# INVESTIGATING THE EFFECTS OF WEATHER, ARTIFICIAL LIGHTING, AND POLARIZED LIGHT ON BIRD-BUILDING COLLISIONS IN THE DOWNTOWN AREA OF A MAJOR U.S. CITY


By

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Bachelor of Science in Environmental Science

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2012


Submitted to the Faculty of the
Graduate College of the
Oklahoma State University
in partial fulfillment of
the requirements for
the Degree of
MASTER OF SCIENCE
May, 2019

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ACKNOWLEDGEMENTS

This work would not have been possible without the help of many collaborators, mentors, and peers. Thank you to: Dr. Scott Loss for his invaluable guidance and support as an advisor; Dr. Tim O'Connell and Dr. Bruce Robertson for their insightful input and advice as committee members; Abigail Anderson, Dr. Rob Blair, Joanna Eckles, and Reed Turner for their instrumental role in the design and implementation of this research; Cooper Crose, Malin Kunerth, Grace Milanowski, and April Strzelczyk for collecting the collision data and handling the challenges of urban field work; and the Minnesota Sports Facilities Authority and Minnesota Vikings Football, LLC for providing the funding that made this research possible. Finally, I would also like to thank members of the Loss and O'Connell labs for their helpful feedback and my friends and family for their support.

Name: SIRENA LAO

Date of Degree: MAY, 2019

Title of Study: INVESTIGATING THE EFFECTS OF WEATHER, ARTIFICIAL LIGHTING, AND POLARIZED LIGHT ON BIRD-BUILDING COLLISIONS IN THE DOWNTOWN AREA OF A MAJOR U.S. CITY

Major Field: NATURAL RESOURCE ECOLOGY & MANAGEMENT

Abstract: Collisions with buildings are a major source of human-caused mortality of birds, killing up to 1 billion birds annually in the United States. Most bird-building collision studies have focused on building and landscape-related factors that contribute to collisions, such as glass area and the amount of surrounding vegetation. Some studies have also considered characteristics of birds, such as migratory behavior and feeding habits, that cause some groups to be more vulnerable to collisions. Nocturnally migrating birds are especially susceptible to collisions, and the combination of poor weather conditions and artificial light at night (ALAN) is frequently cited as causing large collision events. However, little research has formally analyzed these factors. As part of a study evaluating collisions at 21 buildings in downtown Minneapolis, Minnesota, USA, we assessed the effects of nightly weather conditions on collisions across all study buildings. We also evaluated the relationship between collisions and two types of light pollution—ALAN and polarized light pollution (PLP), which has never been analyzed as a collision factor—at 48 façades of 13 buildings.

For weather, we found that favorable migration conditions (e.g., tailwinds) early in the night and poor weather conditions (e.g., low clouds) later in the night correlated with collisions. We also found that time lag effects (conditions from one and two additional nights before surveys) were especially important in the spring, while collisions were primarily associated with weather conditions from the night before surveys in the fall. These results provide support for using weather and bird migration forecasts to predict collisions, allowing advance action to be taken to reduce collisions.

For light pollution, we found that the area of windows emitting ALAN and the proportion of lighted glass were important factors influencing collisions, even after accounting for glass area. This result provides strong support for turning off lights at night to reduce bird-building collisions. We found no relationship between PLP and collisions, but additional research is needed to better understand bird responses to PLP. Nonetheless, reducing both types of light pollution by turning off lights and reducing reflective surfaces should contribute to significantly reducing bird-building collisions.

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## CHAPTER I

# THE EFFECT OF WEATHER ON BIRD-BUILDING COLLISIONS IN THE DOWNTOWN AREA OF A MAJOR U.S. CITY

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## Abstract

Up to 1 billion birds die annually from collisions with buildings in the United States. Most building collision victims are nocturnally migrating birds moving between breeding and non-breeding grounds in spring and fall. Although weather plays an important role in bird migration, little research has investigated how weather influences bird collisions with human-built structures, including buildings. To study the relationship between weather and bird-building collisions, we used daily collision monitoring data at 21 buildings in downtown Minneapolis, Minnesota, during spring and fall of 2017 and 2018. Using hourly weather data for each night preceding morning collision surveys, we characterized weather variables for different periods of the night (sunset, first and second halves of night, sunrise, and entire night). We also included time lag effects to determine if weather conditions one and two additional nights before surveys influenced collisions. We found that collisions correlated with both favorable migration conditions (e.g., tailwinds), especially early in the night, and with poor weather conditions (e.g., headwinds, low clouds, and precipitation), especially later in the night, when collisions likely occur for in-transit birds that "fall out" of migration. We also found seasonal variation in weather effects: warm temperatures, the absence of headwinds, precipitation, and low atmospheric pressure were associated with higher spring collisions; north winds, high visibility, cloudy conditions, low clouds, and high atmospheric pressure were associated with higher fall collisions. Collisions were not only associated with weather conditions the night before surveys, but also conditions one and two additional nights before surveys. Our results provide unprecedented information about the role of weather in bird-structure collisions and suggest that weather and bird migration forecasts are likely effective for predicting and reducing building collisions.

**Introduction**

Humans have radically changed the environment through land conversion and development. As the human population grows, landscapes become increasingly urbanized, and while some wildlife, including birds, are able to thrive in urban areas, many species face numerous human-caused threats associated with living in cities. Migratory birds are especially vulnerable to multiple sources of direct anthropogenic mortality associated with urban development, such as predation by cats and collisions with human-made structures (Calvert et al. 2013, Loss et al. 2015). Bird collisions with buildings are the second-greatest source of direct anthropogenic mortality of birds in the United States, killing an estimated 365 to 988 million birds per year (Loss et al. 2014). These fatalities include species of conservation concern, such as Golden-winged Warbler (*Vermivora chrysoptera*), Canada Warbler (*Cardellina canadensis*), and Wood Thrush (*Hylocichla mustelina*; Partners in Flight 2016). The effect of window collisions on populations of these and other species is unclear, though likely important in some cases (Arnold and Zink 2011, Schaub et al. 2011, Klem et al. 2012, Longcore et al. 2013, Machtans et al. 2013, Loss et al. 2014).

Several studies have identified factors affecting bird-building collision rates. Birds collide with windows because they are unable to perceive transparent glass as a barrier and/or they see continuous habitat reflected in or on the other side of the glass (Klem 1989). Consistent with these mechanisms, the amount of glass area on buildings and proximity of vegetation to windows correlate positively with collisions (Klem et al. 2009, Borden et al. 2010, Hager et al. 2013, 2017, Cusa et al. 2015). Higher numbers of collisions also generally occur during spring and fall migration periods than in summer and winter, when most bird species are relatively sedentary (Gelb and Delacretaz 2006, Hager et al. 2008, O'Connell 2001, Borden et al. 2010, Schneider et al. 2018). Additionally, many birds migrate at night and may become attracted to and disoriented by lights emitted from buildings, causing them to become grounded in urban areas and be more susceptible to collisions (Evans Ogden 1996, 2002, Zink and Eckles 2010, La Sorte et al. 2017, Van Doren et al. 2017). Hence, migrating birds are especially vulnerable to building collisions, particularly in urban areas where the above conditions are prevalent.

Bird collisions are also likely influenced by weather because factors such as temperature, wind speed, and wind direction strongly influence bird migration (Nisbet and Drury 1968, Åkesson and Hedenström 2000, Tøttrup et al. 2010, Wainwright et al. 2016). Research indicates that weather variables can be used to predict intensity of bird migration from regional to continental scales, suggesting that such weather-based models can be used to predict and reduce bird collisions with structures (Van Doren & Horton 2018). However, few studies have formally assessed the relationship between weather and bird collisons with buildings, or with any other human-built structures. Descriptive accounts suggest that severe weather conditions can lead to large bird mortality events from collisions with buildings and other structures (Erickson et al. 2005, Kerlinger et al. 2010, Ramirez et al. 2015), and a recent analysis showed that collisions of American Woodcock (*Scolopax minor*) during spring migration increase with strong headwinds and low cloud base heights (Loss et al. *in prep*). Additional preliminary support for poor weather leading to more collisions is provided by a study that found cloud cover and rainfall to be positively correlated with numbers of nighttime bird fatalities in downtown Toronto, Canada (Evans Ogden 2002). However, at two residences in Illinois, USA, most collisions were anecdotally observed to occur during calm (i.e., low-wind) conditions with no precipitation (Klem 1989), suggesting that fair weather may lead to more collisions in some cases. Despite these observations, additional data and rigorous analyses are needed to better understand the effect of weather on bird-building collisions and improve prediction and mitigation of collisions.

As part of a study of bird collisions at 21 buildings in downtown Minneapolis, Minnesota, USA, we sought to: a) determine which nighttime weather conditions correlate with collisions of nocturnal migrants during the spring and fall migration seasons; b) determine if conditions at certain times of night are particularly important in influencing collisions; and c) explore time lag effects of weather on collisions by comparing effects of conditions from the night preceding surveys to conditions 1 and 2 additional nights prior to surveys, because weather in the days leading up to a migration event can affect migration intensity (Van Belle et al. 2007, Van Doren and Horton 2018). We hypothesized that conditions favorable for migration, such as clear skies and tailwinds (south and north winds in spring and fall, respectively) would increase collisions because more birds are migrating and therefore more birds are likely to collide with buildings. A complementary hypothesis is that severe weather conditions that cause poor visibility (e.g., fog and precipitation) also cause more collisions because migrating birds may fly at lower altitudes and/or become grounded in urban areas, both of which may increase collisions either independent of or interacting with effects of nighttime lighting from buildings.

## Methods

### *Study Site*

We conducted this study in downtown Minneapolis, Minnesota, USA (Fig. 1.1). This highly urbanized city center is bounded to the north and east by the Mississippi River and is characterized by both tall skyscrapers and low-rise buildings (e.g., offices, apartments, shopping centers). Minneapolis is located in the Mississippi Flyway, an important regional pathway for birds during the spring and fall migration seasons. As part of the Mississippi River Twin Cities Important Bird Area, green spaces in the city are used by migratory birds as stopover habitat, making these birds especially vulnerable to collisions (Homayoun and Blair 2015). Because of this threat, Audubon Minnesota initiated Project BirdSafe, a program where volunteers collected collision data from numerous Minneapolis buildings from 2007 to 2016 (Zink and Eckles 2010, Nichols et al. 2018). This collision monitoring data formed the basis of the building selection for the current study.

**Figure 1.1** Image of study site in downtown Minneapolis, Minnesota, USA. Locations of specific monitored buildings are not shown due to terms of the funding agreement for this study.

*Building Selection*

As part of a companion study investigating the factors influencing variation in collisions among buildings, we selected 21 buildings in downtown Minneapolis using four criteria designed to capture spatial variation and a wide range in expected numbers of collisions. First, we referenced total collision counts from 2007 to 2015 for 64 buildings surveyed for Project BirdSafe. These previously monitored buildings were binned into five equal percentile ranges ("quintiles;" i.e., 0 to $20^{th}$ percentile of observed collisions; $20^{th}$ to $40^{th}$ percentile, etc.): the 1st quintile included buildings with zero observed collisions; the $2^{nd}$ quintile had buildings with 1–2 collisions; the $3^{rd}$ quintile had buildings with 3–6 collisions; the $4^{th}$ quintile had buildings with 7–16 collisions; and buildings in the $5^{th}$ quintile had ≥17 collisions (maximum 843). Second, we prioritized buildings based on perimeter access to allow surveyors to monitor as many façades of each building as possible. Third, we chose buildings based on their spatial distribution in the downtown area to minimize spatial clustering of buildings from the same quintile and to capture buildings with varying distances from the Mississippi River. Finally, from buildings meeting the preceding criteria, we randomly selected three buildings from each quintile (n=15) for monitoring to represent a range of previously observed collision rates. Because one of the selected buildings from the 5$^{th}$ quintile was partially inaccessible for the first month of surveys in spring 2017, we added one additional building from the same quintile to balance monitoring effort. Five additional buildings with no previous monitoring data were also included in the survey; four of these were selected randomly within the parameters of the building selection criteria described above, and one building, a large multi-use stadium, was included due to interests of the funding organizations. Buildings selected for monitoring ranged in height from 2 to 57 stories.

*Collision Monitoring*

During 2017 and 2018, we surveyed buildings every morning during spring migration from 15 March to 31 May and during fall migration from 15 August to 31 October. Following a standardized survey protocol adapted from Hager and Cosentino (2014), trained surveyors walked a fixed route and surveyed accessible portions of every building perimeter. To account for time-of-day effects, the route began at a different building each day, and to account for lighting effects, surveyors monitored each building in a clockwise direction on even dates and a counter-clockwise direction on odd dates. During spring 2017, the buildings were separated into two fixed routes, and the start building for each route shifted to the next building in the sequence each day. Because we found that individual surveyors were able to easily complete both routes within a desired timeframe of ~1.5–2.5 hours, we merged the routes starting in fall 2017 and selected the start building each day using a random number generator.

