Consistent with previous assessments (8, 16, 34, 40), the area of lighted windows in the building had a dramatic effect. After accounting for meteorological conditions and migration intensity, predicted collision counts were 11 and 6 times higher (in spring and fall, respectively) when all windows were lighted compared to when half were darkened. Collisions were most frequent when winds were from the west and south, concentrating birds along the Chicago lakefront.

Much attention in scientific and popular literature has focused on the contribution of high-rise buildings to avian mortality. This

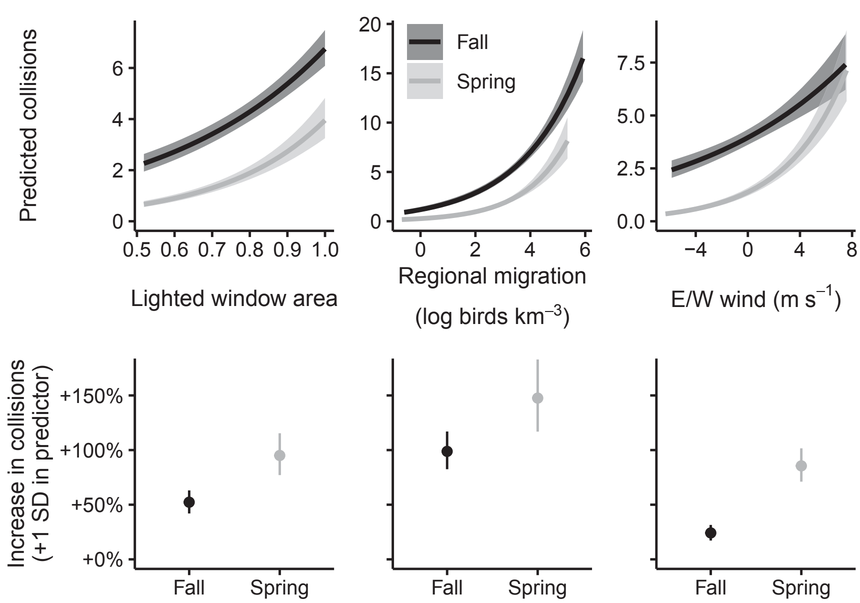

Fig. 4. Number of collisions by light, winds, and migration intensity. (*Upper*) Line plots show model predictions for three important variables. Positive values of the E/W wind component indicate winds blowing from west to east. For predictions, other predictors are held at their average value (continuous variables) or reference level (categorical variables). Continuous predictions are shown between the 0.01 and 0.99 quantiles of observed data. (*Lower*) Model-estimated coefficients by season with 95% CIs. See *SI Appendix*, Figs. S3 and S4 for plots of all predictors and *SI Appendix*, Tables S1 and S2 for all coefficient estimates.

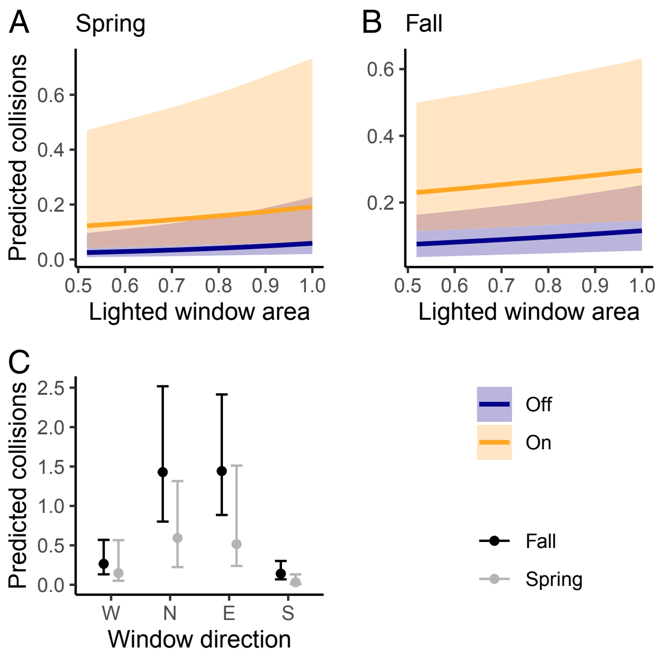

Fig. 5. Predicted number of collisions per window bay. The response variable was the number of collisions at a given window bay, accounting for its size. (*A* and *B*) Predicted collisions by total building lighted window area (*x* axis) and whether the focal window was emitting light (shading color). Continuous predictions are shown between the 0.01 and 0.99 quantiles of observed data. (*C*) Predicted collisions by window direction. See *SI Appendix*, Tables S4 and S5 for coefficient estimates.

study provides a key example of a low-rise building that poses substantial risk to migrating birds. In locations with high migration traffic, lighted window area may be a more important risk factor for collision than building height (13, 15, 26).

Darkening Individual Windows Reduces Mortality. In spring and fall, whether an individual window bay emitted light was the most important variable in predicting fatal bird collisions at that bay. Colliding birds appear to be attracted to specific light sources and are not simply disoriented by overall city or sky glow. This result strongly suggests that reducing the number of lighted windows, even in an otherwise brightly lit area, may make a difference in decreasing local bird mortality. This is consistent with research showing that birds immediately resume normal migratory behavior when bright lights are extinguished (7).

Our results are most applicable to structures with large areas of lighted windows, which raises an additional question: If individual windows are darkened, is this likely to decrease total mortality or simply cause birds to collide with other lighted windows? If the latter were true, we would expect that collisions at a given window bay would increase when surrounding lights are extinguished. However, we observed the opposite: After accounting for individual window-bay lighting, we see a positive, though subtle, relationship between total building lighted window area and predicted collision counts (Fig. 5). This suggests that each darkened window makes it less likely for birds to collide with nearby windows. Additional experiments focused on the effects of individual window lighting would be informative.

Efficacy of Turning Off Lights on High-Risk Nights. Our modeling results show that reducing internal lighting during the entire migration season would be an effective way to reduce collisions, resulting in an ∼60% reduction in collision counts from observed totals. In the years before formal light monitoring began in 2000, McCormick Place was constantly fully lighted. The building began regularly turning off lights starting in 1999, and bird mortality abruptly decreased (Fig. 3*A*). Although we cannot rule out a contribution of long-term population declines to this decrease in collisions (1), the sharp change shown in Fig. 3*A* suggests that the change in lighting was an important factor in the subsequent decrease in collision counts.

Seasonal Variation. We observed seasonal differences in the strength of the associations between collision counts and weather, moon illumination, lighting, and migration; most relationships were stronger in spring than in fall (Fig. 4). Seasonal differences in flight altitudes might explain some of this variation. The average altitude of nocturnal migration was 23% (96 m) higher in fall compared to the spring of the same calendar year (*SI Appendix*, Fig. S11). Birds migrating at higher altitudes may be less likely to interact with illuminated structures on the ground, resulting in weaker observed associations in fall. The underlying cause of this seasonal difference in flight altitude is unclear, but it has been documented elsewhere in North America (41) and may relate to seasonal atmospheric dynamics or behaviors over open water.

Directional Associations. The north and east faces of the building had the greatest number of predicted collisions after accounting for lighting in both seasons. This may reflect topography, habitat, and building configuration. A natural area lies to the northeast and Lake Michigan to the east. Lighting fixtures and possibly bulbs differ between north and south faces, and trees grow adjacent to the north and east sides, while the south and west have less vegetation. Collisions with the eastern face were closely associated with westerly winds in both seasons, suggesting that colliding birds may be flying into headwinds when trying to reach land from open water. When encountering headwinds, birds are expected to fly at lower altitudes (42), increasing collision risk. This may also explain increased collisions on the northern face in fall under unfavorable southerly winds.

Spatiotemporal Scales. Current bird-migration analysis and forecasting tools (31) across North America make predictions using vertical reflectivity profiles constructed from data aggregated over a 37.5-km radius from each Next Generation Radar network (NEXRAD) Doppler radar station. We found that adding finer-resolution local migration data meaningfully improved collision models. Studies could incorporate local migration data from spatially explicit weather radar analyses, individual small radars, or automated acoustic monitoring (43). However, the relatively small estimated effect sizes of local metrics, compared to regional, indicates that regional data likely contain sufficient information for most modeling purposes.

The middle third of the night—generally the peak period of nightly bird migration—was the most relevant time for predicting collision counts from migration and weather. However, our analysis does not reveal exactly when collisions occurred, and behaviors such as dawn reorientation over open water (37–39) may still be a contributing factor. Indeed, the predictive importance of radar measures over Lake Michigan hints that migrants flying over water may show a particularly strong attractive response to coastal light pollution, possibly in combination with a general tendency to seek nearby land. These hypotheses should be further investigated.

Conservation Implications and Recommendations. This study can help inform conservation efforts to protect bird populations through reducing collisions. Current guidelines for collision reduction highlight the contribution of light pollution to mortality and the need to reduce unnecessary lighting (44–46). Our

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findings affirm these recommendations and provide information that can be incorporated into policy initiatives.

In our study, lighted window area strongly predicts fatal collisions, highlighting the need for lights-out initiatives to reduce nocturnal lighting. Given the difficulty of fully reducing nighttime lighting across urban centers, the efficacy of lights-out programs and other conservation efforts to mitigate collisions could be improved by targeting nights of increased collision risk for mitigation action. As we show, both migration intensity and weather conditions meaningfully influence collision risk, often at a local scale. Therefore, we propose incorporating both weather and migration forecasts (31, 32) into lights-out advisories. Associations with weather conditions may be idiosyncratic, varying by city, building, and even window orientation; thus, effective advisories for particularly problematic structures may require on-the-ground efforts to determine the optimal mitigation strategy.

