FACTORS AFFECTING
BIRD-WINDOW COLLISIONS
IN A SMALL URBAN AREA:
STILLWATER, OKLAHOMA

By

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Chapter 2. As of this writing (March 2019), this chapter is in review at *Scientific Reports*. Coauthors include the venerable Tim O'Connell and the inestimable Scott Loss.

Chapter 3. This chapter is to be submitted shortly to a high-quality outlet, pending final review by my dissertation committee. Coauthors include the veracious Tim O'Connell and the indispensable Scott Loss.

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Abstract: This dissertation consists of four concurrent studies of bird-building collisions, which primarily occur at glass surfaces (e.g., windows) and are a major source of direct anthropogenic mortality for birds globally. Although research, public, and policy interest concerning bird-window collisions are increasing, this issue has primarily been studied in larger metropolitan areas, particularly in the eastern third of North America. It is unknown if bird-window collisions in smaller urban areas in other regions (e.g., the U.S. Great Plains) are influenced similarly by the same factors. Chapter 1 examined some biases that cause researchers to underestimate the number of fatal bird-window collisions. Because of high carcass persistence and observer detection rates, we estimated that across seasons we detected about 88% of fatal collision victims. Also, we provided formal definitions to distinguish scavenging and removal events to promote consistent terminology use. Chapter 2 investigated the temporal patterns of fatal and non-fatal window collisions. We found that more collisions occurred at night or early morning than late morning or afternoon. In addition, weekly and monthly variation indicated more collisions during migratory periods, especially spring, and greater mortality of non-migrating individuals than expected. Chapter 3 assessed the fine-scale spatial patterns of window collision mortality. The inter-seasonal and inter-species variation that we found across building façades suggested that targeted mitigation efforts may be applied at small spatial scales but need to identify conservation goals for maximum effect. Chapter 4 considered the effects of artificial lighting at night on building collision frequency. We did not find a strong spatial relationship between the lightscape (variation in nocturnal light intensity) and the collision mortality intensity, but there were several factors that may have confounded our results. Overall, our findings both corroborated and disputed results from previous studies, indicating that although the general phenomenon of bird-window collisions is similar across various contexts, the details of urban development, geographic region, and building façade structure may strongly influence local outcomes. These findings should help inform conservation efforts to reduce bird-window mortality and suggest that further research should be conducted in under-studied localities.

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CHAPTER I

FACTORS INFLUENCING EXPERIMENTAL ESTIMATION OF SCAVENGER REMOVAL AND OBSERVER DETECTION IN BIRD-WINDOW COLLISION SURVEYS

Abstract. Wildlife collisions with human-built structures are a major source of direct anthropogenic mortality. Understanding and mitigating the impact of anthropogenic collisions on wildlife populations requires unbiased mortality estimates. However, counts of collision fatalities are underestimated due to several bias sources, including scavenger removal of carcasses between fatality surveys and imperfect detection of carcasses present during surveys. These biases remain particularly understudied for bird-window collisions, the largest source of avian collision mortality. In Stillwater, Oklahoma, USA, we used bird carcasses collected during window collision monitoring to experimentally assess factors influencing scavenging and observer detection, and we employed trail cameras to characterize the scavenger community and timing of scavenging. We recorded 9 scavenger species, but the domestic cat and Virginia opossum were responsible for 73% of known-species scavenging events. The most frequent scavenger species were primarily nocturnal, and 68% of scavenging events occurred at night. Scavenger species best predicted time to first scavenging event, season best predicted carcass persistence time, and both season and carcass size predicted whether any carcass remains persisted after scavenging. Our results also suggest that observer detection was influenced by substrate, with greater detection of carcasses on artificial substrates. Our findings related to scavenging timing have important implications for the unbiased estimation of collision mortality because the timing of peak scavenging relative to timing of peak mortality can substantially influence accuracy of adjusted mortality estimates. Further, the differences in correlates for time to first scavenging and time to carcass removal (i.e., persistence time) illustrate the importance of explicitly measuring these often-independent events that are frequently conflated in the anthropogenic mortality literature.