For all birds and bird parts found within approximately 5 meters of a building façade, surveyors entered the date, time, location, species, and photos in an ArcGIS Online form. Most dead birds were collected and placed in sealable plastic bags and stored in freezers. A subset of dead birds were left in place and tagged with a twist-tie around one leg to conduct scavenger removal trials as part of the companion study, which quantified how long carcasses persisted before a scavenger or human removed them from the survey area (Hager et al. 2012, Bracey et al. 2016, Kummer et al. 2016, Riding and Loss 2018). For birds that were found alive but stunned after colliding with a building, surveyors attempted to capture the bird when possible and place it in an unlined paper bag. Captured stunned birds were eventually released in a park outside of the downtown area or brought to a rehabilitation center if unable to fly away. Birds were collected under U.S. Fish & Wildlife Service Scientific Collecting Permit #MB05120C-1 and Minnesota Department of Natural Resources Salvage Permit #20412. Animal handling protocols were also approved by the Institutional Animal Care and Use Committee at Oklahoma State University (#AG-17-6).

Because this study focused on effects of weather on collisions of nocturnally migrating birds, we removed from collision counts species that are permanent residents and diurnal migrants (see Table S1 for list of excluded species). We also removed individuals we could not identify to species unless they were likely to be nocturnal migrants (e.g., warblers, sparrows). Because we used daily collision data, we also removed from counts carcasses that likely resulted from a collision from before the previous night (i.e., old carcasses that may have fallen from inaccessible areas, that surveyors failed to detect in previous surveys, or that surveyors missed due to construction or public events that prevented access). After removing old carcasses and birds that were not nocturnal migrants, we tallied unadjusted daily collision counts across all buildings; these daily counts, which served as the basis for the weather analysis, included stunned birds and dead birds, including partial carcasses. We included partial carcasses to account for birds that collided and were later scavenged, but some of these also likely included birds that did not collide but were instead depredated by birds of prey or other predators. Nonetheless, we retained all partial carcasses in counts because we could not determine cause of death, and furthermore, because in a highly urbanized city center like downtown Minneapolis, weather likely has similar effects on the abundance of migratory birds available for both predation and collisions. We did not adjust collision counts for scavenger removal or searcher efficiency (imperfect detection of carcasses that are present; Bracey et al. 2016, Riding and Loss 2018) because we did not have enough removal and detection data to produce reliable daily adjusted count estimates.

*Weather Data Collection*

We used hourly weather data collected at the Minneapolis-Saint Paul International Airport weather station (NOAA 2018), located ~10.5 km from downtown Minneapolis. For each date collision surveys were conducted, we compiled all weather data from approximately sunset on the previous night to approximately sunrise of the date of the survey. Of the available weather variables, we selected a subset that we hypothesized would influence collisions (Table 1). In addition to averaging the selected subset of variables across the entire night from sunset to sunrise, we averaged values within four different time periods to determine if variables during certain times of night play a particularly important role in influencing collisions. These time periods included within one hour before and after sunset, the first half of the night (starting 1 hour after sunset), the second half of the night (ending 1 hour before sunrise), and within one hour before and after sunrise. All these time periods shifted daily as a result of seasonal changes in sunset and sunrise times. We also converted a subset of weather variables to binary data to determine if collisions responded to the presence or absence of certain conditions within each period of the night. These binary variables included presence/absence of north wind (all northerly wind components, including N, NE, NW, NNE, and NNW), south wind (all southerly wind components, including S, SE, SW, SSE, SSW), precipitation (rain, snow, and drizzle), thunderstorms, and conditions that obscure visibility independent of precipitation (fog, mist, and haze; hereafter collectively referred to as fog). Because fog was highly correlated with visibility for all monitoring seasons, we removed fog from analysis, prioritizing visibility because it includes the effects of fog and is a continuous variable. For each date, we also considered potential time lag effects by including data for all weather variables at all periods of the night for one night before (t-1) and two nights before (t-2) the survey date; hereafter, we refer to these as 1- and 2-day time lag variables.

**Table 1.1.** Weather variables selected for analysis from NOAA dataset for the Minneapolis-St. Paul International Airport. Variables in the left column were averaged for each of four periods of the night (see text). Cloud base height was estimated by subtracting temperature from dew point and dividing the result by 4.4 (FAA, 2016). Cloud conditions range from 0-8, where 0 represents clear conditions and 8 represents overcast conditions. Variables in the right column were converted to binary to assess the effect of the presence/absence of these factors for each time of night.

| **Averaged Variables** | **Binary Variables** |
|---|---|
| Cloud base height (ft) | Precipitation |
| Cloud conditions | Thunderstorm |
| Precipitation (in) | N wind |
| Pressure (in) | S wind |
| Temperature (°F) | |

| |
|---|
| Visibility (mi) |
| Wind speed (mph) |

*Data Analysis*

All analyses were performed in R 3.5.2 (R Core Team, 2018). Because the total number of weather variables, including for each time of night and each time lag, resulted in over 130 possible predictor variables for each season, we applied methods to reduce the number of variables carried forward to the final analyses and to assist in identifying informative variables. First, we conducted correlation analyses among all possible variable pairs and removed one of each pair of highly correlated variables ($r \geq |0.7|$). We initially prioritized retaining variables from the immediately preceding night (t-0) over variables with time lags when they were highly correlated with each other. We also prioritized retaining variables from the first half of the night when they were correlated with variables from other time periods because many migratory songbirds initiate flight within the first 2 hours after sunset, which results in comparatively high migration volume during this period (Nisbet and Drury 1968, Bolshakov and Bulyuk 1999). Furthermore, large pulses of migratory movements in the Minneapolis area appear to begin during the first half of the night according to Cornell's BirdCast Live Migration Maps (The Cornell Lab of Ornithology 2018).

For variables remaining after the above correlation analyses, we used R package *Boruta*, which implements an algorithm that outputs important variables based on Random Forest variable importance (Kursa and Rudnicki 2018). *Boruta* determines which variables are important by assessing how each variable performs in predicting collisions compared to randomly shuffled subsets of the predictor variables. To validate the results, we obtained additional variable importance rankings from conditional (includes a parameter that accounts for correlations among variables) and unconditional Random Forest using the ‘cforest’ function in R package *party* (Strobl et al. 2008).

We used generalized linear models (GLM) to test different combinations of the weather variables identified by *Boruta* and Random Forest. Fall and spring data were analyzed separately because we expected weather to influence collisions differently in each season. We treated days as replicates and considered variables with data from 2017 and 2018 included in the same analysis to increase replication and assess patterns across years. Notably, we felt there was no need to account for variation among years by treating year as a random effect; most ecological studies do this to account for weather-related variation, and we explicitly accounted for weather with the fixed effects in our analyses. To assess the implications of the scale at which weather variables are averaged, we also conducted a separate series of analyses with weather variables averaged across the entire night. For both analyses, because the dependent variable was count data and not normally distributed, we first used Poisson regressions and checked for overdispersion using R package *AER* (Kleiber and Zeileis 2008). Because the data were overdispersed, we used negative binomial regressions for the final analyses.

When constructing models for both analyses, we first tested variables identified by *Boruta*, then added any additional variables identified by both conditional and unconditional Random Forest variable importance rankings to check if these variables improved the model. Based on the resultant set of variables, we constructed full additive models (i.e., containing all variables identified by the previous process, but without interaction terms) and full models with the addition of two-way interaction terms for weather variables included more than once as an important variable. For example, in the analysis with variables averaged for different parts of the night, we added an interaction between cloud base height during the first half of the night and cloud base height at sunrise because both factors were identified as important variables by *Boruta* or Random Forest. We then implemented backward and forward stepwise regressions in R package *MASS* (Venables and Ripley 2002) for both sets of models and assessed model fit using Akaike's Information Criterion (AIC; Burnham and Anderson 2002). When inclusion of two-way interactions prevented models from converging, we selectively removed interaction terms for variables dropped from the full additive model after performing stepwise regressions. We validated the result by testing all combinations of the important variables and obtaining relative variable importance (i.e., the sum of AIC weights of all models with $\Delta AIC < 7$) using R package *MuMIn* (Bartoń 2016). For the top model, we also substituted back any highly correlated variables that were previously removed in the preliminary correlation analysis and re-tested whether model fit improved. This final step was conducted because we had prioritized retaining variables without a time lag and from the first half of the night when conducting the preliminary correlation analysis, and we sought to avoid biasing conclusions about the relative importance of different lag periods and times of night.

## Results

During morning surveys in spring and fall of 2017 and 2018, we found 847 total bird-building collision victims that were nocturnal migrants, including fatal and non-fatal collisions (93 in spring 2017, 280 in fall 2017, 88 in spring 2018, 386 in fall 2018). Here, we focus on presenting results related to the analyses with weather variables averaged for different parts of the night. Results for analyses with weather variables averaged for the entire night are included in supplemental materials (Table S2, Fig. S1-S2). AIC tables showing rankings of all models tested for all analyses are also included in supplemental materials (Tables S3-S8).

The top model for spring with weather variables averaged for different parts of the night included five weather variables: precipitation volume, presence of precipitation, pressure, temperature, and presence of north winds (Table 1.2, Fig. 1.2). Precipitation volume from the second half of night with a 1-day time lag was positively associated with collisions. Presence of precipitation at sunset with a 1-day time lag had a negative association with collisions. Pressure was included twice in the model: during the second half of the night preceding surveys (i.e., no time lag) and at sunset with a 2-day time lag. Both pressure variables were negatively correlated with collisions. Temperature at sunset with a 2-day time lag was positively associated with collisions. Finally, the presence of north wind during the first half of the night with a 1-day time lag had a negative association with collisions.

**Table 1.2.** Weather variables included in the top models for spring and fall based on analyses including data from 2017 and 2018 and with weather variables averaged for different parts of the night. For time lags: t-0 = no time lag (i.e., weather conditions the night preceding collision surveys), t-1 = 1-day time lag, t-2 = 2-day time lag. Relative importance indicates the sum of AIC weights for all models with ΔAIC < 7 after testing all possible combinations of variables in R package *MuMIn*.

| Season | Weather Variable | Time of Night | Time Lag | Direction of Effect | Relative Importance |
|---|---|---|---|---|---|
| Spring | Precipitation volume | Second half of the night | t-1 | + | 1 |
| | Presence of precipitation | Sunset | t-1 | - | 1 |
| | Pressure | Second half of the night | t-0 | - | 0.81 |
| | | Sunset | t-2 | - | 0.95 |
| | Temperature | Sunset | t-2 | + | 0.87 |
| | Presence of N wind | First half of the night | t-1 | - | 0.97 |
| Fall | Cloud base height | First half of the night | t-0 | - | 0.91 |
| | | Sunrise | t-0 | - | 0.98 |
| | Interaction of cloud base height | First half of the night, Sunrise | t-0 | + | 0.9 |
| | Cloud conditions | Sunrise | t-2 | + | 0.92 |
| | Pressure | Second half of the night | t-0 | + | 0.82 |
| | Visibility | First half of the night | t-0 | + | 1 |
| | Presence of N wind | Second half of the night | t-0 | + | 1 |
| | Presence of S wind | Sunset | t-0 | - | 0.87 |
| | | | t-1 | - | 0.92 |
| | Interaction of N and S wind | Second half of the night, Sunset (respectively) | t-0 | + | 0.68 |

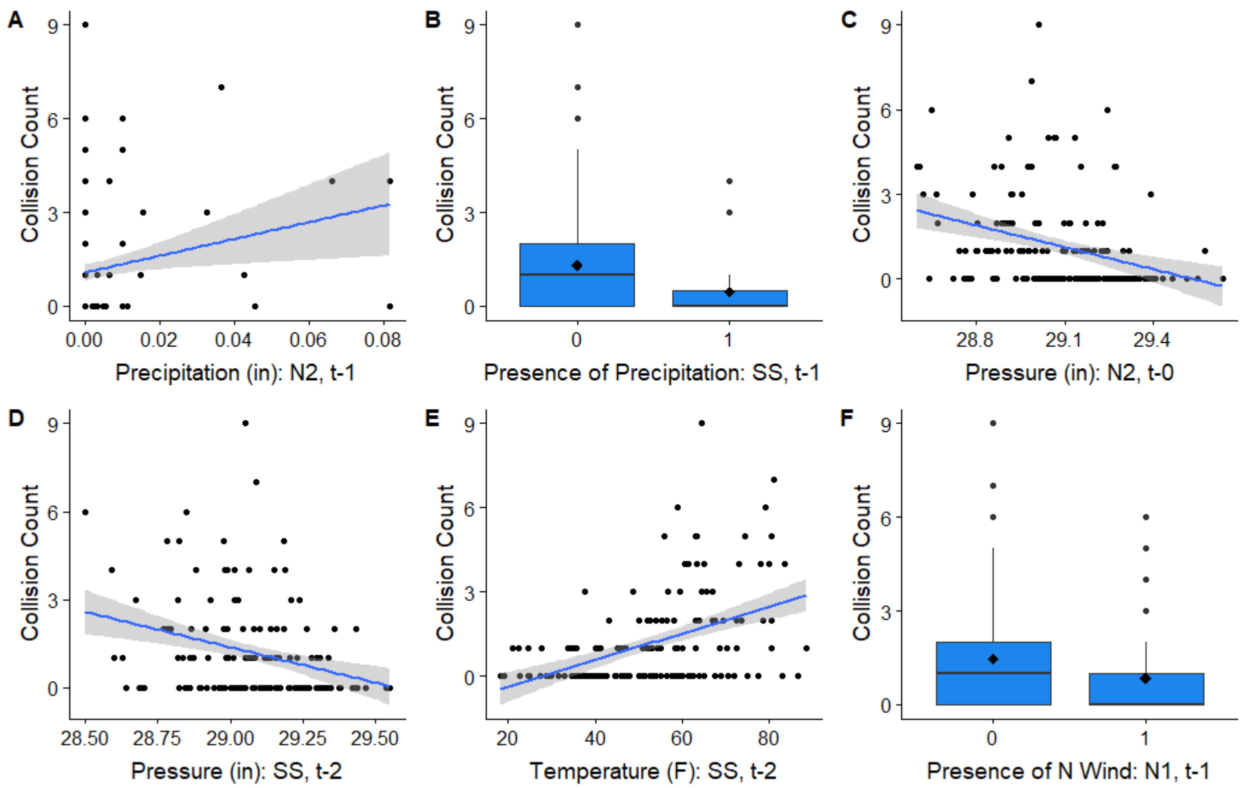


**Figure 1.2.** Plots for spring 2017-2018 analysis with weather variables averaged for different parts of the night, showing relationships between daily collision counts and weather variables in the top-ranked model. SS = sunset, N1 = first half of the night, N2 = second half of the night, SR = sunrise; t-0 = no time lag [i.e., weather conditions during the night preceding collision surveys], t-1 = 1-day time lag, t-2 = 2-day time lag. A) precipitation volume during the second half of the night with a 1-day time lag; B) presence of precipitation at sunset with a 1-day time lag; C) pressure during the second half of the night preceding collision surveys; D) pressure at sunset with a 2-day time lag; E) temperature at sunset with a 2-day time lag; and F) presence of north wind during the first half of the night with a 1-day time lag.