Ultimately, although selective reduction of lighting can make a meaningful difference in reducing bird mortality and help to raise public awareness of the issue, permanent reductions in lighted window area are likely to have a greater positive impact on bird populations. Where possible, permanent lighting adjustments, such as downshielding lighting, changing lighting color (47), and automating the usage of window blinds between certain hours, will reduce the load on individual actors and decrease the risks posed to nocturnally migrating birds by light pollution.

Methods

Collision Monitoring. The McCormick Place Lakeside Center is a large building that is part of a larger convention center located on Chicago's lakefront (Fig. 1). The building contains three stories above ground with large window bays that are illuminated from within and recessed beneath a roof. Since 1978, from early March to June and from mid-August through November, personnel from the Field Museum have surveyed the building daily at dawn for birds that have collided with the windows (Fig. 2). The surveyed perimeter length of the building is 1.5 km, and search effort has been standardized throughout the survey. Birds are collected from a smooth, cement-like walking surface. As a result, detection probability is consistent and not influenced by seasonal vegetation.

Over this 43-y period, over 40,000 birds have been collected in this manner (48). Prior to 1999, interior lights were on nearly continually. Starting in 1999, lighting became more variable, depending on activity in the building. Since 2000, the number of birds and lighting status of each window bay have been recorded during dawn collision monitoring. In this period, Field Museum personnel have conducted combined light and bird monitoring for a median of 77 d (range: 25 to 87) each spring between 28 February and 4 June and 93 d (range: 71 to 109) each fall between 12 August and 2 December, resulting in a total of 3,463 d of monitoring over 21 y. Of these, we removed 9 d due to ambiguous light or collision records.

The majority of collisions at this building are songbirds (34, 48), but some nonpasserine species collide in appreciable numbers as well (e.g., American Woodcock and Yellow-Bellied Sapsucker).

Light Scoring. Winger et al. (34) defined light output at McCormick Place based on whether each of 17 window bays that form the exterior of the building's ground level were illuminated from within. As the windows are of unequal size, we refined this definition by dividing some large bays to consider a total of 21 individual window bays, with nightly lighting status and number of collisions recorded at each (*SI Appendix*, Fig. S12). Because multiple window bays look out from the same interior space, they often change lighting simultaneously. The architecture of the building contains clear separations, such that there was generally no ambiguity in assigning collisions to window bays. Where these separations are lacking, birds close to the border between two bays were assigned to the nearest bay. The data for bays 16 and 17 were not always collected separately, so we combined these two bays in our analysis.

We considered a window bay or bay division lighted if the interior lighting was on and visible from the exterior. Our building light score was the proportion of lighted window bays, accounting for the size of each bay. At least seven window bays were always lighted (bays 14 to 21), representing circa 50% of the surveyed area. Thus, our light index takes values from approximately 0.5 (half of building window area lighted) to 1 (all windows lighted).

Migration Intensity. To quantify nightly bird-migration activity, we used reflectivity measures from the National Oceanographic and Atmospheric Administration's NEXRAD radar network. Specifically, we used nocturnal radar scans from the nearest radar station (KLOT; 41.605°N, −88.045°W) from 2000 to 2020 to characterize spring (March to May) and fall (August to November) movements. We extracted biological measures at two scales: regional and local. For regional migration activity, we calculated profiles of reflectivity from 0 to 1,000 m above ground level at 100-m intervals using well-established methods (49, 50). We used MistNet (51) to remove precipitation and clutter from radar imagery and retained only biological targets. Any pixels classified as precipitation were coded as 0 birds per km^3 because few birds typically migrate in these conditions (52). Following standard practice, we constructed profiles from the lowest five elevation scans (0.5° to 4.5°) and aggregated measures from 5 to 37.5 km from the radar location. We used these vertical profiles of reflectivity from the KLOT radar as a measure of regional bird-migration activity, focusing on altitudes below 1,000 m to specifically quantify densities of birds migrating closer to the ground and, therefore, most likely to interact with terrestrial structures.

Second, we obtained local measures of migration intensity by extracting KLOT radar returns within a given radius of the McCormick Place study site from the lowest elevation scan (0.5°). We extracted mean bird densities for circles with radii 4, 8, 16, and 32 km from the study site to investigate the scale at which radar data best explain collisions, averaging over all biological returns (i.e., not precipitation or clutter) extracted by MistNet (51). We separately quantified migration densities in airspace over land and over Lake Michigan to investigate whether bird numbers over land or over water better explain collisions. Because local and regional migration measures were highly correlated, for modeling, we also constructed relative metrics describing whether local measures were higher or lower than the regional measure: We divided the local measure by the regional measure and log-transformed this ratio.

For local and regional migration metrics, we converted standard radar units of reflectivity factor (dBZ) to reflectivity (dBη) following: η[dB] = Z[dBZ] + β, where $\beta = 10 log_{10}(10^3 \pi^5 |K_m|^2/\lambda^4)$ (53). We then converted η to an estimate of the number of individual birds by dividing by 11 cm^2, a representative average radar cross-section per bird (54), yielding birds per km^3. Ground clutter can result in strong radar returns, particularly in urban environments, and we removed this potential contamination with a combination of static and dynamic clutter masks. For each season, we applied yearly static clutter masks by summing a minimum of 100 low-elevation scans (0.5°), starting on 1 January (16:00 Coordinated Universal Time [UTC] to 18:00 UTC) and continuing to 15 January. We classified any pixel above the 85th percentile of the summed reflectivity as clutter and masked it from our analyses. We removed dynamic clutter in two ways: We excluded any pixel with radial velocity between −1 and 1 ms^{-1} and those with reflectivity >35 dBZ (51). For local migration measures, we applied an additional mask as an extra precaution against clutter: We took the mean of all spring and fall measures and removed any pixels with an average value greater than 10 dBZ, reflecting consistently high reflectivity, as well as those in the upper 5% of remaining reflectivity values in each radar scan. Because we were focused on measuring nocturnal bird migration, we retained data only between local sunset and sunrise. Night lengths in our dataset ranged from 9 to 14.9 h. We split the night into thirds (early/middle/late) and averaged data across each third to investigate which period of the night best explained collision counts.

Local Weather and Moon Illumination. Like the radar data, we split the night into thirds (early/middle/late) and averaged data across each third. Migrating birds respond strongly to wind conditions (52, 55), so we obtained local hourly wind speed and direction, cloud ceiling height, and visibility data from the Integrated Surface Database (56). The closest weather station operating continually during our study period was located at Chicago Midway Airport (ID: 14819), 13.4 km from the study site. Nightly moon illumination (range from zero to one) was calculated by using the R package suncalc (57).

Statistical Analyses.

Drivers of daily collision counts.

Model structure. We modeled daily fatal collision counts derived from early morning surveys using conditions and behavior during the preceding night of migration. We standardized all continuous variables to have a mean of zero and a variance of one so that coefficient estimates could be directly compared across parameters with different units. We constructed separate models for spring and autumn, with the following main effects:

- Regional migration intensity, mean $< 1{,}000$ m above ground (birds per km^3, log-transformed)
- Local migration intensity relative to regional (ratio of local:regional, log-transformed)
- Lighted window area, measured as a proportion of total window-bay area emitting light from within the building, ranging from $\sim$0.5 to 1 because at least 50% of bay area was always lighted
- Zonal (east/west) wind speed component ($m \cdot s^{-1}$; positive values indicate winds blowing from west to east)
- Meridional (north/south) wind speed component ($m \cdot s^{-1}$; positive values indicate winds blowing from south to north)
- Cloud ceiling height (m)
- Visibility (categorical: $>$15 km, 7.5 to 15 km, $<$7.5 km)
- Moon illumination fraction (daily measure ranging from zero to one)
- Day of year (ordinal, including quadratic term)
- Year (continuous)

In addition, we tested six pairwise interactions chosen a priori because of direct relevance to our hypotheses about bird behavior and how it may be modified by atmospheric conditions. Given historical and anecdotal evidence that large mortality events at lighted structures are often associated with cloud and fog (10, 18–20), we tested whether a low cloud ceiling or low-visibility conditions might amplify the association with light pollution or influence the relationship between migration intensity and collision counts. We also expected that lighted window area might affect the relationship between migration intensity and collisions; that cloud cover might affect the relationship between moon illumination and collisions (i.e., if the moon is hidden by clouds); and that moon illumination might impact the relationship between light pollution and collisions. Finally, we expected that wind conditions might affect the relationship between migration intensity and collisions—for example, if westerly winds cause migrants to concentrate along the Chicago lakefront. Thus, we added the following interactions:

- Cloud ceiling × lighted window area
- Visibility × lighted window area
- Cloud ceiling × regional migration intensity
- Visibility × regional migration intensity
- Lighted window area × regional migration intensity
- Cloud ceiling × moon illumination
- Lighted window area × moon illumination
- Zonal wind × regional migration intensity

Model fitting and spatiotemporal scale selection. We fit our collision model using a Bayesian framework, specifying the model with JAGS (Just Another Gibbs Sampler) implemented in the R package rjags (58). For all parameters, we specified Gaussian priors with a mean of 0 and SD of 100. We fitted our model structure as a generalized linear model with a negative binomial distribution, as opposed to a Poisson distribution, because the collision count data were substantially overdispersed. Negative binomial models estimate a parameter to account for overdispersion. We used BLISS (36) to choose the spatial and temporal scales of our predictors that best explained collision data. Using BLISS, we determined whether weather and migration data from early, middle, or late nocturnal periods best explained collision counts. We also compared several spatial scales for local migration data. Our intention here was to determine if local, spatially explicit migration information above Chicago was important in addition to regional migration measures and, if so, the optimal local area size. To this end, we compared local migration data from 4-, 8-, 16-, and 32-km circles centered on Chicago, further subdivided into airspace above land or above water (i.e., above Lake Michigan).

