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Inclement weather and American woodcock building collisions during spring migration

Scott R. Loss, Sirena Lao, Abigail W. Anderson, Robert B. Blair, Joanna W. Eckles and Reed J. Turner

S. R. Loss (https://orcid.org/0000-0002-8753-2995) ✉ (scott.loss@okstate.edu) and S. Lao, Dept of Natural Resource Ecology and Management, Oklahoma State Univ., 008C Ag Hall, Stillwater, OK 74078, USA. – A. W. Anderson and R. B. Blair, Dept of Fisheries, Wildlife and Conservation Biology, St. Paul, MN, USA. – J. W. Eckles and R. J. Turner, Audubon Minnesota, St. Paul, MN, USA. JWE also at: The Raptor Center, College of Veterinary Medicine, Univ. of Minnesota, St. Paul, MN, USA.

Weather appears to influence collisions of migratory birds with human-built structures including buildings, but formal analyses are lacking. In 2018, as part of a two-year study at 21 buildings in Minneapolis, Minnesota, USA, we observed a large number of American woodcock *Scolopax minor* collisions during two early spring snowstorms. We describe these events, analyze associations between weather and woodcock collisions during spring 2018, and compare observations to past studies across the woodcock's range. Most spring 2018 woodcock collisions (11 of 15; 73.3%) occurred in association with the two snowstorms. Analyses indicated collisions were positively associated with maximum and average wind speeds the night before collision surveys, and most collisions occurred with north winds. Collisions also increased with lower cloud base height two nights before surveys. These results support that woodcock collisions were greatly influenced by inclement weather, specifically the coincidence of strong north wind and low clouds. Comparing results to past studies illustrates that building collisions could be a major range-wide source of woodcock mortality, especially in spring migration when mortality is likely additive. Although more research is needed to understand range-wide, population-level effects of woodcock collisions, management to reduce building collisions during migration may benefit woodcock populations. Additional research is needed to clarify effects of weather on bird collisions because management efforts could be refined if collisions of woodcocks and other bird species were forecastable like the weather.

Keywords: American woodcock, artificial lighting at night, bird collision, bird–building collision, bird–window collision, migration, urban ecology, weather

Weather and climate play crucial roles in the lives of migratory birds (Alerstam 1990, Gordo 2007). Along with climate averages, weather extremes such as intense storms and abnormally hot, cold, dry or wet conditions, have strong implications for bird behavior, reproduction and survival (Parmesan et al. 2000, Kozlovsky et al. 2018). Storms in particular can cause catastrophic reproductive failure and mass fatality events that may affect population abundance and even threaten species persistence (Butler 2000, Newton 2007, Pearce-Higgins and Green 2014).

Storms and inclement weather may also increase susceptibility of migratory birds to human-related stressors like light pollution and collisions with structures (Rich and Longcore 2006, Newton 2007). Heavy precipitation, strong winds, fog and low clouds – often interacting with disorienting effects of artificial light at night – cause large numbers of migrating birds to fly at lower altitudes or to be grounded, leading many to collide with structures such as offshore oil platforms, lighthouses, communication towers and wind turbines (Kemper 1996, Johnson et al. 2002, Jones and Francis 2003). Building collisions, particularly collisions with windows, are the largest source of bird collision mortality in North America (Loss et al. 2014) and also appear to be influenced by inclement weather (Evans Ogden 1996). However, except for descriptive accounts of storms causing large numbers of birds to collide with a variety of structures including buildings (Roberts 1907, Johnston and Haines 1954), no published studies specifically describe bird–building collision events in association with inclement weather or include formal analyses linking weather to bird collision rates.

In spring 2018, we documented a large number of American woodcock *Scolopax minor* collisions while conducting a two-year study at 21 buildings in Minneapolis, Minnesota, USA. Initial observations suggested most collisions were associated with two major snowstorms during the peak of woodcock migration in the region. This mortality

is of conservation concern because the American woodcock has undergone a long-term population decline across its range in eastern North America (Seamans and Rau 2018, Saunders et al. 2019), and the mortality was surprising because it occurred in spring when most migratory birds experience fewer collisions relative to fall (Loss et al. 2015). Spring mortality is a management concern because it occurs immediately before the breeding season, when relatively little time exists for population-level processes (e.g. positive density-dependent survival) to compensate for mortality and minimize declines in the abundance of breeding individuals (Boyce et al. 1999). Here, we describe the unusually large number of woodcock collisions observed in our study; conduct a statistical analysis to determine if variables reflecting inclement weather (precipitation, wind, cloud base height) explain daily collision observations; and, to provide context for our observations, compare them to a previous 10-year study in Minneapolis and 14 other collision studies in eastern North America.