The top model for fall included six weather variables: cloud base height, cloud conditions, pressure, visibility, the presence of north wind, and the presence of south wind (Table 1.2, Fig. 1.3). Cloud base height from the night preceding collision surveys was included twice in the model: during the first half of the night and at sunrise. Both cloud base height variables were negatively correlated with collisions. Cloud conditions at sunrise with a 2-day time lag had a positive association with collisions (i.e., overcast conditions were correlated with collisions). Both pressure and the presence of north wind during the second half of the night preceding surveys were positively correlated with collisions. Visibility from the first half of the night preceding surveys also had a positive association with collisions. Finally, the presence of south wind at sunset was included twice in the model: for the night preceding surveys (negative association with collisions) and with a 1-day time lag (positive association with collisions).

In addition to the above additive effects, the top model for fall included two-way interactions. For cloud base height during the first half of the night preceding surveys and at sunrise the morning of surveys, the interaction between periods was primarily driven by low clouds (i.e., there is no clear interaction between the two time periods for moderate and high values of cloud base height); specifically, the effect of low clouds during one part of the night was stronger when low clouds were also present during the other part of the night (Fig. 1.3C). For wind direction, south winds at sunset interacted with north winds during the second half of the night (Fig. 1.3J). Specifically, north winds during the second half of the night always resulted in more collisions than if no north winds occurred during this period; however, this effect was greatest when north winds followed south winds at sunset. The fewest collisions occurred when south winds were present and north winds were absent.

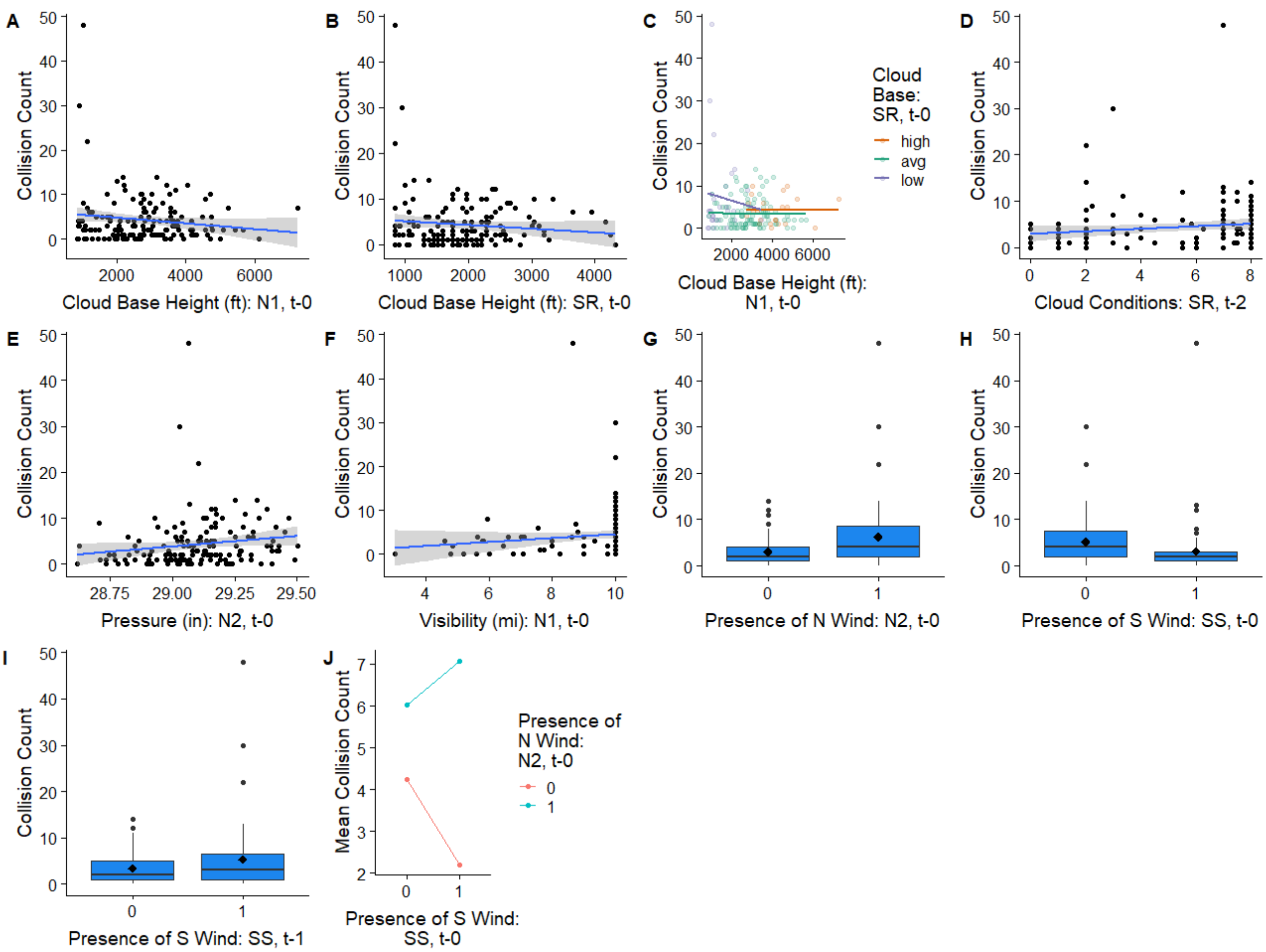


**Figure 1.3.** Plots for fall 2017-2018 analysis with weather variables averaged for different times of night, showing relationships between daily collision counts and weather variables in the top-ranked model. SS = sunset, N1 = first half of the night, N2 = second half of the night, SR = sunrise; t-0 = no time lag [i.e., weather conditions the night preceding surveys], t-1 = 1-day time lag, t-2 = 2-day time lag. A) cloud base height during the first half of the night preceding surveys; B) cloud base height at sunrise the day of surveys; C) the interaction of cloud base height during the first half of the night preceding surveys and at sunrise the day of surveys, where "high" and "low" are 1 standard deviation from the mean cloud base height; D) cloud conditions at sunrise with a 2-day time lag; E) pressure during the second half of the night preceding surveys; F) visibility during the first half of the night preceding surveys; G) presence of north wind during the second half of the night preceding surveys; H) presence of south wind at the sunset preceding surveys; I) presence of south wind at sunset with a 1-day time lag; and J) the interaction of north wind during the second half of the night preceding surveys and south wind at the sunset preceding surveys.

In Table 1.3, we summarize the major categories of weather conditions (i.e., independent of the time of night or time lag for which they were measured) that appeared in top models for both the analysis of different parts of the night (i.e., the results described above), and of variables averaged across the entire night (Table S2). In spring, the results for the entire-night analysis included some weather conditions that were absent from the time-of-night analysis (cloud base height and presence of south wind), and some conditions from the time-of-night analysis were absent from the entire-night analysis (presence of precipitation and presence of north wind). Three weather conditions were included in top models for both analyses: precipitation volume, pressure, and temperature. In fall, the results for the entire-night analysis included only 3 types of weather conditions that were all included in the time-of-night analysis: presence of north wind, presence of south wind, and visibility. However, the model included more interactions between wind direction variables across multiple nights.

**Table 1.3.** Summary of weather conditions included in the top models for the time-of-night analysis and entire-night analysis.

| Season | Weather Variable | Time of Night | Entire Night |
|---|---|---|---|
| Spring | Cloud base height | | x |
| | Precipitation volume | x | x |
| | Presence of precipitation | x | |
| | Pressure | x | x |
| | Presence of N wind | x | |
| | Presence of S wind | | x |
| | Temperature | x | x |
| Fall | Cloud base height | x | |
| | Cloud conditions | x | |
| | Pressure | x | |
| | Presence of N wind | x | x |
| | Presence of S wind | x | x |
| | Visibility | x | x |

## Discussion

We found that weather variables correlate with building collisions of nocturnally migrating birds during both spring and fall migration. Further, our results provide support for both of our hypotheses; specifically, weather variables associated with both favorable and poor migration conditions, sometimes when both occur during the same night, appear to contribute to elevating bird-building collision rates. We also show that the effect of weather is complex, with different weather variables predicting collisions in different seasons, differential effects of weather variables for different times of night and different time lags (from the night preceding collision surveys to two nights before surveys), and interactions of weather variables across times of night. Below we describe in detail the specific weather-related factors that predicted collisions in spring and fall migration for different parts of the night.

In spring, we generally found that conditions favorable for migration—warm temperatures and the absence of north winds (headwinds) and of precipitation—positively correlated with collisions. These weather conditions appeared particularly important near sunset and during the first half of the night (4 of 6 variables in the final model were for these periods), suggesting that favorable migration conditions early in the night, when nocturnal migrants typically initiate migration, may contribute disproportionately to spring collisions. However, high precipitation volume and low pressure (both indicative of stormy conditions) during the second half of the night also correlated with more collisions; this finding may reflect large numbers of collisions that occur when birds initiating migration early in the night encounter precipitation and are forced to “fall out” late in the night. Notably, most of the factors that predicted collisions were especially important for the nights prior to the night preceding collision surveys (i.e., 1- or 2-day lag effects for 5 of the 6 variables), suggesting that weather-based predictions of spring collisions may benefit from forecasts up to 2 days in advance. For example, even though low pressure from the second half of the immediately preceding night correlated with more collisions, a similar effect was also observed for low pressure two nights before surveys. This finding may reflect that decreasing pressure up to two days before the arrival of approaching low-pressure (i.e., storm) systems generates south winds and warm conditions (Bagg 1950) conducive to high-intensity spring migration (Wainwright et al. 2016) and increased collisions. Additionally, time lag effects may reflect conditions from other locations from which birds initiated migration, and therefore additional research analyzing conditions at other weather stations may be informative.

In fall, we also found that conditions favorable for migration (high pressure, high visibility, and the presence of north wind) as well as poor weather conditions (low cloud base height, overcast skies, and the presence of south wind) positively correlated with collisions. Some of these variables followed similar patterns as those found for spring, with collisions elevated in association with favorable migration conditions (high visibility and the absence of south wind) early in the night and poor conditions (low clouds and overcast conditions) later in the night, which again suggests the possibility of collisions occurring for migrating birds forced to fall out or fly at lower altitudes. However, other patterns of weather effects were also evident in the fall. For example, high pressure during the second half of the night was positively correlated with collisions, likely because high-pressure systems are associated with cool, dry air masses that are favorable for migration, especially following passage of a cold front and in association with north winds that occur on the east side of the system (Able 1973). Although pressure variables from all periods of the night were strongly correlated, our results suggest that the disproportionate importance of pressure late in the night may reflect an increased likelihood of north winds during this period, as collisions increased when each of these factors occurred during the second half of the night (Table 1.2).

In fall, weather variables also interacted across time periods to influence collisions. For the night preceding surveys, south wind at sunset followed by north wind during the second half of the night led to more collisions than the presence of north wind alone. This interaction also likely influenced the unexpected positive relationship between collisions and the presence of south wind at sunset with a 1-day time lag. We hypothesize that these patterns reflect large numbers of birds initiating migration in response to a shift to north winds following an extended period of south winds unfavorable for fall migration. Such an intense peak in migration activity late in the night may be expected to result in a higher number of collisions than if north winds had been occurring for a more extended period. There was also an interacting effect of low clouds the night preceding surveys; specifically, low clouds later in the night increased collisions, but the strength of this effect was intensified when there were also low clouds early in the night, a pattern that may increase the total number of low-flying or grounded birds relative to nights when low clouds are present for only part of the night. Finally, we also note that, in contrast to spring, most of the supported weather variables for fall (6 of 8 variables) had no time lag, suggesting that fall collisions are primarily influenced by weather conditions the night immediately preceding collision surveys. This difference in time lag effects may reflect increased urgency for birds to migrate in the spring to arrive early at breeding sites (Nilsson et al. 2013); therefore, birds may be less selective in waiting for optimal migration conditions in spring than in fall.