For both spring and fall, we ran the JAGS model for 110,000 iterations, including 10,000 burn-in iterations. For each multiscale covariate, we calculated the posterior probabilities of each spatial or temporal scale considered using indicator variables to represent the selection of a particular scale. We then retained the scale with the highest posterior probability. We used the subset of Markov chain Monte Carlo iterations with these selected scales for model inference.

Cross-validation of model performance. We assessed model performance across years (n = 21 folds) by retraining the model on data excluding those from a focal year and then testing performance on the withheld year. To assess performance, we calculated the MAE of predictions on the response (count) scale.

Drivers of Daily Mortality at Individual Window Bays. After selecting the best spatial and temporal scales for predictors and identifying drivers of collisions across the study site, we conducted an additional analysis in which the response variable was the daily collision count at individual window bays, as opposed to summed across the whole building. Our goals were twofold: 1) to understand how lighting of individual window bays interacts with building-wide lighted window area; and 2) to understand how weather conditions mediate the spatial pattern of collisions and the particular window bays that pose the greatest risk.

We fit this second model in the same Bayesian framework as above, with the following modifications: 1) We did not perform scale selection; instead, we used the scales selected by the daily mortality models in the previous step. 2) The response variable was the number of collisions recorded at the individual window-bay level on a given night. (3) We added an offset term for the length of each window bay (in meters of perimeter) to account for window bays of different sizes. Thus, our predictions can be interpreted as the number of expected collisions per 100 m. 4) We added a random intercept term of window-bay identity and a fixed effect of the direction the window faced (north/south/east/west). 5) We added a binary fixed effect describing lighting at the individual window bay (on/off), with off (no light) as the reference level. 6) We added an interaction between individual window-bay lighting and the proportion of lighted window area for the entire building. 7) We added two interactions between window-bay direction (north/south/east/west) and wind conditions (with zonal and meridional winds, respectively).

Causal Inference. Although we did not perform a formal causal analysis, we present two lines of evidence that our measured association between window-bay lighting and collision counts likely reflects a causal relationship. First, we constructed a directed acyclic graph with DAGitty (59) to determine whether any variables could potentially confound the estimated effect of lighting on collision counts (60) (*SI Appendix*, Fig. S5). Second, we performed multivariate matching with the R package Matching (61) to compare collision data for nights with and without window lighting that were otherwise highly similar in all other covariates (e.g., weather, migration intensity, date, etc.). This procedure created two matched groups of data that were as similar as possible, except for the light treatment, allowing us to infer a causal effect of this treatment (*SI Appendix*, Fig. S6).

Data Availability. All data and code used in this analysis are publicly accessible on Mendeley Data (http://dx.doi.org/10.17632/mjvt3yxdkv.1) (62).

ACKNOWLEDGMENTS. We thank Ben Marks and Glenn Gabanski for contributions to data collection and Conor Taff, Judy Shamoun-Baranes, and three anonymous reviewers for helpful input. We thank Stephen Parry of the Cornell University Statistical Consulting Unit for assistance with statistical analysis. This material is based on work supported by NSF Grants 1522054, 1661259, 1633206, and MSB-NES-2017554, in addition to the 2017–2018 Belmont Forum and BiodivERsA joint call for research proposals, under the BiodivScen ERA-Net COFUND program, NSF Integrative and Collaborative Education and Research Grant 1927743. The Amon G. Carter Foundation, a Cornell Presidential Postdoctoral Fellowship, Leon Levy Foundation, Lyda Hill Philanthropies, the Marshall Aid Commemoration Commission, and the University of Michigan also supported this work.

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Supplementary Material

Drivers of fatal bird collisions in an urban center
Published in *PNAS*

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Table S1: **Predictors from negative binomial model of daily fatal collisions in spring.** Shown are exponentiated coefficients and 95 percent credible intervals. We standardized all continuous variables to a mean of zero and a variance of one so that coefficient estimates can be compared.

Term	exp(Estimate)	CI
(Intercept)	1.416	[1.240,1.616]
Cloud ceiling height	0.739	[0.671,0.810]
Cloud ceiling height × Lighted window area	0.863	[0.788,0.943]
Cloud ceiling height × Regional migration intensity (log-transformed)	1.185	[1.075,1.311]
Date	0.681	[0.617,0.753]
Date^2	0.788	[0.720,0.862]
Lighted window area	1.951	[1.771,2.154]
Lighted window area × Regional migration intensity (log-transformed)	1.058	[0.972,1.151]
Local relative migration intensity (log-transformed)	1.095	[1.003,1.194]
Regional migration intensity (log-transformed)	2.476	[2.169,2.829]
Moon illumination	0.890	[0.823,0.962]
Moon illumination × Cloud ceiling height	1.056	[0.974,1.144]
Moon illumination × Lighted window area	1.018	[0.940,1.101]
Zonal (east/west) wind	1.856	[1.711,2.016]
Zonal (east/west) wind × Regional migration intensity (log-transformed)	1.078	[0.990,1.173]
Meridional (north/south) wind	1.415	[1.300,1.538]
Year	1.019	[0.943,1.100]
Lighted window area × Visibility = 7.5-15 km	0.677	[0.541,0.849]
Lighted window area × Visibility = <7.5 km	0.590	[0.432,0.810]
Regional migration intensity (log-transformed) × Visibility = 7.5-15 km	0.916	[0.736,1.142]
Regional migration intensity (log-transformed) × Visibility = <7.5 km	1.052	[0.767,1.449]
Visibility = 7.5-15 km	1.384	[1.110,1.732]
Visibility = <7.5 km	1.613	[1.134,2.303]

Table S2: **Predictors from negative binomial model of daily fatal collisions in fall.** Shown are exponentiated coefficients and 95 percent credible intervals. We standardized all continuous variables to a mean of zero and a variance of one so that coefficient estimates can be compared.

Term	exp(Estimate)	CI
(Intercept)	4.183	[3.827,4.588]
Cloud ceiling height	1.020	[0.957,1.086]
Cloud ceiling height × Lighted window area	0.991	[0.932,1.055]
Cloud ceiling height × Regional migration intensity (log-transformed)	0.986	[0.926,1.050]
Date	1.837	[1.704,1.980]
Date^2	0.493	[0.457,0.532]
Lighted window area	1.523	[1.420,1.631]
Lighted window area × Regional migration intensity (log-transformed)	1.040	[0.979,1.105]
Local relative migration intensity (log-transformed)	1.109	[1.039,1.184]
Regional migration intensity (log-transformed)	1.988	[1.825,2.170]
Moon illumination	0.971	[0.922,1.025]
Moon illumination × Cloud ceiling height	0.999	[0.948,1.053]
Moon illumination × Lighted window area	0.989	[0.935,1.046]
Zonal (east/west) wind	1.242	[1.172,1.315]
Zonal (east/west) wind × Regional migration intensity (log-transformed)	0.995	[0.941,1.053]
Meridional (north/south) wind	1.184	[1.108,1.264]
Year	1.061	[1.005,1.120]
Lighted window area × Visibility = 7.5-15 km	1.034	[0.874,1.224]
Lighted window area × Visibility = <7.5 km	0.746	[0.551,1.016]
Regional migration intensity (log-transformed) × Visibility = 7.5-15 km	0.830	[0.715,0.965]
Regional migration intensity (log-transformed) × Visibility = <7.5 km	0.995	[0.728,1.382]
Visibility = 7.5-15 km	1.134	[0.966,1.332]
Visibility = <7.5 km	1.312	[0.929,1.903]

Table S3: **Effect of individual window lighting on collision count, measured with multivariate matching.** Estimates measure the effect of lighting for individual window bays using a dataset where confounding predictors have been balanced across treatment (lighting) groups. Bays for which balancing failed are omitted. Control data (lights off) were matched to treatment data (lights on) with replacement. The exponentiated estimate can be interpreted as the predicted proportional increase in collision counts if the window bay emits light. P-values have been adjusted for multiple tests with the Benjamini & Yekutieli method. The average predicted increase in collision count for lighted window bays was 5x in spring and 3.6x in fall.

Season	Bay	Bay length (m)	N On	N Off	Estimate	SE	P-value	exp(Estimate)
Spring	B7	32.9	1028	377	1.25	0.14	<0.001	3.48
Spring	B9	14.6	626	779	2.63	0.29	<0.001	13.89
Spring	B10	36.6	527	878	1.37	0.35	<0.001	3.92
Spring	B11	43.3	505	900	1.18	0.31	0.001	3.26
Spring	B12	32.3	481	924	1.95	0.50	<0.001	7.00
Spring	B13	15.8	579	826	2.44	0.46	<0.001	11.43
Fall	B2	25.6	949	839	1.26	0.13	<0.001	3.51
Fall	B3	40.2	954	834	1.72	0.11	<0.001	5.60
Fall	B4	36.0	984	804	1.08	0.12	<0.001	2.93
Fall	B5	14.6	1034	754	1.23	0.19	<0.001	3.43
Fall	B6	7.3	1035	753	1.09	0.19	<0.001	2.96
Fall	B8	7.3	1038	750	1.38	0.20	<0.001	3.98
Fall	B9	14.6	1058	730	0.84	0.14	<0.001	2.31
Fall	B10	36.6	978	810	1.84	0.30	<0.001	6.29
Fall	B11	43.3	964	824	1.02	0.18	<0.001	2.77
Fall	B12	32.3	937	851	0.96	0.23	<0.001	2.62

Table S4: **Predictors from negative binomial model of *window-specific* daily fatal collisions in spring.** Shown are exponentiated coefficients and 95 percent credible intervals. We standardized all continuous variables to a mean of zero and a variance of one so that coefficient estimates can be compared.