Material and methods

We monitored for bird collisions at 21 buildings in downtown Minneapolis, Minnesota, which is adjacent to the Mississippi River and part of the Minneapolis-St. Paul (i.e. Twin Cities) metro area (population: ~3.1 million people). Due to funder interests, our study focused on a large multi-use stadium, and we included 20 other buildings as a comparison for bird collision rates (building comparisons are beyond the scope of this paper and covered in Loss et al. 2019). Of the 20 comparison buildings, we selected 16 from a set of 64 that were monitored from 2007 to 2016 for Project BirdSafe (Zink and Eckles 2010). Due to objectives of the companion study comparing collision rates among buildings, we sought to capture a sample of buildings with a range of bird collision rates. Therefore, the sample we selected was not completely random; instead, we grouped the 64 buildings into quintiles based on total bird collisions in the earlier study. From each quintile, we randomly selected three buildings (15 total) with the constraints that 50–100% of building perimeters were accessible and that selected buildings captured a spatial cross-section of the downtown area. We later selected one additional building from the fifth quintile (80th–100th percentile of collisions) because part of one selected building from this quintile was temporarily inaccessible in spring 2017 (yet we continued monitoring the rest of that building). Because the stadium was spatially separate from these 16 comparison buildings, we also selected four previously unmonitored buildings within 0.5 km of the stadium and under the same access constraint as above. The final set of 21 buildings ranged from 2 to 57 stories tall and included hotels, apartment complexes and commercial office buildings.

In 2017 and 2018, daily collision monitoring was conducted at all buildings during spring (15 Mar–31 May) and fall migration (15 Aug–31 Oct). One day before each season, 'clean sweep' surveys were conducted in which we removed existing bird carcasses and remains to avoid counting birds from non-surveyed periods. Each survey entailed walking a fixed route among all 21 buildings starting at approximately sunrise. The route started at a different building each day to account for time-of-day effects, and the direction in which each building circumference was monitored alternated between a clockwise and counter-clockwise direction on even and odd dates, respectively, to account for directional effects. Trained technicians and the authors searched for birds within ~5 m of each building. For all carcasses and remains (e.g. feather piles, wings, feet), close-up photos were taken, the nature of injuries was noted, the location was marked on a map, and carcasses and remains were placed in plastic bags and stored in a freezer until the authors confirmed species identification. Dead woodcocks with fully-intact carcasses were assumed to be collision victims based on their location near a building and observation of visible injuries consistent with collision (blood in the mouth cavity; a fractured or damaged bill; and/or evidence of other skeletal fractures; Veltri and Klem 2005). For purposes of analysis, we also assumed that dead woodcocks with only partial remains (e.g. feet, heads or decapitated bodies) found within 5 m of buildings were collision victims that were subsequently depredated or scavenged; however, in the Results, we describe a test of this assumption that recognizes some partial remains could have resulted from predation events, not collisions.

When we found a live woodcock near a building, we approached it slowly, and if it did not fly away, attempted to catch it by hand and place it in an uncoated paper bag. All captured stunned birds in this paper recovered sufficiently to be released after the day's survey. We assumed live birds were victims of non-fatal collisions, not physiologically stressed birds that had been grounded by inclement weather and/or were seeking shelter near buildings without experiencing a collision. In support of this assumption, we directly observed one of the live woodcocks colliding with a building prior to our approaching it, and all three live birds were found at buildings and building façades where we also found either dead woodcocks or fatal collisions of a variety of other bird species (Loss et al. 2019).

For spring 2018, which included 15 of 19 (78.9%) woodcock collisions in our study, we analyzed associations between weather variables reflecting inclement weather and the total number of woodcock collisions observed on a daily basis across all 21 buildings (i.e. unit of replication = total woodcock collisions per day; n = 78 days). We did not include other years in the analysis because relatively few woodcock collisions occurred outside of spring 2018 (a mean of two collisions each spring in the Project Birdsafe study and four total collisions across the three other seasons in this study), which would have resulted in an exceptionally high proportion of zero observations and complications in fitting statistical models. Further, the set of buildings monitored varied between the earlier and current studies (i.e. five previously unmonitored buildings in the current study), which limits comparisons among years.