Our collective results demonstrate the importance of considering weather conditions during different parts of the night, time lag effects up to two days in advance of collision events, and interactions across times of night. Further, the temporal grain at which weather variables are averaged also matters, as supported by our finding that top models for both migration seasons differed depending on whether variables were characterized for the entire night or parts of the night. In spring, only 3 major categories of weather conditions—precipitation volume, pressure, and temperature—were included in both analyses. In fall, the top model for the entire-night analysis included only 3 of the 6 major categories of conditions identified in the respective time-of-night analysis (presence of north wind, presence of south wind, and visibility). Given our observation that collisions correlated with favorable migration conditions early in the night and poor conditions late in the night, we argue that time-of-night analyses allow more specific predictions about the timing of conditions that influence collisions, and therefore, more targeted recommendations for reducing collisions (e.g., turning off lights during specific periods of the night). However, when logistically infeasible to compile and interpret weather variables for different times of night, our analyses suggest that the weather variables supported in both analyses could be used to predict collisions regardless of the resolution at which weather forecast information is available.

Our results provide the first formal, multi-year assessment of the effects of weather on bird collisions with buildings, or with any human-built structures. Therefore, this study provides a framework and additional follow-up hypotheses for future similar research in other regions. Because both weather patterns and characteristics of avian migration vary by geographic region, conducting this analysis in different regions could lead to identifying different weather-related predictors of collisions. For example, temperature may not be as important in the spring in areas where temperature fluctuations are small (e.g., lower-latitude and coastal locations) compared to our study area. Additionally, in rural and residential settings, different weather variables may affect collisions, or weather may have no effect at all, because the presence of birds could be more heavily influenced by other factors such as food and habitat availability. Because high collision rates can also occur in the summer (Hager and Craig 2014, Schneider et al. 2018, Riding et al. *in review*), future studies may also consider the effect of weather during the summer breeding season, although we predict that weather is of reduced importance when most birds are in a sedentary portion of their annual cycles. Furthermore, our analysis focuses on nocturnal migrants and primarily includes passerines; diurnal migrants and other avian taxonomic groups may respond differently to weather. For example, in the same study area, American Woodcock, a nocturnally migrating, terrestrial shorebird species with a much earlier spring migration window than most other bird species, collided with buildings at unusually high rates during early spring snowstorms in 2018 (Loss et al. *in prep*). Analyzing the effect of weather on building collisions for specific bird species or families may be of interest to wildlife managers and conservation groups and may reveal species-specific correlates of building collisions that provide clues to the mechanisms behind bird collisions. These analyses will be especially relevant as climate change increases the frequency of extreme weather events (IPCC 2013) and may disproportionately affect species of conservation concern.

Our results have management implications for reducing the impact of buildings on migratory birds. Because many of the predictive weather variables are associated with favorable migration conditions, the results of this study support using weather forecasts and tools like Cornell's BirdCast forecasts to predict when high numbers of collisions are likely based on migration intensity. However, our results demonstrate relatively nuanced effects of weather, including time lag effects and changes in weather between fair and poor migration conditions during different parts of the same night. Bird migration forecasts may need to incorporate these more detailed types of information to maximize their utility for predicting collisions. Having access to weather-informed migration forecasts can allow homeowners and building managers to take actions to reduce collisions, such as turning off nighttime lighting when high migration intensity and/or fallout of migrants is likely to occur. Because collisions appear to be influenced by favorable migration conditions early in the night and poor conditions late in the night, building managers could focus mitigation efforts during these times depending on weather forecasts. However, further research and collision monitoring to validate the predictions arising from our analyses are also needed, especially regarding mitigation efforts focused during different parts of the night. Finally, it is often assumed that artificial lighting emanating from and near buildings exacerbates fallouts of migrating birds in urban areas; however, very few studies have analyzed nightly interactions of weather and lighting (but see Evans Ogden 2002). Further research is needed to better understand which specific weather and lighting conditions most strongly influence bird collisions, as this information could lead to additional collision mitigation recommendations.

**Conclusion**

This study shows that weather influences bird-building collisions during both spring and fall migration. Collision counts were generally associated with favorable migration conditions early in the night, when most birds begin migrating, and poor conditions later in the night, which cause migrating birds to fly at lower altitudes or become grounded in urban areas. We also found that conditions up to two nights prior to a collision event were important in the spring, which suggests a need for advanced planning of any collision reduction efforts. However, in the fall, collisions were primarily related to conditions the night preceding surveys, suggesting that fall management decisions can be made up to the night before a collision fatality event is predicted to occur. These results also suggest that weather and bird migration forecasts may be useful for predicting large collision events, and that predictions may become more accurate if they incorporate time lag effects and interactions of fair and poor weather conditions during different times of night. By using weather information to improve predictions of bird-building collisions, building managers and homeowners can take better-informed actions to reduce numbers of birds killed by this major source of human-caused mortality.

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## Supplemental Materials

**Table S1**. Species removed from daily collision monitoring counts due to classification as permanent residents or diurnal migrants.

| Common Name | Species Name |
|---|---|
| American Robin | *Turdus migratorius* |
| Black-capped Chickadee | *Poecile atricapillus* |
| Blue Jay | *Cyanocitta cristata* |
| Common Grackle | *Quiscalus quiscula* |
| Downy Woodpecker | *Picoides pubescens* |
| House Finch | *Haemorhous mexicanus* |
| House Sparrow | *Passer domesticus* |
| Rock Dove | *Columba livia* |
| Ruby-throated Hummingbird | *Archilochus colubris* |
| White-breasted Nuthatch | *Sitta carolinensis* |
| White-winged Crossbill | *Loxia leucoptera* |

**Table S2.** Weather variables included in the top models for spring and fall based on analysis including data from 2017 and 2018 and with weather variables averaged across the entire night. For time lags, t-0 = no time lag (i.e., weather conditions the night preceding surveys), t-1 = 1-day time lag, t-2 = 2-day time lag. Relative importance indicates the sum of AIC weights (i.e., proportion of all models that include the variable) after testing all possible combinations of variables in R package *MuMIn*.

| Season | Weather Variable | Time Lag | Direction of Effect | Relative Importance |
|---|---|---|---|---|
| Spring | Cloud base height | t-1 | + | 0.81 |
| | | t-2 | + | 0.69 |
| | Precipitation volume | t-2 | + | 0.84 |
| | Pressure | t-0 | - | 0.72 |
| | | t-2 | - | 0.82 |
| | Temperature | t-2 | + | 0.77 |
| | Presence of S wind | t-1 | + | 0.81 |
| | | t-2 | + | 0.77 |
| Fall | Visibility | t-0 | + | 0.82 |
| | Presence of N wind | t-0 | + | 0.96 |
| | | t-1 | + | 0.91 |
| | | t-2 | + | 0.65 |
| | Presence of S wind | t-0 | + | 0.79 |
| | | t-1 | + | 0.96 |
| | Interaction of N wind | t-0, t-2 | - | 0.44 |
| | Interaction of S wind | t-0, t-1 | - | 0.39 |
| | Interaction of N and S wind | t-2, t-0 (respectively) | - | 0.53 |

**Figure S1.** Plots for spring 2017-2018 analysis with weather variables averaged across the entire night, showing relationships between daily collision counts and weather variables in the top-ranked model. t-0 = no time lag [i.e., weather conditions the night preceding surveys], t-1 = 1-day time lag, t-2 = 2-day time lag. A) cloud base height with a 1-day time lag; B) cloud base height with a 2-day time lag; C) precipitation volume with a 2-day time lag; D) pressure the night preceding surveys; E) pressure with a 2-day time lag; F) temperature with a 2-day time lag; G) presence of south wind with a 1-day time lag; and H) presence of south wind with a 2-day time lag.

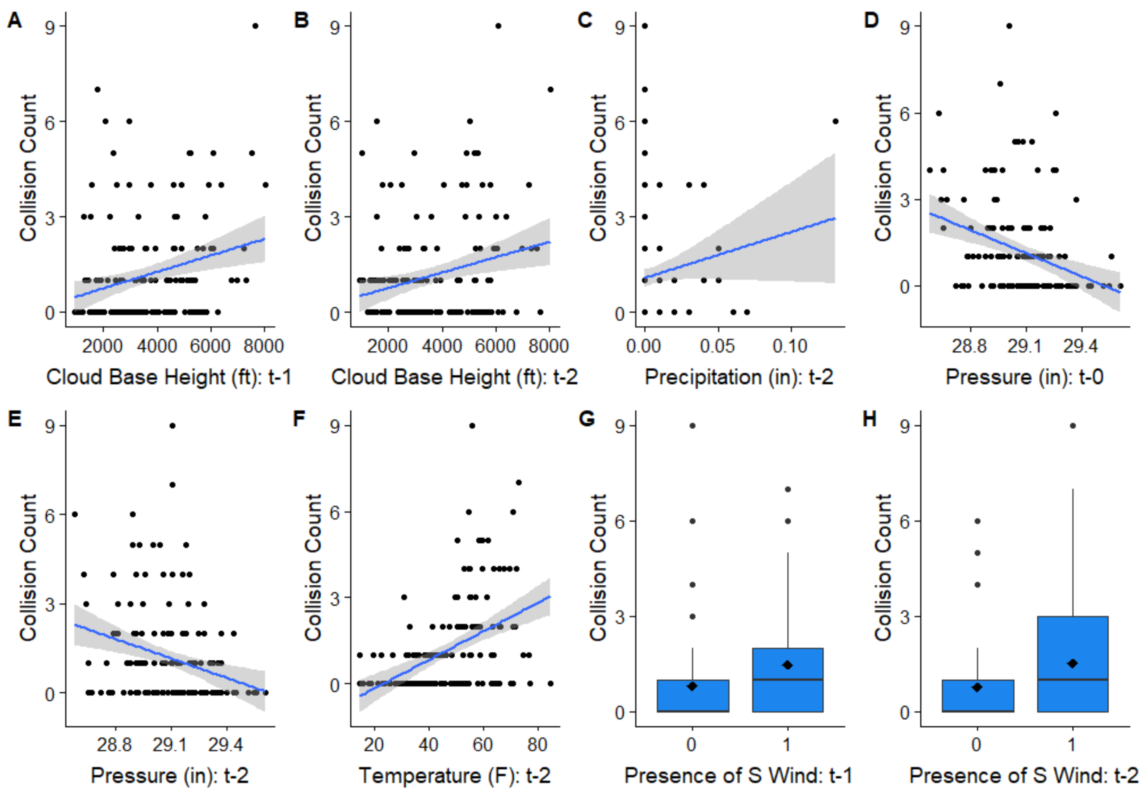

**Figure S2.** Plots for fall 2017-2018 analysis with weather variables averaged across the entire night, showing relationships between daily collision counts and weather variables in the top-ranked model. t-0 = no time lag [i.e., weather conditions the night preceding surveys], t-1 = 1-day time lag, t-2 = 2-day time lag. A) visibility with no time lag; B) presence of north wind the night preceding surveys; C) presence of north wind with a 1-day time lag; D) presence of north wind with a 2-day time lag; E) presence of south wind the night preceding surveys; F) presence of south wind with a 1-day time lag; G) the interaction of north wind the night preceding surveys and north wind with a 2-day time lag; H) the interaction of south wind the night preceding surveys and south wind with a 1-day time lag; and I) the interaction of south wind the night preceding surveys and north wind with a 2-day time lag.