Term	exp(Estimate)	CI
(Intercept)	0.036	[0.012,0.137]
Cloud ceiling height	0.767	[0.683,0.855]
Cloud ceiling height × Lighted window area	0.909	[0.808,1.028]
Cloud ceiling height × Regional migration intensity (log-transformed)	1.188	[1.117,1.265]
Date	0.691	[0.648,0.736]
Date^2	0.812	[0.766,0.860]
Lighted window area	1.367	[1.165,1.590]
Lighted window area × Regional migration intensity (log-transformed)	1.025	[0.905,1.162]
Window lighting = On	4.122	[3.483,4.893]
Total lighted window area × Window lighting = On	0.865	[0.734,1.028]
Local relative migration intensity (log-transformed)	1.094	[1.034,1.155]
Regional migration intensity (log-transformed)	2.332	[2.060,2.648]
Moon illumination	0.913	[0.868,0.960]
Moon illumination × Cloud ceiling height	1.089	[1.036,1.144]
Moon illumination × Lighted window area	0.970	[0.926,1.019]
Zonal (east/west) wind	1.797	[1.597,2.029]
Zonal (east/west) wind × Regional migration intensity (log-transformed)	1.079	[1.023,1.139]
Meridional (north/south) wind	0.825	[0.738,0.927]
Year	1.003	[0.957,1.052]
Zonal (east/west) wind × Direction window facing = N	0.857	[0.740,0.987]
Zonal (east/west) wind × Direction window facing = E	1.100	[0.958,1.258]
Zonal (east/west) wind × Direction window facing = S	0.947	[0.756,1.179]
Lighted window area × Visibility = 7.5-15 km	0.767	[0.675,0.878]
Lighted window area × Visibility = <7.5 km	0.731	[0.603,0.894]
Regional migration intensity (log-transformed) × Visibility = 7.5-15 km	1.048	[0.914,1.205]
Regional migration intensity (log-transformed) × Visibility = <7.5 km	1.017	[0.848,1.224]
Meridional (north/south) wind × Direction window facing = N	1.955	[1.696,2.241]
Meridional (north/south) wind × Direction window facing = E	1.845	[1.616,2.096]
Meridional (north/south) wind × Direction window facing = S	0.826	[0.662,1.024]
Visibility = 7.5-15 km	1.270	[1.106,1.461]
Visibility = <7.5 km	1.370	[1.084,1.716]
Direction window facing = N	3.860	[0.757,12.545]
Direction window facing = E	3.461	[0.770,14.077]
Direction window facing = S	0.208	[0.031,1.097]

Table S5: **Predictors from negative binomial model of *window-specific* daily fatal collisions in fall.** Shown are exponentiated coefficients and 95 percent credible intervals. We standardized all continuous variables to a mean of zero and a variance of one so that coefficient estimates can be compared.

Term	exp(Estimate)	CI
(Intercept)	0.096	[0.047,0.206]
Cloud ceiling height	1.028	[0.943,1.124]
Cloud ceiling height × Lighted window area	0.992	[0.903,1.087]
Cloud ceiling height × Regional migration intensity (log-transformed)	0.974	[0.936,1.013]
Date	1.826	[1.731,1.926]
Date^2	0.478	[0.451,0.505]
Lighted window area	1.186	[1.059,1.323]
Lighted window area × Regional migration intensity (log-transformed)	0.982	[0.895,1.075]
Window lighting = On	2.746	[2.426,3.165]
Total lighted window area × Window lighting = On	0.930	[0.824,1.050]
Local relative migration intensity (log-transformed)	1.068	[1.025,1.110]
Regional migration intensity (log-transformed)	1.987	[1.812,2.187]
Moon illumination	0.989	[0.954,1.024]
Moon illumination × Cloud ceiling height	0.986	[0.954,1.021]
Moon illumination × Lighted window area	0.973	[0.937,1.010]
Zonal (east/west) wind	0.948	[0.864,1.037]
Zonal (east/west) wind × Regional migration intensity (log-transformed)	0.988	[0.953,1.024]
Meridional (north/south) wind	1.111	[1.004,1.228]
Year	1.039	[1.004,1.075]
Zonal (east/west) wind × Direction window facing = N	1.038	[0.934,1.154]
Zonal (east/west) wind × Direction window facing = E	1.531	[1.385,1.696]
Zonal (east/west) wind × Direction window facing = S	1.150	[1.001,1.324]
Lighted window area × Visibility = 7.5-15 km	1.022	[0.918,1.139]
Lighted window area × Visibility = <7.5 km	0.721	[0.591,0.879]
Regional migration intensity (log-transformed) × Visibility = 7.5-15 km	0.811	[0.734,0.894]
Regional migration intensity (log-transformed) × Visibility = <7.5 km	0.989	[0.807,1.224]
Meridional (north/south) wind × Direction window facing = N	1.369	[1.221,1.538]
Meridional (north/south) wind × Direction window facing = E	1.022	[0.915,1.140]
Meridional (north/south) wind × Direction window facing = S	0.962	[0.828,1.119]
Visibility = 7.5-15 km	1.126	[1.013,1.255]
Visibility = <7.5 km	1.337	[1.073,1.667]
Direction window facing = N	5.336	[2.237,11.960]
Direction window facing = E	5.458	[1.903,14.018]
Direction window facing = S	0.523	[0.187,1.448]

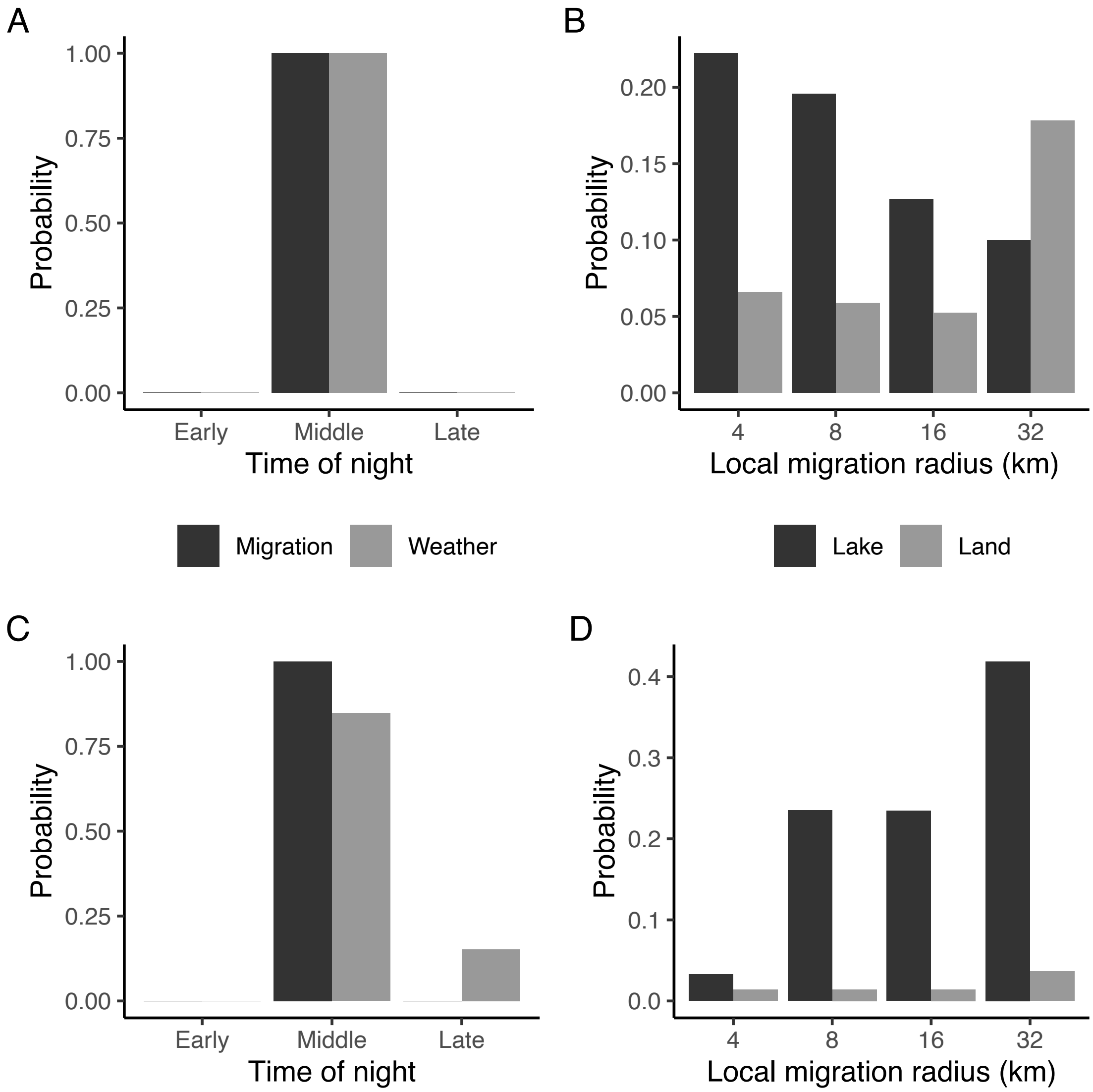

Figure S1: **Posterior distributions of spatial and temporal scales of predictors of fatal avian collisions as estimated by BLISS**. **(A-B)** Spring **(C-D)** fall. Probabilities reflect the proportion of MCMC iterations where the candidate scale was selected; the scale with the highest posterior probability represents the scale that best explains the observed data. For each season, we selected the scales of migration and weather variables independently, so the posterior probabilities of migration and weather temporal scales each sum to 1 (A, C). When conducting spatial scale selection on migratory bird numbers over land and lake (B, D), scales were considered jointly, so the probabilities of all spatial scales sum to 1 (i.e., we wanted to select a single land vs. water predictor combination that best explained collisions, rather than choose both a best land scale and water scale).