We used hourly weather data from Minneapolis-St. Paul International Airport, 11 km south of our study area (NOAA 2019), to generate candidate predictor variables for average wind speed, maximum wind speed, minimum cloud base height, snowfall and total precipitation. Because most building collisions in downtown areas occur overnight or in the early morning (Evans Ogden 1996), all weather variables except snowfall were calculated for the overnight period before each survey (i.e. one hour before sunset the evening prior to one hour after sunrise the morning of surveys).

We calculated minimum cloud base height because ceilometer data (and thus direct measures of cloud ceiling height) were unavailable; we estimated cloud base height by dividing the difference between air temperature and dew point at ground level by 400 (FAA 2016). Because hourly snowfall data were unavailable, we used total snowfall for the date of each survey (i.e. midnight to midnight the day of the survey). For all five weather-related factors, we also generated variables reflecting one- and two-day lag effects to determine if collisions were associated with weather conditions two and three nights before surveys (for average and maximum wind, total precipitation and cloud base height) or one and two days before surveys (for snowfall). We assumed such time lag effects were possible based on past field observations and analyses (Lao 2019) suggesting bird–building collisions can be influenced up to two days after a weather event. For example, passage of a strong cold front and its associated north winds during spring may cause large numbers of northward-migrating birds to be grounded in an area for multiple days; thus collision rates may be elevated for greater than one day after the weather event. To summarize, we generated a total of fifteen candidate predictor variables (a no time lag variable and one- and two-day lag effects for each of five weather-related factors). Most of these variables were not strongly correlated (Pearson's $r < 0.7$), with the exception of average and maximum wind speed, which were always correlated with each other for the same time period (e.g. average wind speed two nights before was correlated with maximum wind speed two nights before; $r = 0.90$) but never between time periods (e.g. average wind speed two nights before was not correlated with average wind speed three nights before; $r = 0.31$) (Supplementary material Appendix 1 Table A1).

We conducted all analyses in R ver. 3.6.1 (<www.r-project.org>). We conducted several preliminary analyses to determine which type of model to use to assess weather effects on collisions. First, we tested for potential temporal autocorrelation in the data set by comparing: 1) a simple linear model ('lm' function in R's base statistics package) with woodcock collisions as the response variable and date as a numerical predictor, and 2) a similar generalized least squares (GLS) regression model ('gls' function in 'nlme' package; Pinheiro et al. 2019) that included specification of a first-order, autoregressive correlation structure for date. Model comparison using Akaike's information criterion (AIC) indicated the GLS model did not greatly improve on the simple linear model, so we did not further consider temporal autocorrelation. Second, we assessed whether to use a Poisson or negative binomial distribution to model collision count data because of the relatively small sample size ($n = 78$) and potential overdispersion; a likelihood ratio test based on an intercept-only model (with daily woodcock counts as the response variable) indicated no support for a negative binomial model improving on a Poisson model ($\chi^2 = 1.96$; $df = 2$; $p = 0.16$), so we used the latter (however, we also assessed sensitivity of our results to this decision by re-running analyses with negative binomial models). Third, because we found zero woodcocks on 65 of 78 (83.3%) days, we assessed whether a zero-inflated model was appropriate using a Vuong test (Vuong 1989); all test statistics indicated there was no support for a zero-inflated model improving on a standard Poisson model (Raw z-statistic = −0.49; AIC-corrected z-statistic = 0.14; BIC-corrected z-statistic = 0.89; all p-values > 0.19); thus, we used standard Poisson generalized linear models (GLMs) for the following analyses.

We conducted model selection using a two-step process. First, we ran a null (i.e. intercept-only) model and single-variable models for all 15 weather variables, and we compared these models using AIC corrected for small sample sizes (AICc). Second, for variables in models with $\Delta AICc \leq 2$, we constructed two-variable additive models and ranked these along with single-variable models. We did not consider interaction models, or additive models with more than two variables, because the above procedure resulted in only two single-variable models with $\Delta AICc \leq 2$, and therefore only a single two-variable model being ranked. Notably, this two-variable model contained an uninformative parameter; in other words, it varied from the model ranking ahead of it by only including one additional parameter and having $\Delta AICc$ within two of that higher model (Arnold 2010). This indicates minimal support for drawing inferences from models with two or more variables, so we focused on single-variable models only.