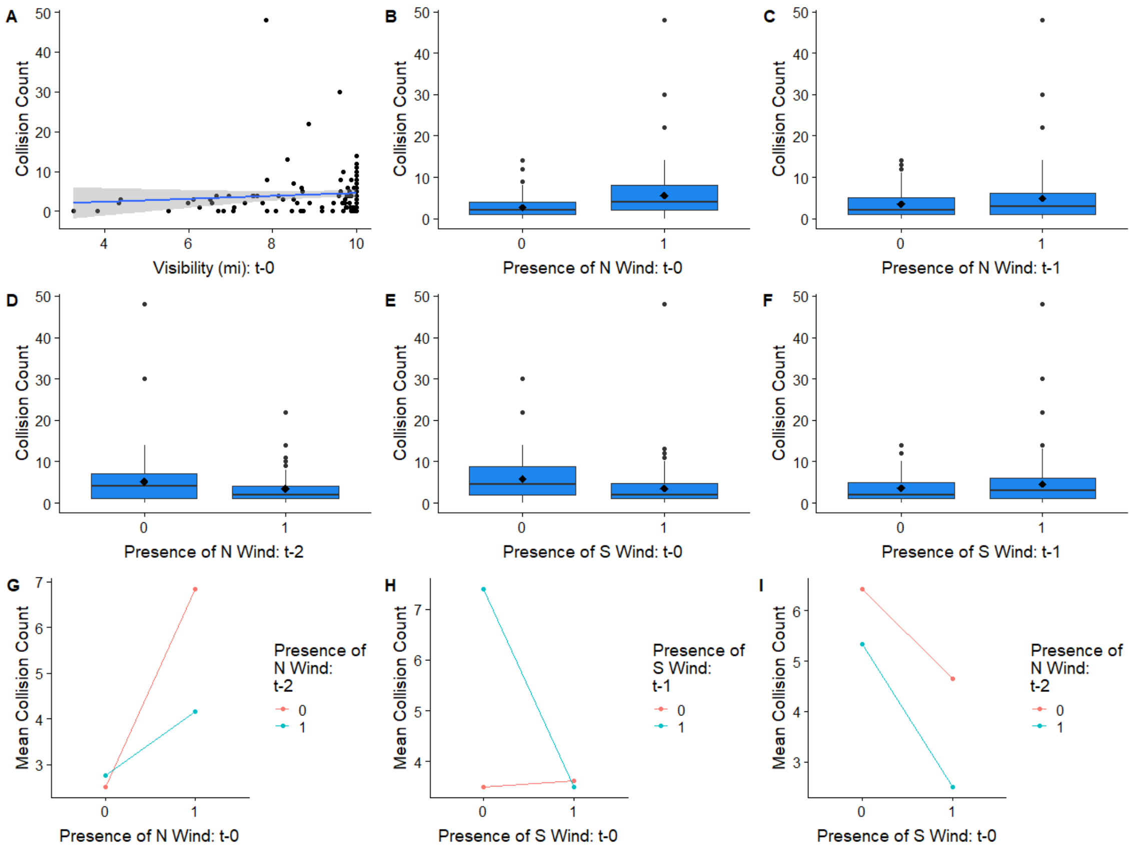

**Table S3.** Model selection results for analysis of weather variables associated with bird-building collision counts in spring 2017 and 2018 averaged over different parts of the night. See Table S7 for the final model selection results after substituting back highly correlated variables in the top-ranked model. Time of night is represented by: SS = sunset; N1 = first half of the night; N2 = second half of the night; SR = sunrise. Time lags are represented by numbers at the end of each variable: 0 = no time lag (i.e., weather conditions the night preceding surveys); 1 = 1-day time lag; 2 = 2-day time lag.

| **Models** | **AIC** | **∆AIC** | **df** | **weight** | **Resid Dev** |
|---|---|---|---|---|---|
| N_N1_1 + Precip_in_N2_1 + Precip_SS_1 + Pressure_N1_0 + Pressure_N1_2 + Temp_N1_0 | 412.4 | 0 | 8 | 0.4028 | 147.7 |
| CloudBase_N1_2 + N_N1_1 + Precip_in_N1_2 + Precip_in_N2_1 + Precip_SS_1 + Pressure_N1_0 + Pressure_N1_2 + Temp_N1_0 | 412.4 | 0 | 10 | 0.3983 | 150 |
| CloudBase_N1_2 + Precip_in_N1_2 + Precip_in_N2_1 + Precip_SS_1 + N_N1_1 + Pressure_N1_0*Pressure_N1_1 + Pressure_N1_2 + Temp_N1_0 | 414.8 | 2.4 | 12 | 0.1207 | 149.4 |
| CloudBase_N1_1 + CloudBase_N1_2 + N_N1_1 + Precip_in_N1_2 + Precip_in_N2_1 + Precip_SS_1 + Pressure_N1_0 + Pressure_N1_1 + Pressure_N1_2 + Temp_N1_0 + WindSpeed_SR_0 | 418.7 | 6.3 | 13 | 0.0171 | 149 |
| Precip_in_N1_2 + Precip_in_N2_1 + Precip_SS_1 + Pressure_N1_0 + Temp_N1_0 + WindSpeed_SR_0 | 419.2 | 6.8 | 8 | 0.0133 | 148 |
| Precip_in_N1_2 + Precip_in_N2_1 + Precip_SS_1 + Pressure_N1_1 + Temp_N1_0 + WindSpeed_SR_0 | 419.3 | 7 | 8 | 0.0124 | 148.8 |
| Precip_in_N1_2 + Precip_in_N2_1 + Precip_SS_1 + Pressure_N1_0 + Temp_N1_0 | 419.7 | 7.3 | 7 | 0.0105 | 148.3 |
| Precip_in_N1_2 + Precip_in_N2_1 + Precip_SS_1 + Pressure_N1_1 + Temp_N1_0 | 419.8 | 7.4 | 7 | 0.01 | 149.4 |
| Precip_in_N2_1 + Precip_SS_1 + Pressure_N1_1 + Temp_N1_0 + WindSpeed_SR_0 | 420.1 | 7.7 | 7 | 0.0084 | 149.6 |
| CloudBase_N1_1 + Precip_in_N1_2 + Precip_in_N2_1 + Precip_SS_1 + Pressure_N1_0 + Pressure_N1_1 + Temp_N1_0 + WindSpeed_SR_0 | 421.4 | 9.1 | 10 | 0.0043 | 147.4 |
| CloudBase_N1_1 + Precip_in_N1_2*Precip_in_N2_1 + Precip_SS_1 + Pressure_N1_0*Pressure_N1_1 + Temp_N1_0 + WindSpeed_SR_0 | 423.5 | 11.2 | 12 | 0.0015 | 148.6 |
| CloudBase_N1_1*CloudBase_N1_2 + N_N1_1 + Precip_in_N1_2*Precip_in_N2_1 + Precip_SS_1 + Pressure_N1_0*Pressure_N1_1 + Pressure_N1_2 + Pressure_N1_0:Pressure_N1_2 + Pressure_N1_1:Pressure_N1_2 + Temp_N1_0 + WindSpeed_SR_0 | 425.7 | 13.3 | 18 | <0.001 | 147.7 |
| Null | 467.9 | 55.5 | 2 | <0.001 | 236 |

**Table S4.** Model selection results for analysis of weather variables associated with bird-building collision counts in fall 2017 and 2018 averaged over different parts of the night. See Table S8 for the final model selection results after substituting back highly correlated variables in the top-ranked model.
Time of night is represented by: SS = sunset; N1 = first half of the night; N2 = second half of the night; SR = sunrise. Time lags are represented by numbers at the end of each variable: 0 = no time lag (i.e., weather conditions the night preceding surveys); 1 = 1-day time lag; 2 = 2-day time lag.

| **Models** | **AIC** | **ΔAIC** | **df** | **weight** | **Resid Dev** |
|---|---|---|---|---|---|
| CloudBase_N1_0*CloudBase_SR_0 + CloudConditions_SR_2 + N_N2_0*S_SS_0 + Pressure_N1_0 + S_SS_1 + Visibility_N1_0 | 759.9 | 0 | 12 | 0.5394 | 175.2 |
| CloudBase_N1_0*CloudBase_SR_0 + CloudConditions_SR_1*CloudConditions_SR_2 + Pressure_N1_0 + N_N2_0*S_SS_0 + S_SS_1 + VisibilityMi_N1_0 | 760.6 | 0.7 | 14 | 0.3725 | 176.2 |
| CloudBase_N1_1 + CloudBase_SR_0 + CloudConditions_SR_2+ N_N2_0 + Pressure_N1_0 + S_SS_2 + S_SS_1 + Visibility_N1_0 | 765.5 | 5.6 | 10 | 0.0326 | 176.1 |
| CloudBase_N1_0 + CloudConditions_SR_1*CloudConditions_SR_2 + N_N2_0 + Pressure_N1_0 + S_SS_1 + S_SS_2 + Visibility_N1_0 | 766.7 | 6.9 | 11 | 0.0172 | 175 |
| CloudBase_N1_0 + CloudBase_N1_1 + CloudConditions_SR_2 + N_N2_0 + Pressure_N1_0 + S_SS_1 + S_SS_2 + Visibility_N1_0 | 766.8 | 6.9 | 10 | 0.0169 | 176.2 |
| CloudConditions_SR_1*CloudConditions_SR_2 + N_N2_0 + Pressure_N1_0 + S_SS_1 + S_SS_2 + Visibility_N1_0 | 766.9 | 7.1 | 10 | 0.0156 | 173.6 |
| CloudConditions_SR_2 + N_N1_0 + Pressure_N1_0 + S_SS_0*S_SS_1 + S_SS_2 + N_N1_0:S_SS_0 | 770.2 | 10.4 | 10 | 0.003 | 173 |
| CloudBase_N1_0*CloudBase_SR_0 + CloudBase_N1_1 + CloudConditions_SR_1*CloudConditions_SR_2 + S_SS_0 + VisibilityMi_N1_0 | 772.1 | 12.3 | 11 | 0.0012 | 175.7 |
| CloudBase_N1_0 + CloudBase_N1_1 + CloudConditions_SR_1*CloudConditions_SR_2 + N_N1_0*N_N2_0 + Pressure_N1_0 + S_SS_0*S_SS_1 + S_SS_2 + S_SS_0:N_N1_0 + S_SS_0:N_N2_0 + S_SS_1:N_N1_0 + S_SS_1:N_N2_0 + S_SS_2:N_N1_0 + S_SS_2:N_N2_0 + Visibility_N1_0 | 772.4 | 12.6 | 21 | 0.001 | 178.5 |
| CloudBase_N1_0 + CloudBase_N1_1 + CloudBase_SR_0 + CloudConditions_SR_1 + CloudConditions_SR_2 + N_N1_0 + N_N2_0 + Pressure_N1_0 + S_SS_0 + S_SS_2 + S_SS_1 + N_N2_2 + Visibility_SS_0 + Visibility_N1_0 | 773.7 | 13.9 | 15 | <0.001 | 175.8 |
| CloudBase_N1_0*CloudBase_N1_1 + CloudConditions_SR_1*CloudConditions_SR_2 + S_SS_0 + Visibility_SS_0 + Visibility_N1_0 | 777.8 | 17.9 | 14 | <0.001 | 175.4 |
| CloudBase_N1_0 + CloudBase_N1_1*CloudBase_SR_0 + CloudConditions_SR_2*CloudConditions_SR_2 + S_SS_0 + Visibility_N1_0 | 779 | 19.2 | 7 | <0.001 | 173.3 |

| | | | | | |
|---|---|---|---|---|---|
| CloudBase_N1_0 + CloudBase_N1_1 + CloudConditions_SR_1*CloudConditions_SR_2 + S_SS_0 + Visibility_SS_0 | 782.9 | 23 | 9 | <0.001 | 173.4 |
| CloudBase_N1_0 + CloudBase_N1_1 + CloudBase_SR_0 + CloudConditions_SR_1 + CloudConditions_SR_2 + S_SS_0 + Visibility_SS_0 + Visibility_N1_0 | 783.8 | 23.9 | 10 | <0.001 | 173.2 |
| Null | 802.7 | 42.8 | 2 | <0.001 | 259.5 |

**Table S5.** Model selection results for analysis of weather variables associated with bird-building collision counts in spring 2017 and 2018 averaged over the entire night. Temp_0 was highly correlated with Temp_1 and Temp_2; in the final model shown in Table S2, we used Temp_2 because it improved model fit (AIC = 425.1). Time lags are represented by numbers at the end of each variable: 0 = no time lag (i.e., weather conditions the night preceding surveys); 1 = 1-day time lag; 2 = 2-day time lag.

| **Models** | **AIC** | **ΔAIC** | **df** | **weight** | **Resid Dev** |
|---|---|---|---|---|---|
| CloudBase_1 + CloudBase_2 + Precip_in_2 + Pressure_0 + Pressure_2 + S_1 + S_2 + Temp_0 | 426.6 | 0 | 10 | 0.225 | 151.4 |
| CloudBase_1 + CloudBase_2 + Precip_in_2 + Pressure_0*Pressure_1 + Pressure_2 + S_1 + S_2 | 427.2 | 0.6 | 11 | 0.1679 | 149.5 |
| CloudBase_1 + CloudBase_2 + Precip_in_2 + Pressure_0 + Pressure_2 + S_1 + S_2 | 427.2 | 0.6 | 9 | 0.1651 | 152.8 |
| CloudBase_1 + Precip_in_2 + Pressure_0 + Pressure_2 + S_1 + S_2 + Temp_0 | 427.4 | 0.8 | 9 | 0.1485 | 150 |
| CloudBase_1 + CloudBase_2 + Precip_in_2 + Pressure_2 + S_1 + S_2 + Temp_0 | 427.8 | 1.2 | 9 | 0.1248 | 152.5 |
| CloudBase_2 + Pressure_0 + Pressure_2 + Temp_0 | 430.4 | 3.8 | 6 | 0.0331 | 151.4 |
| CloudBase_1 + Pressure_0 + Pressure_2 + Temp_0 | 430.6 | 4.1 | 6 | 0.0297 | 152.3 |
| CloudBase_0 + CloudBase_1 + CloudBase_2 + Precip_in_2 + Pressure_0 + Pressure_1 + Pressure_2 + S_1 + S_2 + Temp_0 | 431.1 | 4.6 | 12 | 0.0229 | 151.3 |
| CloudBase_1 + Pressure_1 + Pressure_2 + Temp_0 | 431.2 | 4.6 | 6 | 0.022 | 151.7 |
| Pressure_0 + Pressure_2 + Temp_0 | 431.4 | 4.8 | 5 | 0.0203 | 150 |
| CloudBase_2 + Pressure_2 + Temp_0 | 431.4 | 4.9 | 5 | 0.0199 | 152.3 |
| CloudBase_1 + Pressure_1 + Temp_0 | 431.7 | 5.2 | 5 | 0.017 | 152.7 |
| CloudBase_0 + CloudBase_1 + CloudBase_2 + Pressure_0 + Pressure_1 + Pressure_2 + Temp_0 | 434.9 | 8.3 | 9 | 0.0036 | 152.4 |
| CloudBase_1 + CloudBase_2 + Precip_in_2 + Pressure_0*Pressure_1 + Pressure_2 + S_1 + S_2 | 440.3 | 13.8 | 19 | <0.001 | 148.4 |
| CloudBase_0*CloudBase_1 + CloudBase_0:CloudBase_2 + CloudBase_1:CloudBase_2 + CloudBase_2 + Pressure_0*Pressure_1 + Pressure_0:Pressure_2 + Pressure_1:Pressure_2 + Pressure_2 + Temp_0 | 445.9 | 19.3 | 15 | <0.001 | 149.2 |
| Null | 467.9 | 41.3 | 2 | <0.001 | 226.2 |