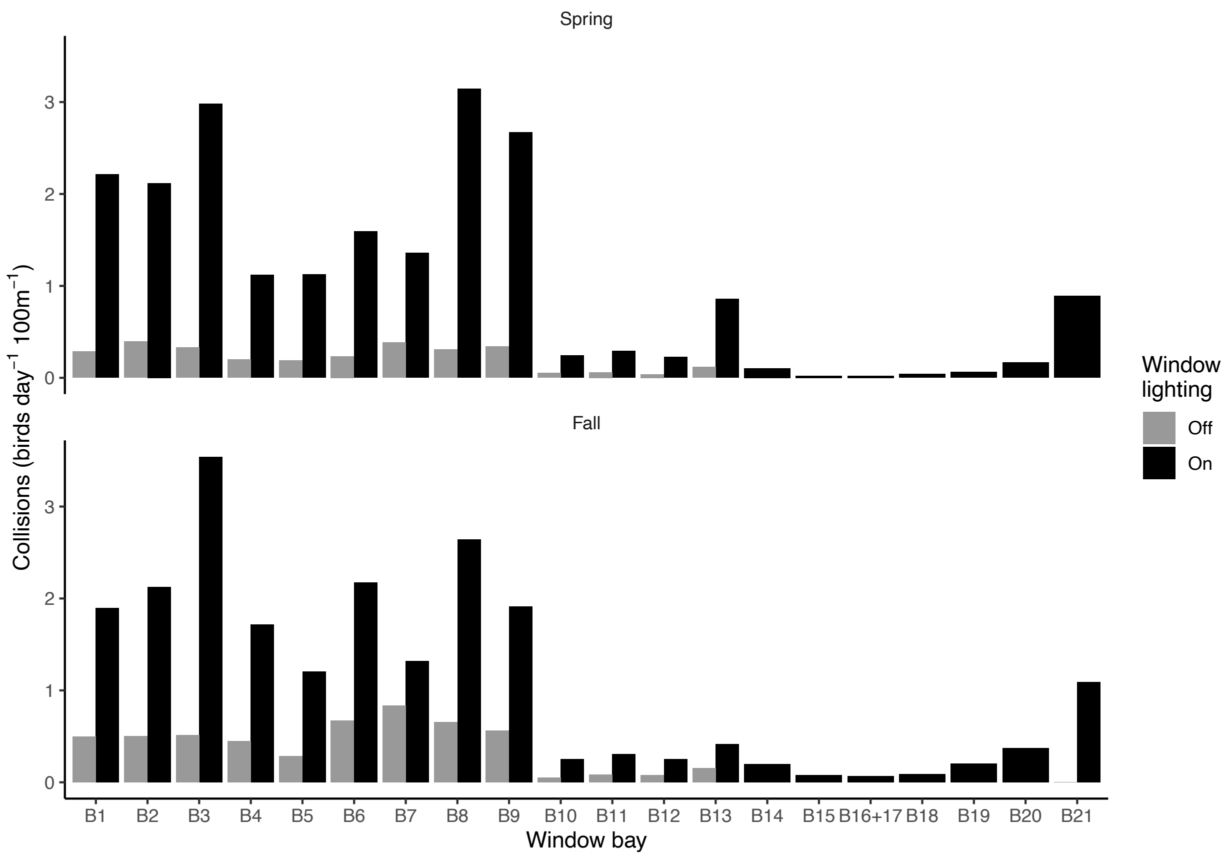

Figure S2: **Recorded collisions by window bay and lighting status.** Bar plots show mean collisions across all window bays. Some window bays were always lit; these bays only show one wide black bar.

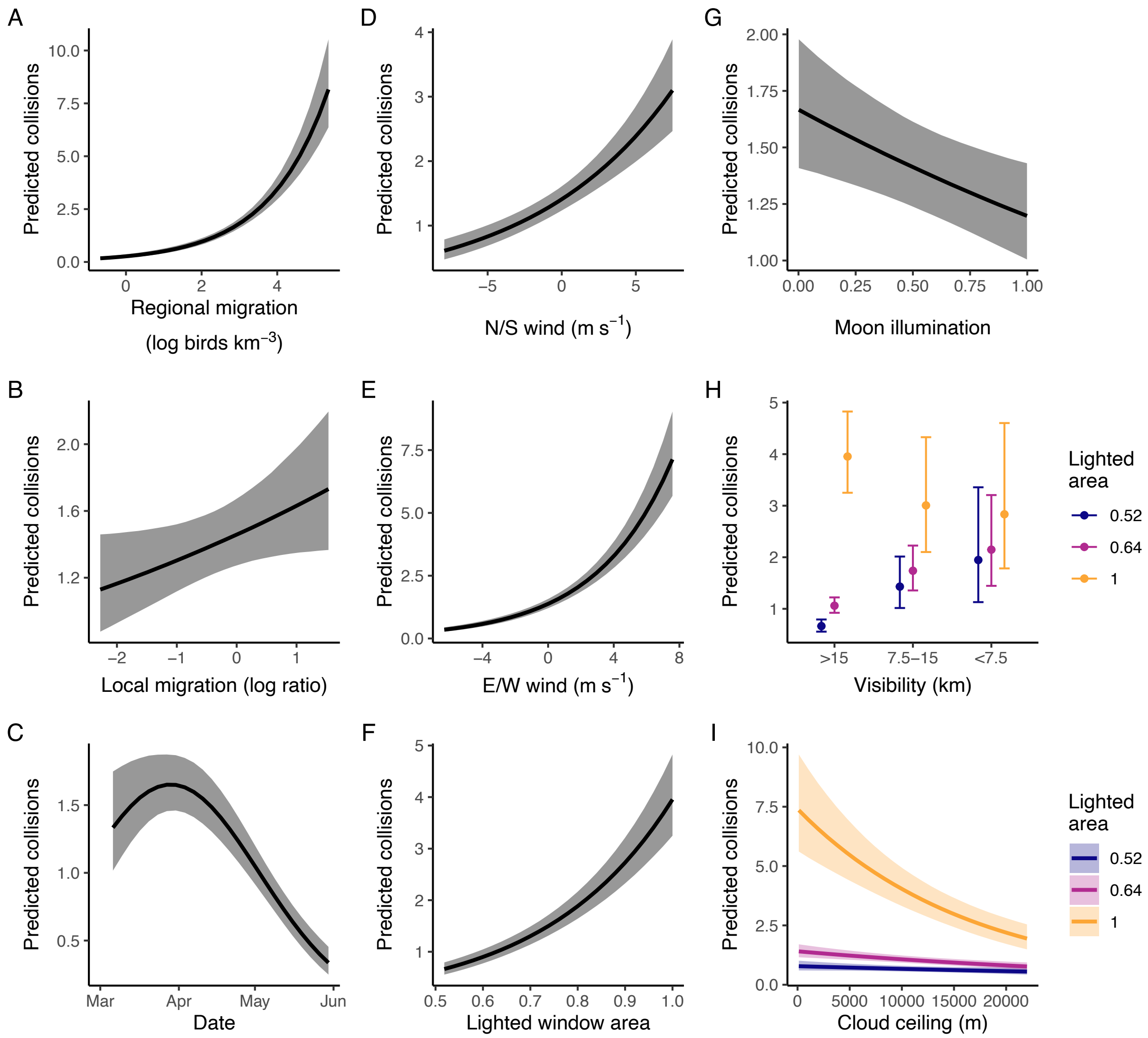

Figure S3: **Predicted number of collisions in spring by migration intensity, lighted window area, and atmospheric conditions.** **(A-G)** Model predictions for single variables, and **(H-I)** important interactions. In all cases, other predictors are held at their average or reference value. Continuous predictions are shown between the 0.01-0.99 quantiles of observed data. For interactions, predictions are plotted at the 0.05, 0.50, and 0.95 quantiles of the interacting variable. See Table S1 for coefficient estimates.