We also descriptively compared numbers of woodcock collisions to Project BirdSafe counts for Minneapolis (2007–2016), to 13 studies (in 11 North American cities) reviewed in Loss et al. (2014) (Table 1), and to a Fall 2014 study of 281 buildings on 40 college/university campuses across North America (including 33 campuses in or near the woodcock's geographic range) (Hager et al. 2017). Project BirdSafe methods are covered elsewhere (Zink and Eckles 2010); however, of relevance to our comparison, spring and fall migration monitoring dates exactly matched dates for the current study. Sampling dates and monitoring protocols were highly variable among the other studies (details in Loss et al. 2014, Hager et al. 2017). For all studies, we tabulated numbers of years and buildings monitored and average, minimum and maximum counts of woodcock collisions for spring and fall migration periods.

Results

Across 21 buildings in spring and fall of 2017–2018, we found 19 American woodcocks, including 16 carcasses or remains and three non-fatally injured (i.e. stunned) birds. Of these, 15 woodcocks (12 carcasses/remains; three stunned birds) were found in spring 2018 at eight buildings (range for these buildings = 1–4 collisions). Six of the spring 2018 observations were partial remains (feet, heads or decapitated bodies), indicating collision casualties that were scavenged or live birds that were depredated near buildings (i.e. not killed by collision), for example by peregrine falcon *Falco peregrinus*, a species often observed during surveys. A large proportion (11 of 15; 73.3%) of spring 2018 collisions occurred around the dates of the two snowstorms (Fig. 1). The first storm occurred from 29 March to 3 April and resulted in ~30 cm of snowfall at Minneapolis-St. Paul International Airport. During this period, we found seven woodcock collisions on surveys and three woodcocks off the survey route that were not included in counts or analyses. The second storm occurred from 13 to 16 April, dropped ~40 cm of snow, and resulted in four woodcock collisions on surveys

Table 1. Seasonal totals of American woodcock building collisions in the current study in Minneapolis, Minnesota (2017–2018), in the same area for a previous study, for 13 studies in downtowns of 11 North American cities (data from Loss et al. 2014), and for a study of 281 buildings on 40 college/university campuses in North America (Hager et al. 2017). Data from Loss et al. (2014) meet that study's inclusion criteria for a species vulnerability analysis at buildings ≥ 12 stories tall, except we excluded a study from Calgary, Canada, for being outside the woodcock range and included a study for Washington, DC, that included buildings up to 11 stories.

Location	Years	No. of buildings[a]	Average spring collisions (range)	Average fall collisions (range)	Source[b]
Minneapolis, Minnesota	2017–2018	21	8.0 (1–15)	1.5 (1–2)	current study
Minneapolis, Minnesota	2007–2016	?	2.1 (0–4)	0.7 (0–2)	Project Birdsafe
Atlanta, Georgia	2005	53	–	0 (0–0)	Sexton 2006
Baltimore, Maryland	2008–2012	16–48	4.6 (2–12)	2.4 (0–4)	Lights Out Baltimore
Chicago, Illinois	2002–2012	?	32.7 (2–75)	16.9 (0–76)	Chicago Bird Collision Monitors
Chicago, Illinois	1978–2012	1	6.3 (1–17)	2.9 (1–14)	McCormick Place
Indianapolis, Indiana	2009–2010	48	0 (0–0)	1.0 (0–1)	Lights Out Indy
Milwaukee, Wisconsin	2007–2011	?	0.4 (0–2)	0.2 (0–1)	Wisconsin Night Guardians
New York, New York	2009–2011	17–31	1.0 (0–2)	0.7 (0–1)	Project Safe Flight New York
New York, New York	2006–2007	?	0 (0–0)	2.0 (2–2)	Klem et al. 2009
Philadelphia, Pennsylvania	2008–2011	10	0 (0–0)	0.8 (0–3)	Pennsylvania Audubon
Toronto, Ontario	2000–2010	74–194	21.8 (8–30)	11.8 (7–19)	Fatal Light Awareness Program
Toronto, Ontario	1967–1969	1	–	0 (0–0)	Ranford and Mason 1969
Washington, DC	2010–2012	21–38	2.0 (1–4)	1.0 (0–3)	Lights Out DC
Winston-Salem, N. Carolina	2011–2012	16	0 (0–0)	0 (0–0)	Lights Out Winston-Salem
40 college/university campuses	2014	281	–	0 (0–0)	Hager et al. 2017