**Table S6.** Model selection results for analysis of weather variables associated with bird-building collision counts in fall 2017 and 2018 averaged over the entire night. Time lags are represented by numbers at the end of each variable: 0 = no time lag (i.e., weather conditions the night preceding surveys); 1 = 1-day time lag; 2 = 2-day time lag.

| **Models** | **AIC** | **ΔAIC** | **df** | **weight** | **Resid Dev** |
|---|---|---|---|---|---|
| N_0 + N_1 + N_2*S_0 + S_1 + N_0:N_2 + S_0:S_1 + Visibility_0 | 773.2 | 0 | 11 | 0.2576 | 173.2 |
| CloudBase_0 + N_0*N_2 + N_1 + S_0 + S_1 + N_1:S_0 + N_2:S_0 + Visibility_0 | 773.3 | 0.2 | 12 | 0.238 | 174.4 |
| CloudBase_0 + CloudBase_1 + N_0*S_1 + N_1 + Visibility_0 | 774.1 | 0.9 | 9 | 0.1649 | 173.7 |
| CloudBase_0 + CloudBase_1 + N_0 + N_1 + S_1 + Visibility_0 | 774.5 | 1.4 | 8 | 0.1302 | 173.3 |
| CloudBase_0 + CloudBase_1 + N_0*N_2 + N_1 + S_0*S_1 + S_2 + N_0:S_2 + N_2:S_0 + Visibility_0 | 775 | 1.8 | 15 | 0.1029 | 175 |
| CloudBase_0 + N_0 + Pressure_0 + Visibility_0 | 777.7 | 4.5 | 6 | 0.0268 | 172.5 |
| CloudBase_0 + CloudBase_1 + N_0 + Visibility_0 | 777.8 | 4.6 | 6 | 0.0253 | 173.2 |
| CloudBase_0 + N_0 + Visibility_0 | 777.8 | 4.7 | 5 | 0.0251 | 172.6 |
| CloudBase_0 + CloudBase_1 + Pressure_0 + N_0 + Pressure_1 + Visibility_0 | 777.9 | 4.8 | 8 | 0.0239 | 173.7 |
| CloudBase_0*CloudBase_1 + N_0 + Pressure_0*Pressure_1 + Visibility_0 | 782.2 | 9 | 10 | 0.0029 | 173.6 |
| CloudBase_0 + CloudBase_1 + N_1 + N_2 + Pressure_0 + N_0 + Pressure_1 + S_0 + S_1 + S_2 + Visibility_0 + WindSpeed_2 | 782.8 | 9.6 | 14 | 0.0021 | 173.8 |
| CloudBase_0 + CloudBase_1 + Pressure_0 + Pressure_1 + N_0*N_2 + N_1 + S_0*S_1 + S_2 + S_0:S_2 + N_0:S_1 + N_0:S_2 + S_0:N_1 + S_0:N_2 + Visibility_0 + WindSpeed_2 | 786.9 | 13.7 | 21 | <0.001 | 174.6 |
| Null | 802.7 | 29.5 | 2 | <0.001 | 232.3 |

**Table S7.** AIC table comparing model fit for the top model for spring (variables averaged over different parts of the night; see Table S5) and models with substitutions of highly correlated pressure and temperature variables. Original top model denoted by ^. Other temperature variables also performed better than the original top model, but were not competitive compared to those reported here. No other substitutions for highly correlated variables performed better than the original top model.

| **Models** | **AIC** | **ΔAIC** | **df** | **weight** | **Resid Dev** |
|---|---|---|---|---|---|
| N_N1_1 + Precip_in_N2_1 + Precip_SS_1 + Pressure_N2_0 + Pressure_SS_2 + Temp_SS_2 | 405.9 | 0 | 8 | 0.34 | 148.6 |
| N_N1_1 + Precip_in_N2_1 + Precip_SS_1 + Pressure_N2_0 + Pressure_SS_2 + Temp_N1_2 | 406.5 | 0.6 | 8 | 0.252 | 147.3 |
| N_N1_1 + Precip_in_N2_1 + Precip_SS_1 + Pressure_N1_0 + Pressure_N1_2 + Temp_SS_2 | 407 | 1.1 | 8 | 0.195 | 149.2 |
| N_N1_1 + Precip_in_N2_1 + Precip_SS_1 + Pressure_N1_0 + Pressure_N1_2 + Temp_N1_2 | 408 | 2.1 | 8 | 0.118 | 148 |
| N_N1_1 + Precip_in_N2_1 + Precip_SS_1 + Pressure_N2_0 + Pressure_SS_2 + Temp_N1_0 | 410.4 | 4.6 | 8 | 0.035 | 147.3 |
| N_N1_1 + Precip_in_N2_1 + Precip_SS_1 + Pressure_N1_0 + Pressure_SS_2 + Temp_N1_0 | 410.7 | 4.9 | 8 | 0.03 | 147.9 |
| N_N1_1 + Precip_in_N2_1 + Precip_SS_1 + Pressure_N2_0 + Pressure_N1_2 + Temp_N1_0 | 411.9 | 6 | 8 | 0.017 | 147 |
| ^N_N1_1 + Precip_in_N2_1 + Precip_SS_1 + Pressure_N1_0 + Pressure_N1_2 + Temp_N1_0 | 412.4 | 6.5 | 8 | 0.013 | 147.7 |

**Table S8.** AIC table comparing model fit for the top model for fall (variables averaged over different parts of the night; see Table S6) and models with substitutions of highly correlated pressure variables. Original top model denoted by ^. No other substitutions for highly correlated variables performed better than the original top model.

| **Models** | **AIC** | **ΔAIC** | **df** | **weight** | **Resid Dev** |
|---|---|---|---|---|---|
| CloudBase_N1_0*CloudBase_SR_0 + CloudConditions_SR_2 + N_N2_0*S_SS_0 + Pressure_N2_0 + S_SS_1 + Visibility_N1_0 | 757.7 | 0 | 12 | 0.43 | 175.1 |
| CloudBase_N1_0*CloudBase_SR_0 + CloudConditions_SR_2 + N_N2_0*S_SS_0 + Pressure_SR_0 + S_SS_1 + Visibility_N1_0 | 757.7 | 0 | 12 | 0.43 | 175.2 |
| ^CloudBase_N1_0*CloudBase_SR_0 + CloudConditions_SR_2 + N_N2_0*S_SS_0 + Pressure_N1_0 + S_SS_1 + Visibility_N1_0 | 759.8 | 2.3 | 12 | 0.14 | 175.2 |

CHAPTER II

# INVESTIGATING THE INFLUENCE OF ARTIFICIAL NIGHT LIGHTING AND POLARIZED LIGHT ON BIRD-BUILDING COLLISIONS

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**Abstract**

Collisions with buildings annually kill up to 1 billion birds in the United States. Bird-building collisions primarily occur at glass surfaces: birds often fail to perceive glass as a barrier and appear to be attracted to artificial light emitted from windows. However, birds perceive light differently than humans and some aspects of avian vision are poorly understood, including how bird responses to different types of light influence building collisions. Some evidence suggests birds can detect polarized light, which may serve as a cue to assist with migration orientation and/or detect water bodies. Dark, reflective surfaces, including glass, reflect high degrees of polarized light, causing polarized light pollution (PLP). However, no studies have analyzed the relationship between bird collisions and artificially polarized light reflected from buildings. Additionally, while artificial light at night (ALAN) is frequently implicated as a major factor influencing bird-building collisions, few studies have analyzed this relationship. We investigated both types of light pollution—PLP and ALAN—and their association with bird collisions at individual façades of 13 buildings in Minneapolis, Minnesota, USA. We found that the area of glass emitting ALAN was the most important factor influencing collisions, even after accounting for overall glass area; this result provides strong support for turning off lights at night to reduce bird-building collisions. Although we found no relationship between artificially polarized light and collisions, designing glass surfaces and retrofitting existing glass to reduce both types of light pollution should contribute to significantly reducing bird-building collisions.

## Introduction

Building collisions are a major source of avian mortality, killing 365–988 million birds each year in the United States (Loss et al. 2014). Bird-building collisions occur primarily at glass surfaces, with birds failing to perceive as barriers panes that are transparent or that reflect sky and/or vegetation (Klem 1989). Susceptibility to collisions could be exacerbated at night, when nocturnally migrating birds seem to be attracted to or disoriented by lighting emanating from windows (Evans Ogden 2002, Keyes and Sexton 2014, Parkins et al. 2015). Supporting these observations, studies have shown that the area and/or proportion of buildings covered by glass and the distance of vegetation from buildings are positively correlated with collisions (Klem et al. 2009, Borden et al. 2010, Cusa et al. 2015, Hager et al. 2013, 2017), and further, that most collision victims are nocturnal migrants (Arnold & Zink 2011, Loss et al. 2014, Nichols et al. 2018). However, few studies have formally analyzed the relationship between artificial light at night (ALAN) and building collisions despite the oft-cited importance of this factor. Moreover, nearly all bird-building collision studies assessing the role of lighting have drawn conclusions based only on light visible to humans, despite the fact that birds perceive and respond differently to light.

ALAN changes natural patterns of light and dark in ecosystems, causing a wide range of effects on animal behaviors and activity patterns (Longcore and Rich 2004). At broad scales, ALAN can disorient birds and concentrate them in urban areas (La Sorte et al. 2017, McLaren et al. 2018, Van Doren et al. 2017). At finer scales within urban areas, lights emitted from and near buildings and other structures can attract birds, particularly on nights with low clouds and/or visibility (Avery et al. 1976, Evans Ogden 2002, Erickson et al. 2005, Kerlinger et al. 2010, Rebke et al. 2019). Anecdotal evidence suggests that ALAN contributes to bird-building collisions, but few peer-reviewed studies have formally analyzed this relationship, except one study that found an association between light emission and bird collisions but was unable to isolate the correlated effects of light emission and glass area (Parkins et al. 2015). Thus, further research is needed to formally assess effects of ALAN relative to other variables influencing bird-building collisions.

In addition to ALAN, other aspects of light may play a role in bird-building collisions. Considering these effects requires recognition that birds have different visual systems and perceive light differently than humans (Maier and Bowmaker 1993, Martin 2011). A poorly understood aspect of avian vision is the degree to which birds detect polarized light and whether it influences behavior and collision risk. Sunlight is *unpolarized* before entering earth's atmosphere, meaning the electric field vectors (E-vector) of light waves vibrate in all directions (Fig. 1). Light is *polarized* when the light source (i.e., *incident light*) reflects off a surface that causes the E-vector of reflected light to vibrate in a single plane. The *degree of polarization* is the percentage of reflected light that is polarized, which depends on characteristics of the reflecting surface and the angle of incident light. Generally, smooth, dark surfaces and low angles of incident light cause high degrees of polarization (Umov 1905).

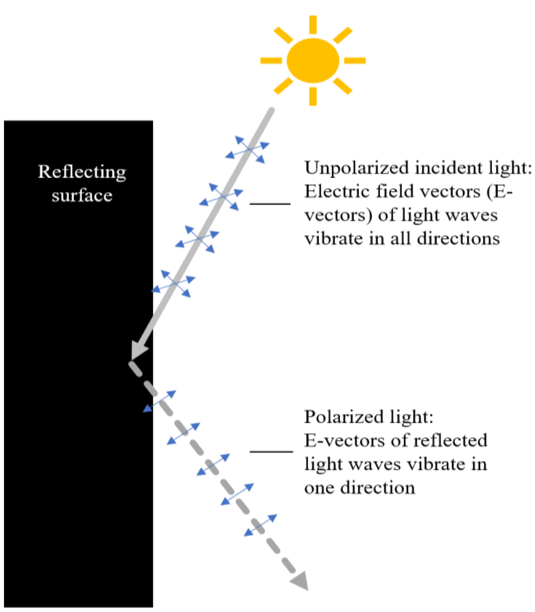


**Figure 2.1.** Example of how unpolarized incident light (e.g., sunlight) becomes polarized after reflecting off a surface.