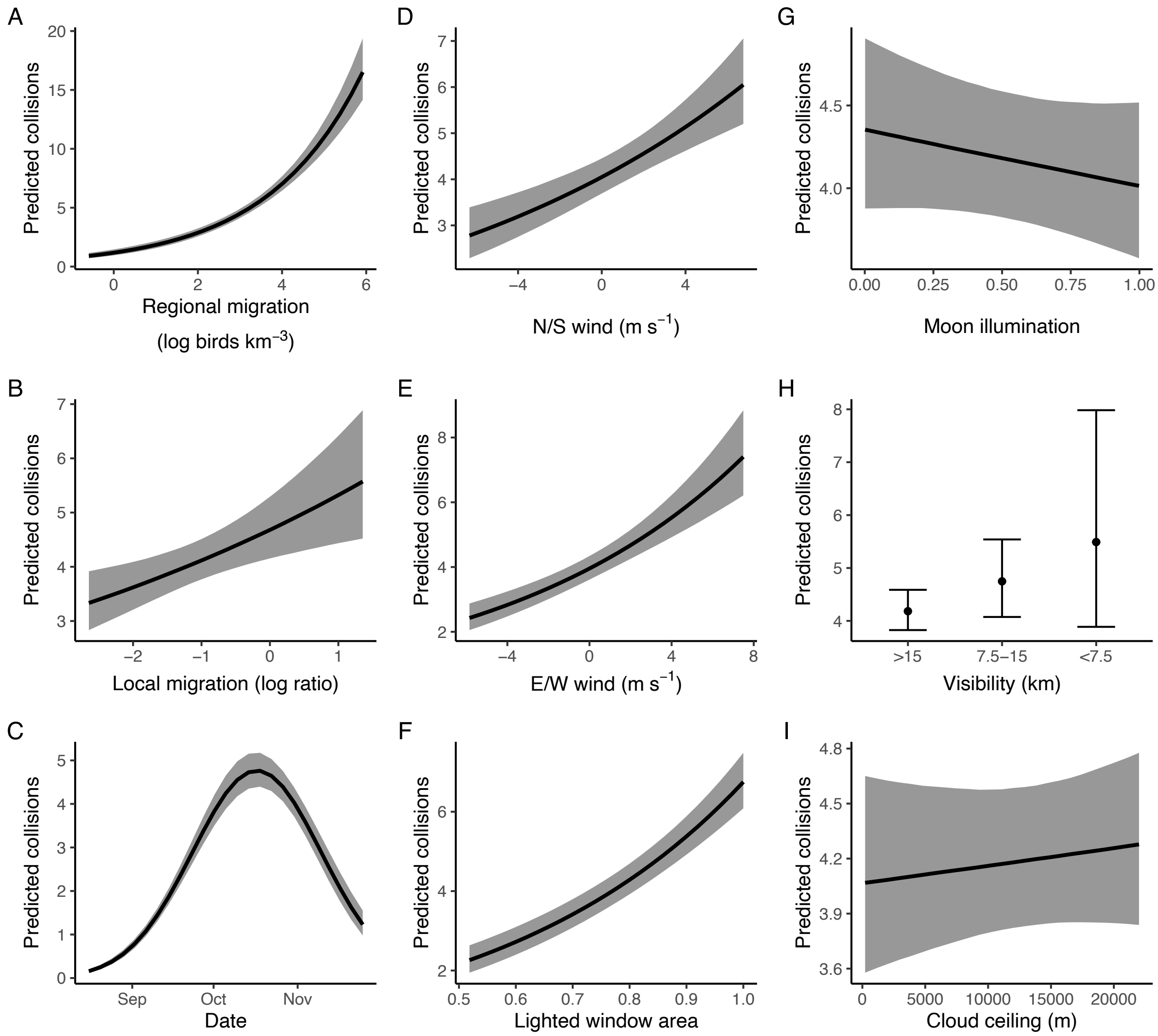

Figure S4: **Predicted number of collisions in autumn by migration intensity, lighted window area, and atmospheric conditions. (A-I)** Model predictions for single variables. In all cases, other predictors are held at their average or reference value. Continuous predictions are shown between the 0.01-0.99 quantiles of observed data. See Table S2 for coefficient estimates.

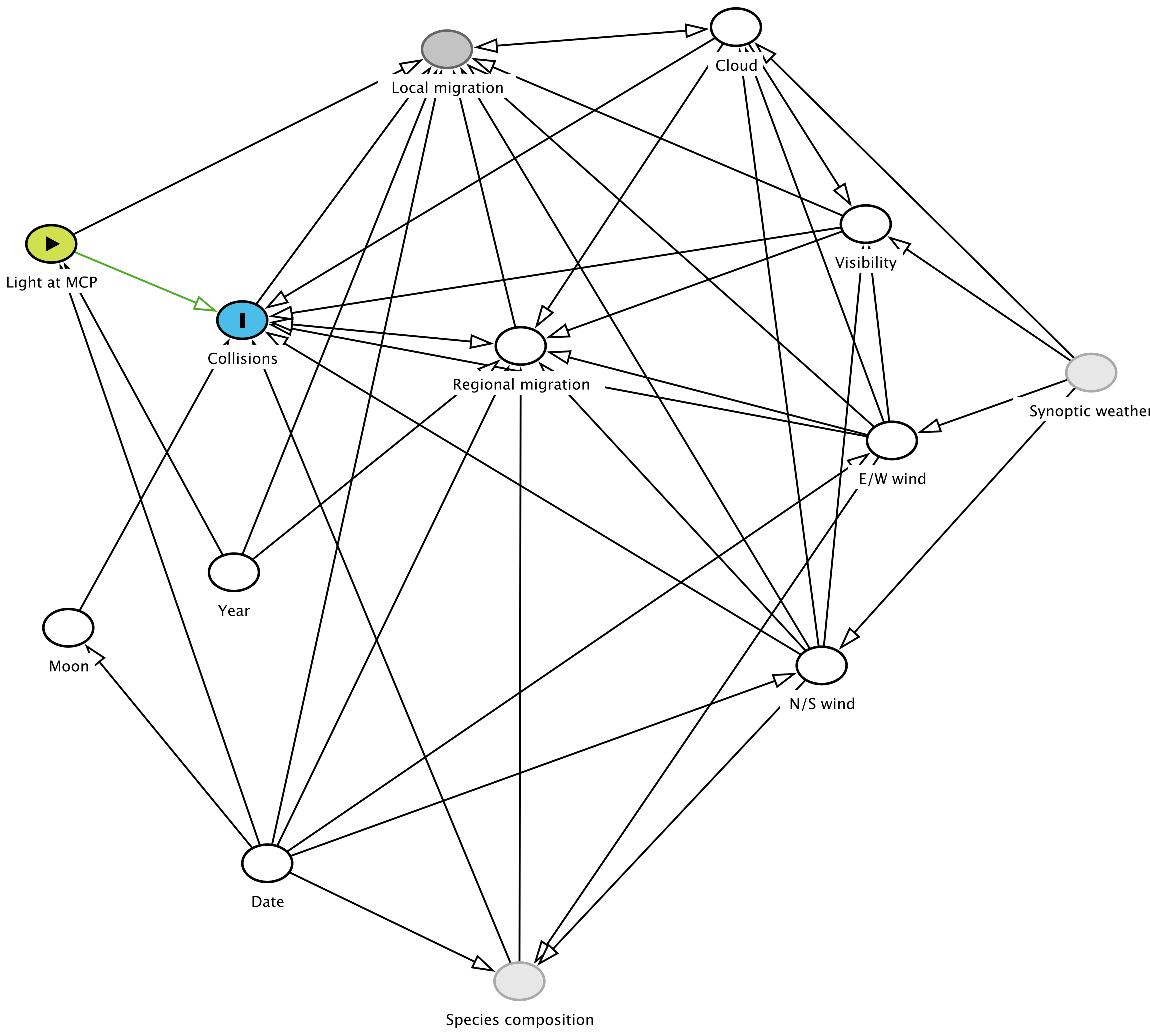

Figure S5: **Predictor and response variables drawn as a directed acyclic graph (DAG) in `DAGitty`, with arrows indicating likely or plausible causal relationships.** The DAG contains nodes corresponding to variables in our model. The green oval indicates the variable of interest, and the blue oval indicates the response variable. White ovals are variables adjusted for in the model, and grayed ovals with gray borders indicate latent variables that are not measured. Analysis of the DAG with `DAGitty` indicated that once date and year were accounted for, no relationships among variables were likely to confound the effect of lighting. Because we considered it plausible that the lights at McCormick Place could have local effects on migration densities detected by radar, the analysis found that it would be necessary to exclude the local migration variable from the model to avoid potential confounding effects. Thus, the graph depicts "local migration" excluded from the model. (The airspace summarized by the regional migration variable did not include Chicago, so we did not consider a causal link to be possible for the regional migration measure.) After constructing our full-building model, we produced another version without the local migration variable because the coefficient of the effect of light on collisions can then potentially be interpreted as a causal effect, given the DAG is accurate.

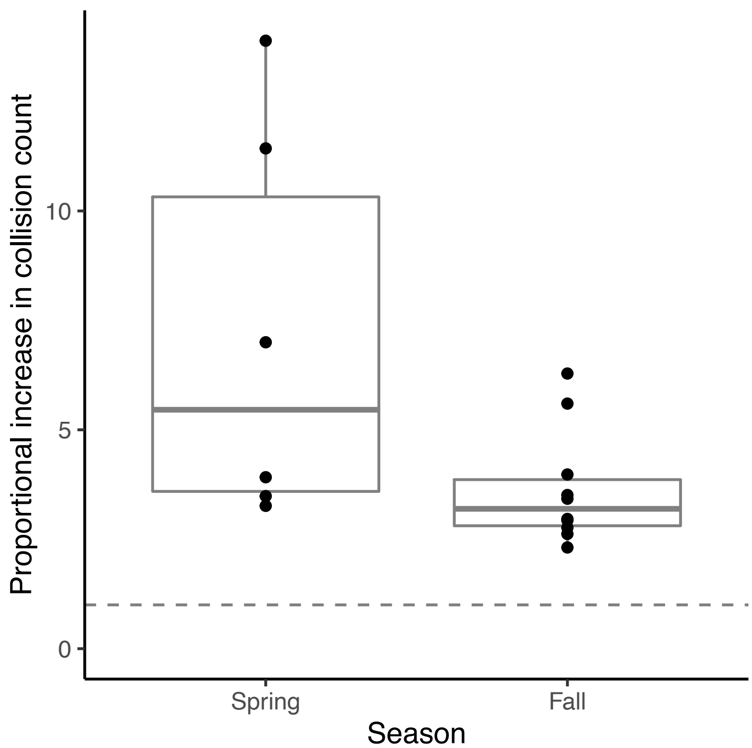

Figure S6: **Effect of individual window lighting on collision count, measured with multivariate matching.** In the matching analysis, we separately analyzed the data from each window bay. We used a genetic search algorithm implemented in `Matching` to balance the following covariates across matched groups: visibility, cloud cover, zonal and meridional winds, date of season, regional migration intensity, and interactions of migration intensity with zonal wind, cloud cover, and visibility. We also attempted to balance total building lighted window area, but this was difficult to achieve because of the correlation between individual bay lighting and full building lighted window area. Therefore, this analysis may not fully isolate the effect of individual window lighting from total building lighting. We considered matched groups to be successfully balanced if no covariates (excluding lighting) significantly differed between matched groups. To estimate the causal effect of window lighting between groups, we fitted negative binomial models for each window bay and season, with collision count as the response and bay lighting (on/off) as the sole predictor. We adjusted p-values for multiple testing using the Benjamini & Yekutieli method, the most appropriate correction for tests that are not independent. We summarized the results by taking the average effect of window bay lighting across bays, weighting the average by the size of each bay. In the future, points show the estimated proportional effect of lighting for individual window bays for which the matching procedure succeeded. Bays for which balancing failed are omitted. The dashed horizontal line marks a proportional effect of 1. The average predicted increase in collision count for lighted window bays was 5x in spring and 3.6x in fall. Full model results are given in Table S3.