[a] Number of buildings monitored; for studies other than the current study, this number was estimated based on average of potential minimum and maximum numbers (Loss et al. 2014); range indicates year-to-year variation in number of buildings monitored.
[b] Data from most sources are unpublished (except Ranford and Mason 1969, Sexton 2006, Klem et al. 2009, Hager et al. 2017); further details regarding these data sources can be found in Loss et al. (2014), and in some cases, on organization websites.

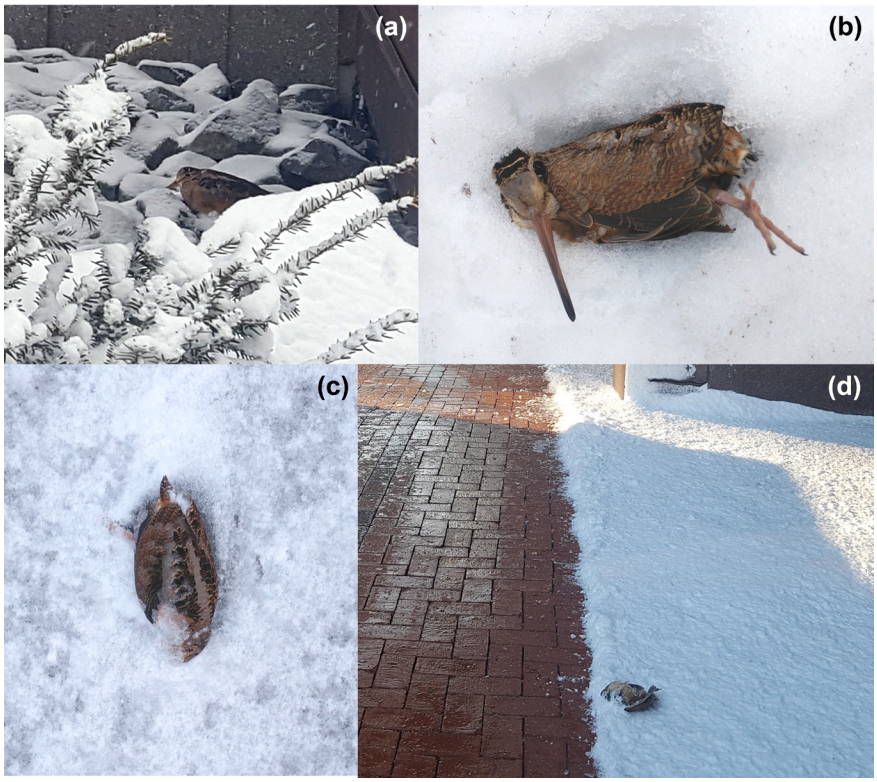

Figure 1. American woodcocks found during building collision monitoring at 21 buildings in spring 2018 in downtown Minneapolis, Minnesota, USA. All individuals shown were found during major early-spring snowstorms that affected the study region during the peak of woodcock migration (late March to mid-April). The woodcock in (a) was non-fatally injured (i.e. stunned) and woodcocks in (b–d) were encountered dead.

during or within two days after the storm. This latter storm resulted in the largest April snowfall ever recorded for most of the region and the second largest snowfall in history (up to ~80 cm) for adjacent areas of Wisconsin (NWS 2018).