In nature, the most common light-polarizing surface is water. However, any smooth, dark surface can polarize light, and human-built surfaces such as buildings, solar panels, and roads create *polarized light pollution* (PLP), which is analogous to ALAN in changing naturally occurring patterns of polarized light in ecosystems (Horváth et al. 2009). PLP is characterized by high degrees of polarization reflected at a horizontal angle, and several animal species perceive horizontally polarized light to locate water-associated breeding areas and food sources (Horváth et al. 2009). These species can be attracted to and entrapped by PLP; for example, aquatic insects like mayflies (Ephemeroptera) and caddisflies (Trichoptera) land in large numbers and attempt to oviposit on highly polarizing artificial surfaces like windows (e.g., Kriska et al. 2008, Malik et al. 2009, Robertson et al. 2010). Birds may also detect polarized light and use it as a navigational cue; specifically, migrating songbirds may use polarization patterns in the sky at twilight to calibrate their magnetic compass (Able and Able 1995, Cochran et al. 2004, Muheim et al. 2006, 2007, 2009). Very little research has assessed if birds are also attracted to polarized light reflected from natural or artificial surfaces, but anecdotally, water birds have been found dead or stranded at night on asphalt roads and parking lots that produce PLP by reflecting light from streetlamps (Horváth et al. 2009). Experiments also suggest that some songbirds are attracted to horizontal surfaces that polarize light (Easthausen 2015). Despite the potential for birds to perceive polarized light, no research has addressed whether PLP at buildings helps explain variation in bird collision rates.

We conducted bird collision monitoring at 48 building façades of 13 buildings in Minneapolis, Minnesota, USA, to assess if collisions are related to: (1) the emission of ALAN from windows at night, after accounting for glass area, and (2) the degree of polarized light reflected from building surfaces. We hypothesized collisions would be positively correlated with both ALAN and PLP due to their potential attraction and entrapment effects. As migratory bird populations have declined precipitously over the last several decades (Soykan et al. 2016), studying all potential factors contributing to mortality, including effects of ALAN and PLP on bird-building collisions, will improve understanding and mitigation of factors contributing to avian declines.

## Methods

### *Study Site and Building Selection*

We conducted this study in downtown Minneapolis, Minnesota, USA as part of a larger study investigating the factors influencing variation in collisions among buildings and through time. Downtown Minneapolis is a highly urbanized city center located adjacent to the Mississippi River and within the Mississippi Flyway, and large numbers of migratory birds use green spaces in this area as stopover habitat during both spring and fall (Homayoun and Blair 2015). For this study, we collected data from individual building façades, which we defined as discrete faces of buildings oriented in different directions. However, for some irregularly shaped buildings, we combined data from adjacent façades when we were unable to distinguish the façade at which collisions occurred. We also excluded some façades from analysis because we were unable to obtain reliable estimates of glass, ALAN, and/or PLP variables due to unusual façade characteristics (e.g., angled glass with setbacks, façades with multiple tiered levels that obstructed views of the entire façade). We ultimately collected data from 48 building façades that are part of 13 buildings, a subset of the 21 buildings we monitored for the other study. These 21 buildings were selected using several criteria to capture spatial variation and a range of expected collision numbers (see Loss et al., *in prep*). We only analyzed the subset of 13 buildings for this study because, in addition to the above façade-related limitations, security and access limitations prevented us from taking high-quality photos in close proximity to some buildings. Nonetheless, this study captured a variety of building types, including low-rises, high-rises, and a multi-use stadium (range: 5–57 floors), and a broad range of observed collisions and building characteristics (e.g., building surfaces, amount of glass).

*Collision Monitoring*

In 2017 and 2018, we surveyed buildings during spring migration (15 March to 31 May), late spring migration/early summer (1 Jun to 30 Jun), and fall migration (15 August to 31 October). Surveys began every morning at approximately sunrise. On a subset of dates, we also conducted additional mid-day and late afternoon surveys at all buildings to evaluate the number of bird collisions throughout the day. Following a standardized survey protocol adapted from Hager and Cosentino (2014), trained surveyors walked a fixed route and surveyed accessible portions of each façade. To account for time-of-day and lighting effects, surveyors began routes at different buildings each day and monitored buildings in a clockwise direction on even dates and a counter-clockwise direction on odd dates. During spring 2017, buildings were assigned to two separate fixed routes, and the start building for each route shifted to the next building in the sequence each day. Because surveyors were able to complete both routes within ~1.5–2.5 hours, we merged the routes starting in June 2017 and used a random number generator to select the start building each day.

For all birds found within ~5 m of a building façade, surveyors entered the date, time, location, species, and photos in an ArcGIS Online form. Most dead birds were placed in sealable plastic bags and stored in freezers. For birds found alive but stunned after colliding with a building, surveyors attempted to capture the bird when possible and place it in an unlined paper bag. Captured birds were later released in parks outside of the downtown area or brought to a rehabilitation center. Birds were collected under U.S. Fish & Wildlife Service Scientific Collecting Permit #MB05120C-1 and Minnesota Department of Natural Resources Salvage Permit #20412, and animal handling protocols were approved by the Institutional Animal Care and Use Committee at Oklahoma State University (#AG-17-6).

As part of the companion study, we left a subset of dead birds in place and attached a twist-tie around one leg to conduct scavenger removal trials, which quantified how long carcasses persisted before a scavenger or human removed them from the survey area (Hager et al. 2012, Bracey et al. 2016, Kummer et al. 2016b, Riding and Loss 2018). Scavenger removal trials and searcher detection trials (to account for imperfect detection of carcasses by surveyors; Bracey et al. 2016, Riding and Loss 2018) were used in the companion study to calculate bias-adjusted mortality estimates at each building. However, for this study of ALAN and PLP, we only considered unadjusted (i.e., raw) collision counts (including both fatal and non-fatal collisions) because we did not have enough replicates of scavenger removal and searcher detection trials at individual building façades to produce reliable bias-adjusted estimates at the façade level. We also removed from counts any birds that were potential skyway collisions (i.e., birds that may have collided with glass walkways connecting the monitored building façades) or parts of birds that may have resulted from predation events instead of collisions.

### *Measuring Artificial Light at Night*

Of note for the following variables, we treated windows and glass as different features; windows were considered areas of glass with openings behind them while glass included both windows and areas of glass without openings behind them. For each of the 48 building façades, we measured the surface area of windows lighted at night (hereafter: lighting area) and the proportion of all glass lighted at night (hereafter: lighting proportion). For lighting proportion, we divided lighting area by area of all glass surfaces because we expected collisions to be influenced by all types of glass. To generate these variables, we first calculated glass area by taking direct measurements of glass panes using a measuring tape whenever possible. When direct measurements were not possible, we photographed all building façades and used ImageJ (Schneider et al. 2012) and a known-dimension reference (e.g., one directly-measured edge of a glass pane) to calculate the area of every pane of glass. To measure ALAN and to capture night-to-night lighting variation, we photographed all building façades on three separate nights at least 1 hour after sunset but before midnight during the collision-monitoring season. Using these photos, we then counted the number of windows emitting any amount of light and calculated lighting area by summing the area of all lighted windows for each night and then averaging across all nights. Finally, we calculated lighting percentage by dividing average lighting area by glass area.

We also calculated several glass variables for each façade to account for correlations between lighting and glass and to compare their relative importance in predicting bird collisions. These glass variables included total glass area (sum of area of all glass panes), glass proportion (glass area divided by the area of each façade), maximum pane area (area of largest individual glass pane), and average pane area (average area of all glass panes).

*Measuring Polarized Light Pollution*

To measure PLP for each building façade, we used a manual polarimeter (Estrato R&D Ltd.), which consisted of a Canon EOS 650D DSLR camera and a Tamron 18–200 mm lens customized with a rotating polarized light filter. For each surface type on a façade (e.g., glass, brick, concrete), we captured a set of three images with the polarizer rotated to a different position for each image (176.9 degrees, 59.8 degrees, and 122.9 degrees). To capture the highest degree of polarization for each surface, we tilted the camera lens upward at an angle of approximately 56 degrees from horizontal, which is the angle at which light reflected from glass is maximally polarized (Brewster 1815). All photos were taken during the day between 0545 and 1400 hours in cloudy or overcast conditions to capture incident light scattered from multiple directions. Photos were then processed in Polarworks (Estrato R&D Ltd.), a program that combines the three images and generates a modified image displaying polarization characteristics for each surface in the photo (Fig. 2).

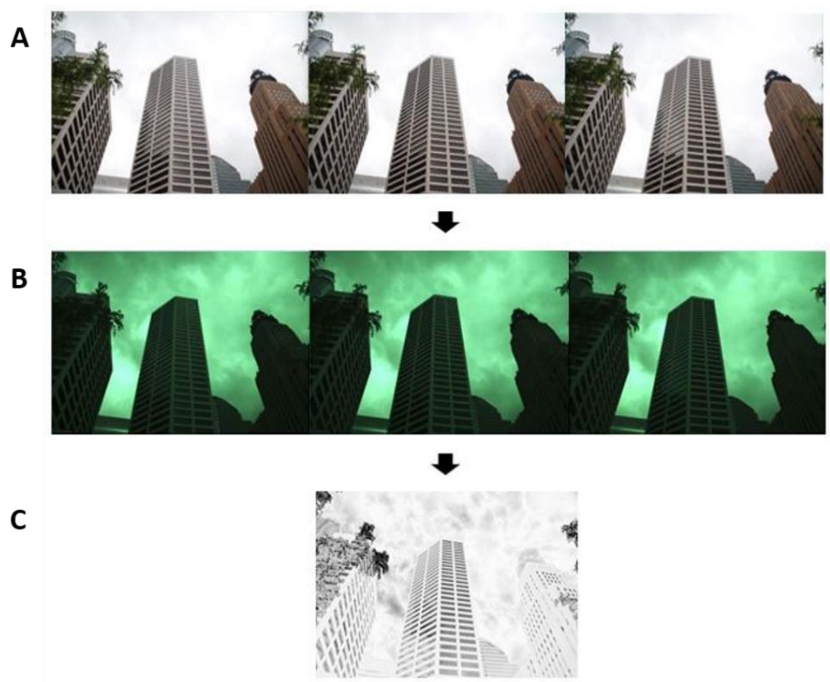


**Figure 2.2.** Steps for obtaining polarized light characteristics of buildings. A) Three photos were taken of every building façade, each with the polarizer rotated to a different position. B) Photos were uploaded to Polarworks (Estrato R&D Ltd.) and converted from RAW to TIF format. C) Polarworks combined the three photos and generated an image depicting polarization characteristics; this image shows the degree of polarization with darker areas indicating surfaces with high degrees of polarization and lighter areas indicating surfaces with low degrees of polarization.

Using ImageJ and the modified images from Polarworks, we quantified PLP metrics for each façade. We changed images to 8-bit format and used the Polygon Selections tool to draw a polygon on each façade surface of interest. We then used the Measure tool to generate mean pixel intensity in the range of 0 to 255, where 0 indicates pure black and 255 indicates pure white. We repeated this process several times for each surface of interest to ensure consistent measurements. By dividing the mean pixel intensity by 255 and multiplying by 100, we obtained the percentage of "whiteness" of each selected area. We subtracted this result from 100 to calculate the degree of polarization of each surface, represented by the percentage of "blackness" of the pixels in the selected area. We then calculated the overall degree of polarization for each building façade by estimating the percentage of each façade surface using ImageJ and multiplying the percentage of each surface by its degree of polarization to generate a weighted average (hereafter: polarization index) that ascribes greater weight to surfaces comprising a larger portion of the façade. In addition to polarization index, we measured three other polarized light variables for each façade: the degree of polarized light reflected from the most-polarizing surface, which was glass in most cases (hereafter: maximum polarization), the degree of polarized light reflected from the least-polarizing surface (hereafter: minimum polarization), and the difference between the maximum and minimum degrees of polarization (hereafter: polarization contrast).

*Statistical Analysis*

All analyses were conducted in R 3.5.2 (R Core Team 2018). To determine which variables to formally analyze, we first tested whether there were any highly correlated pairs of variables among glass variables (glass area and proportion, and maximum and average pane area), ALAN variables (lighting area and proportion), and PLP variables (polarization index, maximum and minimum polarization, and polarization contrast). Only polarization contrast and minimum polarization were highly correlated ($r > |0.7|$). Because Akaike's Information Criterion adjusted for small sample sizes (AICc; Burnham and Anderson 2002) showed minimum polarization to be a better predictor of collisions than polarization contrast (Table 3), we excluded polarization contrast from further analyses.

We used R package *lme4* (Bates et al. 2015) to construct generalized linear mixed models (GLMM) with unadjusted collision counts as the response variable, the above ALAN and PLP variables as fixed effects, and building as a random effect to account for non-independence of individual façades nested within the same building. We also included an offset term for the number of collision surveys conducted at each façade to account for varying effort that arose due to occasional access restrictions (e.g., construction and public events). Because the collision count data were overdispersed, we used negative binomial GLMMs. To evaluate the importance of each ALAN and PLP variable, we constructed a model including additive effects of all five ALAN and PLP variables and conducted a likelihood ratio test using function 'drop1'. We validated the result by constructing models with all additive combinations of lighting and polarized light variables and comparing model fit using AICc. Finally, to evaluate the importance of ALAN and PLP variables relative to glass variables, we used AICc to compare fit of all single-variable models.