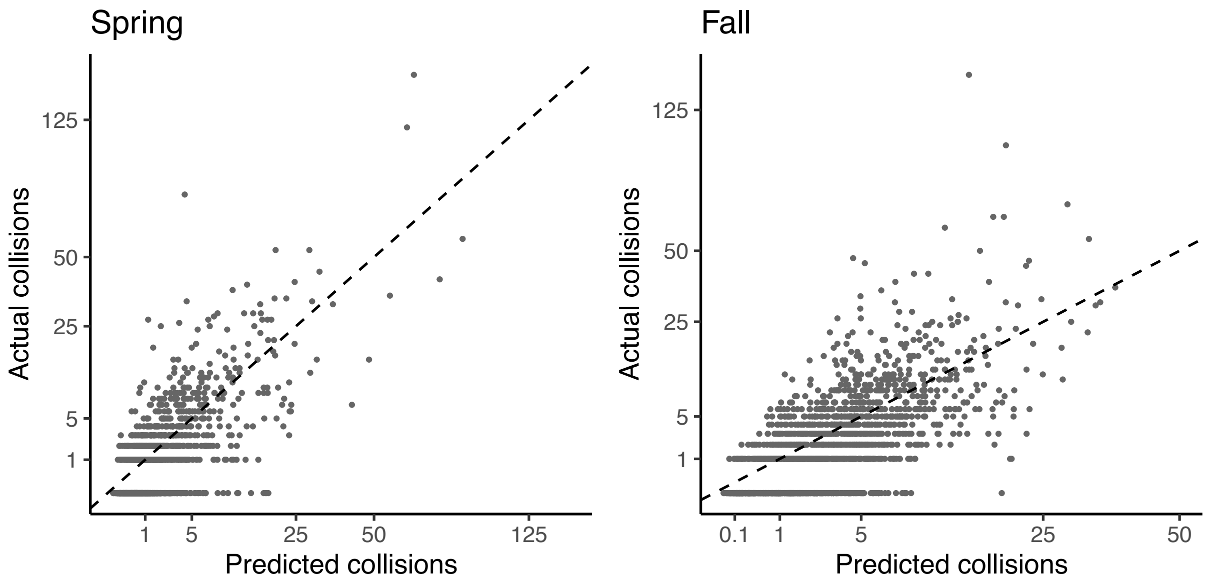

Figure S7: **Predictive performance of collision models.** Full dataset model predictions against observed values for total building model. The dashed line is the identity line.

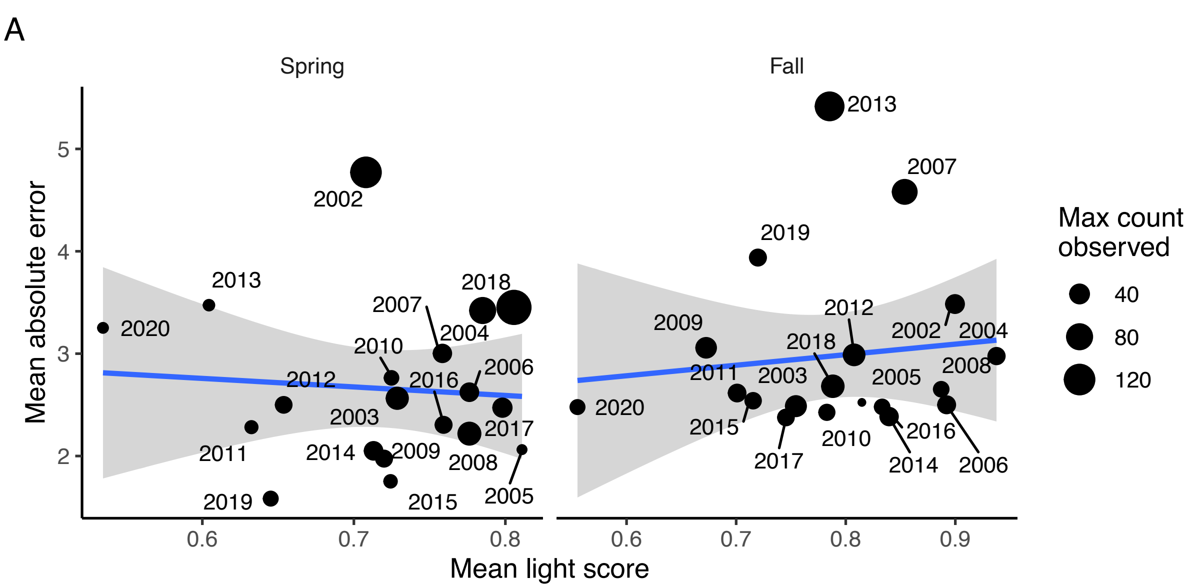

Figure S8: **Prediction performance on cross-validation folds.** Dots show mean absolute error by year in predicting daily collision counts. We tested data for each year using a model trained without those data. Years with few data points (<0.10 quantile) are not shown. Plots show variation in performance by mean light score. Illumination levels did not meaningfully affect model performance.

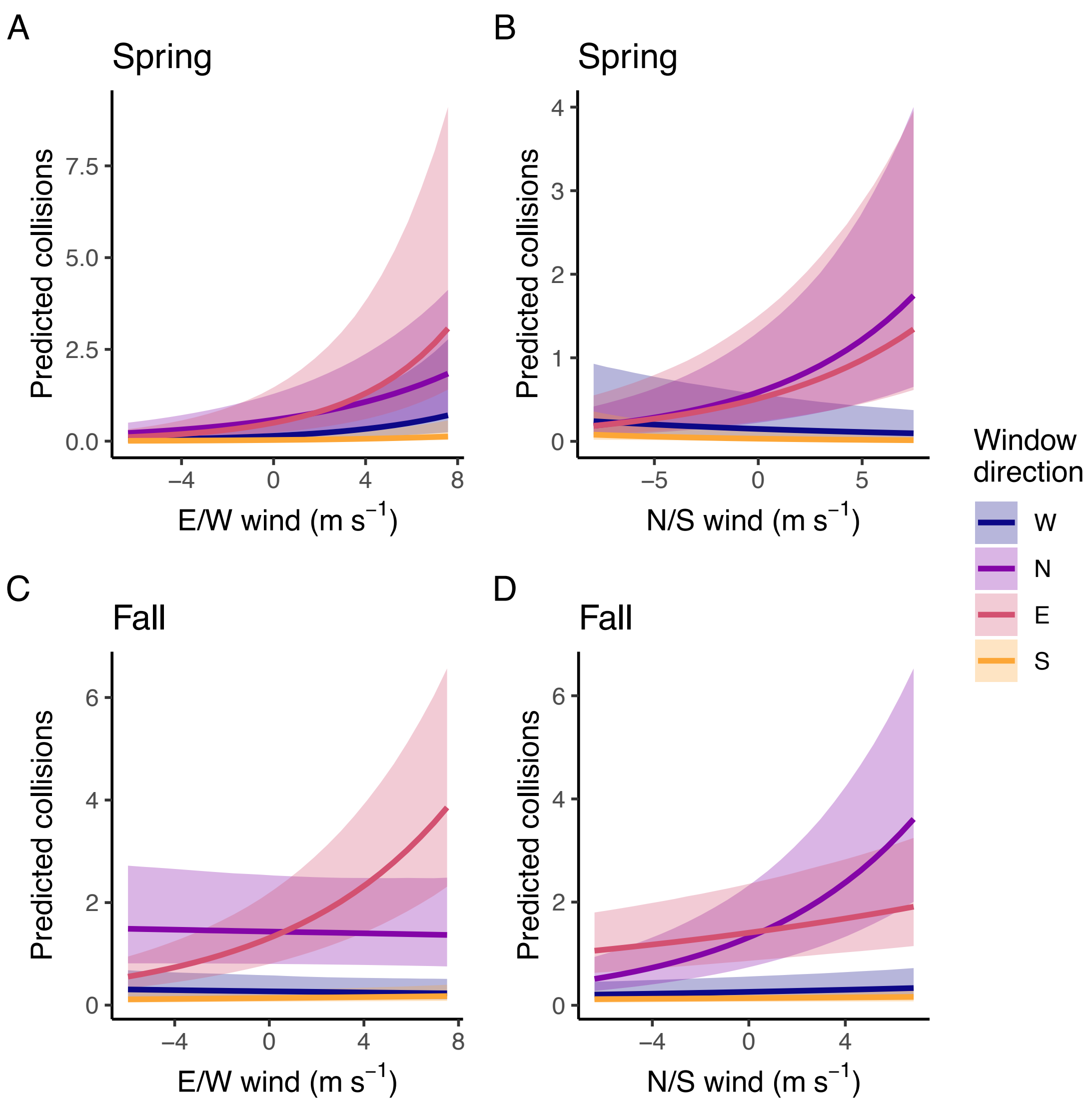

Figure S9: **Predicted number of collisions by window direction under different wind conditions.** Continuous predictions are shown between the 0.01-0.99 quantiles of observed data. For interactions, predictions are plotted at the 0.05, 0.50, and 0.95 quantiles of the interacting variable. See Table S5 for coefficient estimates.