The formal analysis supported observations regarding the association between inclement weather and collisions (Supplementary material Appendix 1 Table A2). When using Poisson models and including all 15 woodcocks from spring 2018, we found strong support for single-variable models with average wind speed ($\Delta AICc = 0.00$; $\omega_i = 0.36$) and maximum wind speed ($\Delta AICc = 1.27$; $\omega_i = 0.19$) the night before surveys; collisions were positively associated with both of these variables (average wind: $\beta \pm 95\%$ CI $= 0.16 \pm 0.10$; maximum wind: $\beta \pm 95\%$ CI $= 0.12 \pm 0.08$). There was marginal support ($\Delta AICc = 3–4$; $\omega_i = 0.05–0.06$) for models with minimum cloud base height two nights before surveys (i.e. a one-day lag effect) and maximum wind speed, average wind speed and minimum cloud base height three nights before surveys (i.e. two-day lag effects). These models indicated that collisions increased with increasing wind speed and lower clouds (maximum wind two-day lag: $\beta \pm 95\%$ CI $= 0.10 \pm 0.08$; average wind two-day lag: $\beta \pm 95\%$ CI $= 0.12 \pm 0.10$; both cloud height variables: $\beta \pm 95\%$ CI $= -0.001 \pm 0.0006$). The two-variable model including both average and maximum wind speed the night before also received marginal support ($\Delta AICc = 2.15$; $\omega_i = 0.12$); however, average wind speed was an uninformative parameter, indicating that this two-variable model does not improve on the single-variable models under the principle of parsimony.

To test the robustness of results to our decision to use Poisson models and include potential predation events, we re-ran analyses twice: first using negative binomial models with all 15 collision records included, and second using Poisson models but including only the nine intact woodcock carcasses. When using negative binomial models, the same two models received strong support, and the same four models received marginal support (Supplementary material Appendix 1 Table A3). When using Poisson models excluding potential predation events, the same two models received strong support, albeit in reverse-order (Supplementary material Appendix 1 Table A4). Further, three of the same four models received marginal support, with the only difference being that the model with the one-day lag effect of maximum wind speed replaced the model with the two-day lag effect of minimum cloud base height. For both sets of re-analyses, the two-variable model with average and maximum wind speed the night before again received marginal support, but with maximum wind speed as an uninformative parameter. Thus, our results are not greatly influenced by the choice to use Poisson models and include potential predation events in analysis.

Given strong support for high winds influencing woodcock collisions, we further explored the role of wind direction, as mechanisms behind elevated collision rates may vary depending on wind direction (e.g. for spring migration, favorable south winds causing birds to collide in transit; unfavorable north winds grounding birds with many subsequently colliding). Based on hourly wind direction data for nights before collision observations, collisions appear largely associated with north winds; 13 of 15 collisions were after nights with no southerly component to the wind direction (bearings between 270° and 90°), and although south winds occurred on the other two nights, north winds also occurred one of those nights.

The number of woodcock collisions we observed in spring 2018 was abnormally high compared to past research in Minneapolis and most other studies in North America. During the earlier Minneapolis study, 25 woodcock collisions were observed over 10 years, with 19 in spring (spring average = 2.1; range = 0–4). Of the other studies we reviewed that included observations of woodcock collisions, most (7 of 10) documented a higher average collision rate in spring than fall (Table 1). Three other studies had a single-spring count of woodcock collisions greater than our 2018 observation of 15 birds. Two of these monitored more buildings (Chicago Bird Collision Monitors: spring average = 32.7 woodcocks; range = 2–75; Toronto Fatal Light Awareness Program: spring average = 21.8; range = 8–30), and all three, including a study focused only on the McCormick Place Convention Center in Chicago (spring average = 6.3; range = 1–17), were along Great Lakes shorelines, which are major migration concentration points. Even if all six partial carcasses that we observed were from predation events, a count of nine woodcocks would still exceed all past studies except those above and an additional study in Baltimore (Lights Out Baltimore: spring average = 4.6; range = 2–12).

Discussion

Inclement weather, specifically strong headwinds and low clouds, influenced within-season variation in the daily number of American woodcock building collisions during spring 2018 in Minneapolis – and may have contributed to the unusually large number of total spring 2018 collisions relative to other migration seasons and years in this and other study areas. Although past studies have described storm-related bird collision events that included building collisions (Roberts 1907, Newton 2007), ours is the first to formally describe and analyze relationships between weather and collisions over an entire migration season. The relationships we show were strongly influenced by two early spring snowstorms that each resulted in relatively large numbers of woodcock collisions. Although total precipitation and snowfall were not related to within-season collision variation in spring 2018, heavy snowfall may have been an important factor leading to the high total count of spring collisions. Indirect evidence for this role of snowfall is provided by a follow-up review of Minneapolis weather records from 15 Mar to 31 May for 2007–2016, the period of spring monitoring for Project Birdsafe, which never documented more than four woodcock collisions in one spring. These data reveal that periods of north wind occurred multiple times each spring, but intense spring snowstorms were rare; across 10 years, only two snowfalls exceeded 12 cm, and both of these (18.3 cm on 20–23 Mar 2008; 18.5 cm on 18–19 Apr 2013) (NOAA 2019) resulted in far less snow than the 2018 storms. We therefore believe the unique combination of exceptionally heavy snowfall combined with strong north winds during the peak of woodcock migration could have led to the large number of woodcock collisions in spring 2018.