## Results

We observed 768 fatal and non-fatal bird collisions at the 48 surveyed façades (range: 0–194 per façade). Based on likelihood ratio tests, we found that lighting area and lighting proportion had statistically significant positive associations with numbers of collisions, with lighting area as the most informative predictor, and that polarized light variables were unassociated with collisions (Table 2.1, Fig. 2.3). This result was supported by the AICc rankings of all possible additive models containing ALAN and PLP variables (Table 2.2); specifically, the top model included positive effects of lighting proportion and average lighting area, no PLP variables, and had an AICc weight roughly five times greater than the next best model.

**Table 2.1.** Results of likelihood ratio test (LRT) with single-term deletions of polarized light and artificial night lighting variables. Differences in AIC values between the full model ("None") and other models represent the change in AIC associated with dropping the variable from the full model; thus, higher AIC values represent greater reduction in model support with exclusion of the focal variable. Asterisks in the right column represent statistically significant variables.

| **Variable dropped** | **AIC** | **LRT** | **p (chi)** |
|---|---|---|---|
| None | 295.06 | | |
| Polarized light index | 293.09 | 0.0331 | 0.85571 |
| Maximum polarization | 293.15 | 0.0879 | 0.76683 |
| Minimum polarization | 294.46 | 1.3980 | 0.23706 |
| Lighting proportion | 299.63 | 6.5709 | 0.01037 * |
| Average lighting area | 315.89 | 22.8270 | 1.773e-06 * |

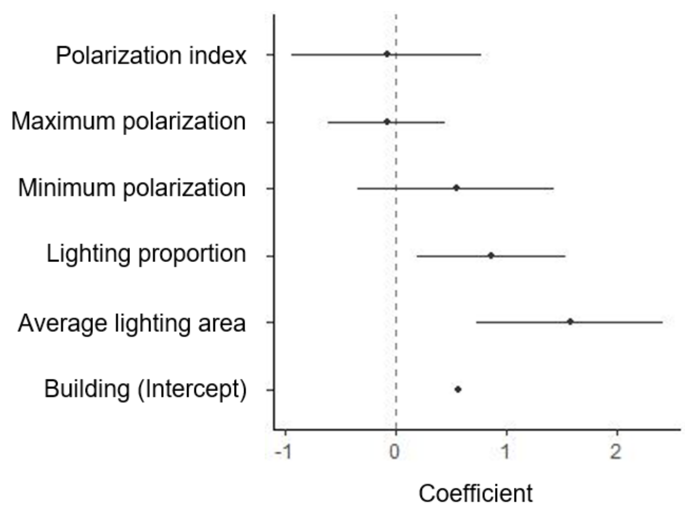


**Figure 2.3.** Dot-whisker plot of fixed effects of polarized light and artificial night lighting variables. Variables were included in a negative binomial GLMM with building as a random effect and number of surveys as an offset term.

**Table 2.2.** Model selection results for analysis of bird-building collisions in relation to artificial night lighting (lighting proportion, average lighting area) and polarized light variables (polarization index, maximum polarization, minimum polarization). All models were negative binomial GLMMs with building as a random effect and number of surveys as an offset term. Only models that do not include uninformative parameters and performed better than the null model are shown.

| Model | AICc | ΔAICc | df | Weight |
|---|---|---|---|---|
| Lighting proportion + Average lighting area | 292.2 | 0 | 5 | 0.83 |
| Average lighting area | 295.4 | 3.2 | 4 | 0.17 |
| Lighting proportion | 310.7 | 18.5 | 4 | <0.001 |
| Null | 317.6 | 25.4 | 3 | <0.001 |

AICc comparisons of all single-variable models for ALAN, PLP, and glass variables showed that lighting area was the best predictor of collisions, followed by average pane area (Table 3). No other single-variable ALAN and window area models were competitive, having ΔAICc ≥ 7 but performing better than the null model. All of the single-variable polarized light models had ΔAICc > 22 and ranked behind the null model.

**Table 2.3.** AICc table comparing fit for all single-variable negative binomial GLMMs with building as a random effect and number of surveys as an offset term.

| Model | AICc | ΔAICc | df | Weight |
|---|---|---|---|---|
| Average lighting area | 295.4 | 0 | 4 | 0.695 |
| Average pane area | 297.2 | 1.8 | 4 | 0.283 |
| Maximum pane area | 302.3 | 7.0 | 4 | 0.021 |
| Total glass area | 310.3 | 15.0 | 4 | <0.001 |
| Lighting proportion | 310.7 | 15.3 | 4 | <0.001 |
| Glass percentage | 316.7 | 21.3 | 4 | <0.001 |
| Null | 317.6 | 22.2 | 3 | <0.001 |
| Minimum polarization | 318.2 | 22.8 | 4 | <0.001 |
| Maximum polarization | 319.7 | 24.3 | 4 | <0.001 |
| Polarization index | 319.8 | 24.4 | 4 | <0.001 |
| Polarization contrast | 319.9 | 24.5 | 4 | <0.001 |

## Discussion

This was the first study to simultaneously evaluate how bird-building collisions are influenced by two different types of light pollution: artificial light at night (ALAN) emanating from building windows and polarized light pollution (PLP) reflected from artificial building surfaces including glass. Our results provide the first evidence that ALAN emanating from building windows correlates with bird-building collisions independent of glass area. Specifically, we found that the area of lighted windows and proportion of glass lighted at night were important predictors of collisions, and that lighting area in particular was a better predictor than total glass area, glass percentage, and the maximum and average sizes of glass panes. However, we did not find any evidence for an effect of polarized light pollution on collisions.

Previous studies that found a relationship between collisions and ALAN at the level of entire buildings analyzed a light index that was calculated by multiplying percent lighting by the number of floors in each building to account for building size (Evans Ogden 2002, Keyes and Sexton 2014, Parkins et al. 2015). However, these studies did not or were unable to parse apart the effects of lighting and glass because the light index was strongly correlated with percent glass. We found that, at the level of individual building façades, lighting variables were not highly correlated with any glass variables, suggesting that these factors may vary independently when analyzed at the façade level instead of the building level. Indeed, a companion study assessing building-level collision correlates analyzed lighting area at the building scale for all 21 study buildings and found a stronger correlation between lighting area and glass area (Loss et al. *in prep*). These differences between façade- and building-level results suggest that analyses focusing on individual façades may reveal additional predictors of collisions that have not yet been identified at larger scales. Our finding that lighting area was a significant predictor of collisions independent of glass area also suggests that lighting could at least partially contribute to the frequently identified importance of glass area in many past studies (Hager et al. 2013, 2017, Schneider et al. 2018). However, we expect the reflective and/or transparent properties of glass to also influence collisions independent of lighting, especially for bird collisions that occur during the daytime when ALAN effects are minimal.

We also found that in addition to lighting area, lighting proportion was an important predictor of collisions. Depending on façade size and glass area, lighting proportion represents different amounts of light emitted from each façade, and therefore, the mechanism for the effect of lighting proportion on collisions is uncertain. We hypothesize that higher proportions of lighting may represent lighted windows occurring closer together (Loss et al. *in prep*), which could create more contiguous areas of lighting that likely play a greater role in attracting birds than isolated windows emitting light. Hence, our results may indicate that buildings with both large areas of lighted windows and high proportions of lighted glass are especially dangerous for birds, attracting and killing migrating birds to a greater degree than buildings with smaller, less contiguous areas of lighted glass. Further research investigating these and other metrics of ALAN emission from building windows, including metrics that more explicitly capture lighting and glass contiguity (e.g., fragmentation indices commonly used in spatial ecology), may help clarify mechanisms for the role of lighting in bird-building collisions.

Our finding that ALAN was an important predictor of bird-building collisions at individual building façades has important implications for management efforts designed to reduce this threat to bird populations. By quantifying the relative effect of ALAN compared to other potential collision correlates, we provide a stronger, data-supported argument for building managers to turn off lights and/or shade windows at night during spring and fall migration to reduce collisions. Along with past research, these results provide evidence that significant reductions in bird-building collisions may be achieved by implementing a combination of measures that reduce ALAN emitted from windows, break up reflections from and reduce transparency of glass, and focus mitigation steps on glass near existing vegetation (Gelb and Delacretaz 2009, Klem et al. 2009, Kummer et al. 2016a, Schneider et al. 2018). Notably, we only quantified the area of glass that appeared to be lit from the building's interior and lacked the equipment necessary to analyze other properties of artificial night lighting (e.g., color and intensity), or other sources of light, such as bright lights emanating from the top or outside surfaces of buildings or from ground-based lighting features near buildings. Because previous studies have shown that shutting off high-intensity exterior lights virtually eliminates disruptive effects on nocturnally migrating birds (Van Doren et al. 2017) and that different types of lights with varying spectral properties (e.g., wavelengths, colors) have differential effects on various wildlife taxa (Longcore et al. 2018), future collision studies should also evaluate exterior building lighting and the direction, intensity, and spectral characteristics of lighting. Such studies will be especially important as building managers and municipalities increasingly adopt high-efficiency light-emitting diodes (LEDs), which typically produce light with short wavelengths that increase sky glow (i.e., reduced night-sky visibility caused by atmospheric scattering of light; Luginbul et al. 2014, Kinzey et al. 2017). Furthermore, decreasing costs of energy consumption associated with LEDs allow for increased installation of lighting in areas that were previously unlit (Kyba et al. 2017), potentially exacerbating the effects of ALAN on migrating birds.

We found no associations between bird-building collisions and any of the variables we measured to quantify the degree of polarized light reflected from buildings. This result suggests that collisions may not be driven by avian responses to PLP. However, the strong effect of artificial night lighting in our analysis may overwhelm any effect of polarized light at any time of day. Specifically, because PLP can occur both during the day and at night—and because artificial light sources are known to diminish polarized light signals (Kyba et al. 2011)—ALAN emanating from the interior of windows at night likely reduces polarized light reflected from the exterior of these windows. Because ALAN reduces the effect of PLP at night, additional research to assess both types of light in a more controlled manner may be beneficial in parsing apart their effects and confirming our negative result of PLP being unassociated with bird collisions. One potential approach to separately evaluate PLP's effects could be to assess it only in relation to bird collisions that occur during the daytime and near twilight, when the effect of ALAN is reduced and polarized light signals may be stronger. Another potential approach could entail focusing only on collisions of bird species that are likely to respond to polarized light, such as songbird species for which evidence exists of the potential use of polarized light as a navigational cue (e.g., White-throated Sparrow [*Zonotrichia albicollis*; Muheim et al. 2009] and Savannah Sparrow [*Passerculus sandwichensis*; Able and Able 1995, Muheim et al. 2006, 2007]). However, as few studies have experimentally determined which species detect and respond to polarized light, additional research is necessary to understand avian perception of polarized light and responses to PLP in order to design rigorous studies of the relationship between polarized light and collisions for specific bird species.

Although we found no evidence that PLP affects collisions, reducing PLP should change other properties of glass in ways that reduce collisions. One study showed that replacing completely reflective solar panels with those covered by white, non-polarizing grid patterns reduced the attractiveness of panels to insects that respond to and are entrapped by PLP (Horváth et al. 2010). Hence, adding contrasting, non-polarizing patterns to glass surfaces and using smaller panes should reduce the degree of polarized light reflected from buildings and also break up reflections of visible light that make glass dangerous for birds, especially since this study and previous studies have shown that sizes of individual panes influence collisions (Kahle et al. 2016, Nichols 2018). Additionally, designing buildings with higher proportions of low-polarizing surfaces, such as brick, will reduce the amount and proportion of glass with which birds can collide. In addition to benefitting birds, reducing PLP should also have broader ecosystem impacts due to its known entrapment effects on aquatic insects, as described above.

## Conclusion

Using data from 48 façades at 13 different buildings, we showed that two variables capturing artificial lighting at night (ALAN), specifically area of windows lighted and proportion of glass lighted, were important predictors of bird-building collisions. This is the first study to demonstrate an association between bird-building collisions and ALAN after accounting for the effect of glass area. This finding provides strong support for recommendations to turn off lights or pull down window shades at night to help reduce bird collisions during the spring and fall migration seasons. Although we found no support for a relationship between artificially polarized light (i.e., polarized light pollution; PLP) and collisions, additional research is needed to better understand avian perception and responses to polarized light and to parse apart the effects of ALAN and PLP on bird-building collisions. Nevertheless, reducing the effects of PLP, for example by adding patterns to reflective surfaces, should also reduce the reflective properties of glass known to affect collisions. Because both ALAN and PLP have negative effects on many wildlife species, reducing both types of light pollution could produce far-reaching benefits for birds, insects, and other organisms.

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VITA

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Major Field: Natural Resource Ecology & Management

Biographical:

Education:

Completed the requirements for the Master of Science in Natural Resource Ecology & Management at Oklahoma State University, Stillwater, Oklahoma in May, 2019.

Completed the requirements for the Bachelor of Science in Environmental Science at University of California, Los Angeles, California in 2012.

Experience:

Program Assistant, Travis Audubon Society, Austin, TX (2015-2017)
Laboratory Manager, UCLA Center for Tropical Research, Los Angeles, CA, (2012-2015)
Field Assistant, UCLA Institute of the Environment and Sustainability, WA (2012)

Professional Memberships:

American Ornithological Society
The Wildlife Society