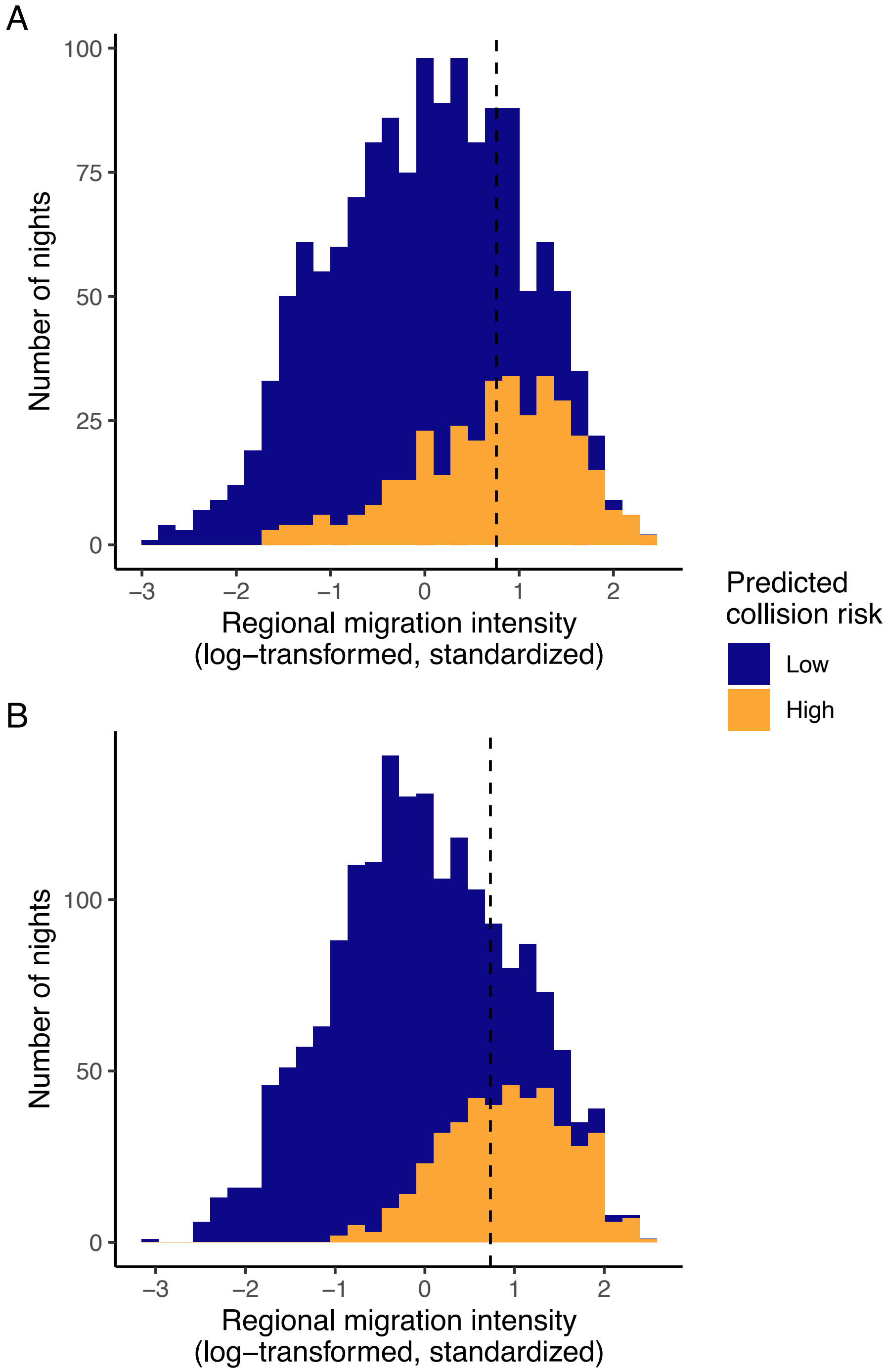

Figure S10: **Distribution of predicted low and high collision count nights by observed regional migration intensity.** High collision risk nights were defined as those with the top 25% of predicted collision counts under an average lighting scenario. **(A)** Spring, **(B)** fall. Dashed lines show the 0.75 quantile of migration intensity. A large proportion of nights with high migration intensities had high predicted collision counts, but many nights with lower migration intensity also had higher risk.

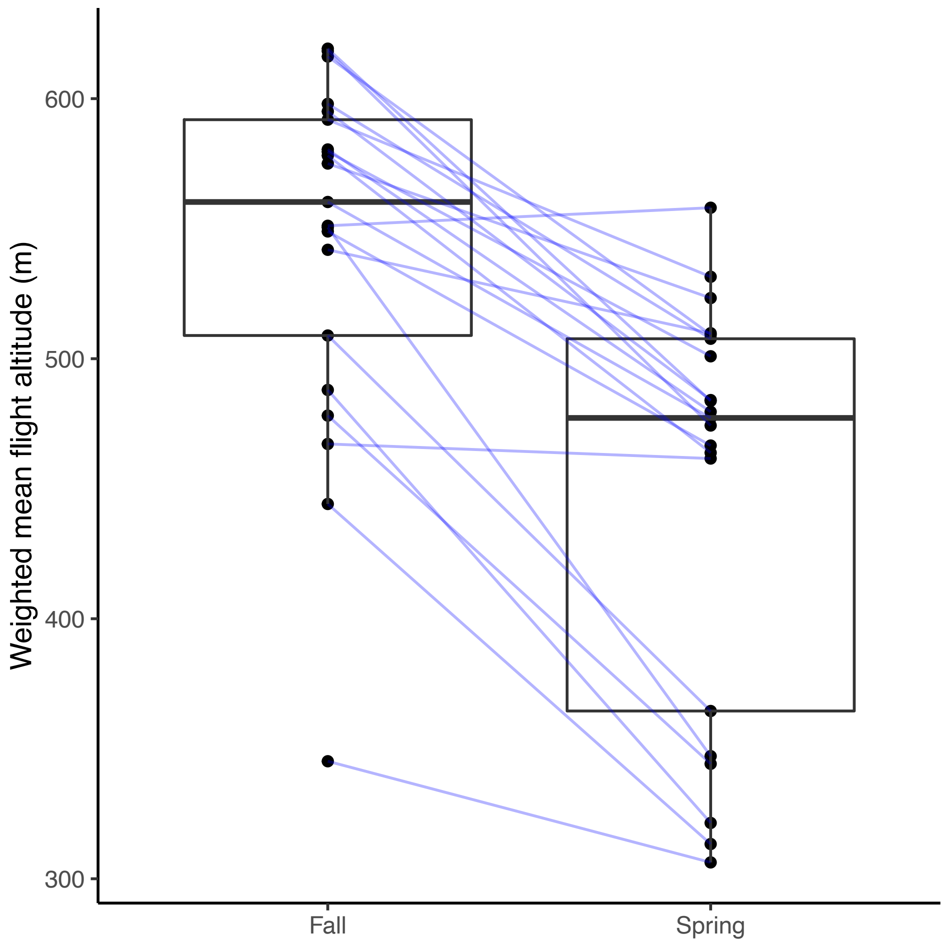

Figure S11: **Seasonal variation in average flight altitude of nocturnal migration at KLOT radar.** Each point represents the weighted mean flight altitude during spring or fall for one year. Averages were calculated from 0-3000 m and weighted by reflectivity (η). Blue lines connect measures from the same calendar year.

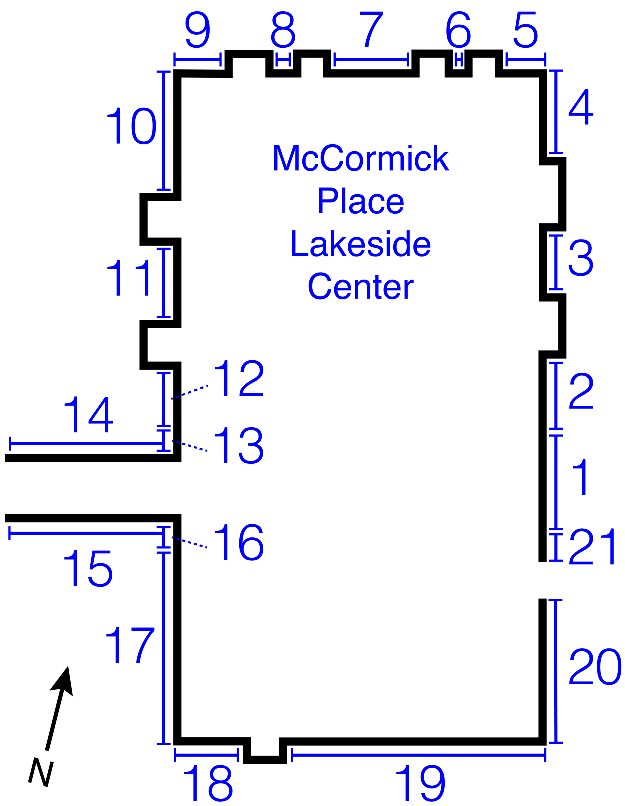

Figure S12: **Locations of surveyed window bays along the perimeter of McCormick Place Lakeside Center.** Each window bay on the northern half of the building (bays 2–12) contains multiple windows. These windows occupy the top two-thirds of the wall and look out from a large central room containing a series of lights arrayed in rows. An exception is bay 7, which contains an additional light that illuminates only that bay. All or some of these lights may be on at a given time and some windows may have curtains drawn. Window bays on the southern half of the building look out from either a large room or more narrow corridors. These windows span the height of the building. The large central room has ceiling lights similar to those in the north section, while the rest are lit by a row of lights running along narrow halls. Finally, the raised walkway connecting the Lakeside Center to the rest of the complex (bays 14 and 15) is solid glass on both north and south sides and interior colored lights run the length of the walkway.