We likely captured only a small portion of much larger, storm-associated collision events that appeared to affect

migrating woodcocks across much of the US upper Midwest. Notably, a Twin Cities wildlife rehabilitation center reported its highest ever count of woodcock admissions from building collisions in spring 2018, with the highest number (6) on 31 Mar during the earlier snowstorm and with admissions coming from a variety of building types ranging from large office buildings to individual residences (T. Vogel, Wildlife Rehabilitation Center of Minnesota; unpubl.). Popular press coverage indicates that woodcock collisions also occurred widely with the later storm in mid-April, including up to at least 500 km southeast of the Twin Cities in southern Wisconsin (DeLong 2018). Because at least small numbers of woodcock collisions have been reported in other US regions in association with spring storms (Rosenberg 2017), such storm-induced collision mortality almost certainly occurs across the species' range.

During the two storms, we observed few collisions of other species, including only one unidentifiable bird during the first storm and two birds during the second storm, a yellow-bellied sapsucker *Sphyrapicus varius* and a mourning dove *Zenaiada macroura* (Loss et al. 2019). This observation and the influence of inclement weather on woodcock collisions provide insight into collision risk factors for this species. Woodcocks are among the earliest spring migrants of all North American birds, arriving in the northern US by early March and in northernmost breeding areas in Canada by early April (McAuley et al. 2013). This early migration makes woodcocks likely to encounter snow and ice storms. For most collision-prone species, peak migration through the northern US does not begin until late April, which likely explains the lack of collisions for other species during the two storms. Woodcocks also migrate at night and are thought to fly at low altitudes (McAuley et al. 2013), which may contribute to collisions even in clear conditions. The weather conditions most likely to lead to large numbers of woodcock collisions could entail a combination of favorable migration conditions (e.g. clear skies and tailwinds) followed suddenly by inclement weather (headwinds, low clouds, and/or precipitation). Upon encountering these inclement conditions, migrating woodcocks may fly even lower and/or be grounded in urban areas. Low-flying and grounded birds may experience elevated collision risk due to disorienting effects of artificial night lighting emitted from and near buildings (Evans Ogden 1996), especially because light pollution 'skyglow' is exacerbated by low clouds and precipitation (Rich and Longcore 2006). Finally, woodcock flight mechanics and vision may contribute to their vulnerability, as this species is plump and short-winged compared to other migratory species – which reduces maneuverability and perhaps the ability to avoid collisions – and has eyes set far back on the head, which may limit visual perception of obstructions.

Other monitoring studies support that building collisions could be a major range-wide source of mortality for woodcocks, and as in our study, most of these studies observed more woodcock collisions in spring than fall. This pattern is surprising because most migratory birds experience the greatest collision mortality in fall (Loss et al. 2014), likely due to larger post-breeding populations. The smaller number of woodcock collisions in fall could result from a reduced frequency of weather conditions that cause migrating woodcocks to fly lower or be grounded. Additionally, the timing of fall woodcock migration (generally Oct to Nov) and the propensity for woodcocks to migrate south with fall cold fronts (McAuley et al. 2013) could reduce encounters with inclement weather regardless of its frequency. Finally, collision monitoring programs often conclude fall sampling in late October or early November (Loss et al. 2014), which likely results in some woodcock fatalities being missed.

The apparent heightened risk of woodcock collisions in spring poses a potentially important threat to the conservation of this declining species because mortality immediately before the breeding season is likely to be additive (i.e. contributing to population declines) – as there is little time for processes like positive density-dependent survival to compensate for mortality and minimize declines in the abundance of breeding individuals (Boyce et al. 1999). Several other factors also likely influence the degree to which woodcock collision mortality is additive. Some of the collision fatalities we observed could represent birds that would have died from other sources of mortality related to inclement weather (e.g. exposure and/or starvation). Additionally, the American woodcock is a game species that is harvested in large numbers during fall migration and/or early winter, depending on the region. Approximately ~230 000 woodcocks were estimated to be taken during the 2017–2018 harvest season (~203 000 birds in the US; ~25 000 birds in Canada), and harvests were historically much greater (Seamans and Rau 2018). Although we observed a small number of collisions relative to the annual harvest, total woodcock mortality from collisions could be substantial enough to have range-wide management relevance. Further, woodcock collisions could increase as more buildings are constructed and because the frequency and intensity of late-winter and early-spring snowstorms may increase in the eastern US due to climate change (Cohen et al. 2018). However, additional research is needed to better understand range-wide, population-level effects of woodcock collisions. Studies are needed to generate precise estimates of fatality rates in different portions of the species' range and in relation to seasonality. Although we did not identify the sex of woodcock collision casualties in our study, future studies that separately estimate male and female collision rates would also be beneficial because this species is polygynous, with a relatively small subset of males contributing to egg fertilization and females providing virtually all parental care. Thus, female collision mortality may be more likely to be additive. Male and female woodcocks may also have different spring migration timing, with males thought to depart wintering grounds before females (McAuley et al. 2013); therefore, depending on the timing of inclement weather, one or the other sexes may be disproportionately represented in mortality events. Finally, information about collision mortality should be integrated into models that consider how woodcock populations are influenced by factors operating in all parts of the annual cycle (e.g. harvest mortality during fall migration and winter, and loss of early-successional habitat in breeding areas) (Saunders et al. 2019).

More broadly, research is needed to clarify effects of weather on bird collisions because efforts to mitigate collisions could be refined if they were forecastable like the weather. Our finding of large numbers of woodcock collisions during spring storms, but few collisions of other species, suggests that weather effects on collisions are variable

among species. This variation may be influenced by migration phenology (early versus late season), migration timing (nocturnal versus diurnal) and behavior (flight height and propensity to migrate in 'risky' conditions), as well as life history (long- versus short-distance migration), visual acuity and physiological tolerances and efficiencies. Thus, to gather more insight into mechanisms behind collisions and the best approaches to manage them, future research could consider links between weather and both total bird fatalities and fatalities of individual species or species groups (e.g. nocturnal migrants). Research could also separately consider mortality of migrants during spring and fall because drivers of collisions are likely to vary among seasons characterized by different weather patterns.

Conclusions and management recommendations

This study can inform management of the American woodcock, a species that has undergone a long-term population decline. Loss of habitat, especially early successional woodlands in breeding areas, is thought to be a major contributor to this decline; however, the woodcock has also been hypothesized to experience greater mortality during migration than any other time in the annual cycle (D. J. Case & Associates 2010). Despite increasing research into woodcock migration, there is little information about woodcock mortality sources during this period. Our study suggests the possibility that building collisions are an important source of mortality for migrating woodcocks, and that the majority of collisions occur in spring when mortality is more likely to contribute to population decline. We therefore suggest that management to reduce building collisions will benefit the American woodcock's overall population. Management steps that have been recommended to reduce collisions of all bird species are also likely to reduce woodcock collisions, including incorporation of bird-friendly design features for new buildings, reduction of artificial lighting emitted from and near buildings at night, and reduction of reflective and see-through effects of glass (e.g. with screens, window films and markers or other treatments) (USFWS 2016, National Audubon Society 2019).

Because weather dictates bird migration timing and intensity, it also likely dictates when factors associated with buildings and their surroundings are especially important in driving collision risk. Recent technological advances allow use of meteorological data and radar systems to predict avian migration on a continental scale (Van Doren and Horton 2018); these weather-based projections are an important step toward predicting collision risk for migrating birds. However, because conditions favoring migration may not always be the same as those influencing collisions, further research is needed to link weather and radar-derived migration variables to observed collisions. Enactment of collision mitigation steps at all times (e.g. reducing or eliminating lighting on all nights during migration periods) is likely to result in the greatest reductions in bird-building collisions. However, such comprehensive management may not always be possible. In these cases, prediction of collisions based on weather may allow for targeted timing of mitigation activities (e.g. turning lights off on nights forecast to experience inclement weather) that greatly benefits conservation of the American woodcock and other migratory bird species.

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Supplementary material (available online as Appendix wlb-00623 at <www.wildlifebiology.org/appendix/wlb-00623>). Appendix 1.