Introduction

Birds and other volant wildlife fatally collide with a wide variety of human-built structures (Avery 1979, Klem 1989, Longcore et al. 2013, Campedelli et al. 2014, Loss et al. 2015). For birds, collisions at windows and other glass surfaces on buildings are the top source of collision mortality, annually killing an estimated 16-42 million birds in Canada and 365-988 million birds in the United States (Machtans et al. 2013, Loss et al. 2014). A major issue in studying and mitigating the impact of wildlife collisions, including bird-window collisions, is accurately estimating the numbers of individuals killed. Bird-window collision mortality is typically quantified by surveying for and generating counts of bird carcasses found around perimeters of monitored buildings (O'Connell 2001, Gelb and Delacretaz 2009, Borden et al. 2010, Hager and Cosentino 2014). However, just as simple counts of live birds are usually biased because they do not account for variation in detection probability among individuals, species, and habitats (Ralph et al. 1995), counts of dead birds are similarly biased. Spatiotemporal comparisons of simple fatality counts and assessments of mortality correlates based on counts are likely to lead to inaccurate conclusions because factors influencing carcass detection can vary greatly among buildings, seasons, regions, and studies. Therefore, an important aspect of quantifying mortality is estimating the values of and identifying factors influencing the different types of estimation bias.

Several processes cause significant under-detection bias for wildlife mortality studies, and two of the largest bias sources are scavenger removal and imperfect observer detection of carcasses. Scavenger removal occurs when a scavenger removes a carcass before it has a chance to be detected. This bias has been assessed for many mortality sources, and studies show that carcass persistence varies with season, carcass size, carcass age (time since carcass deposition), local vegetation, and the surrounding landscape (Rivera-Milán 2004, Prosser et al. 2008, Ponce et al. 2010, Guinard et al. 2012). Scavenging communities also vary spatiotemporally, and different species have variable effects on detectability. For example, studies in two U.S. states (Devault et al. 2004, 2011) found that numbers of scavenger species removing placed rodent carcasses varied greatly between sites. Further, whereas some scavenger species are more likely to consume carcasses in situ, often leaving detectable remains, others are more likely to remove carcasses entirely (Hager et al. 2012). Studies of scavenger removal of window-killed bird carcasses that assessed correlates of carcass persistence (Hager et al. 2012, Bracey et al. 2016, Kummer et al. 2016) have found carcass size, carcass age, vegetation structure, and proximity to certain features (e.g., windows, urban centers) to be important. However, these studies were limited to a single year, season, and/or building type, and no study to date has assessed the potential influence of scavenger species as a correlate of carcass persistence.

In addition to scavenger removal, searchers may not detect all carcasses that are available to be found in the survey area. This observer detection bias has been systematically assessed for many mortality sources and may increase with extensive vegetative cover, poor light conditions, inclement weather, and observer fatigue or inattentiveness (Gehring et al. 2011, Korner-Nievergelt et al. 2013, Mathews et al. 2013, Campedelli et al. 2014). Extensive observer experience has been shown to decrease detection bias in limited instances (Ponce et al. 2010), but experience had no effect in many field tests (Rivera-Milán et al. 2004, Stevens et al. 2011, Schutgens et al. 2014). To date, only a single peer-reviewed study has assessed observer detection in the context of window collisions, and this study did not formally assess any correlates of detection rates (Bracey et al. 2016).

To improve understanding of the biases influencing estimates of bird-window collision mortality, we experimentally evaluated rates and correlates of scavenging and observer detection as part of a bird-window collision study in Stillwater, Oklahoma, USA, a small urban area in the North American Great Plains. In addition to quantifying scavenging and observer detection, our objectives were to: 1) describe which species are the primary scavengers of window-killed bird carcasses, 2) determine the frequency and distribution of scavenging events throughout the day, and 3) formally assess factors influencing both scavenging (e.g., season, scavenger species) and observer detectability of carcasses (e.g., substrate, observer experience). Additionally, to provide a unified framework for the study of mortality estimation biases, both for bird-window collisions and anthropogenic wildlife mortality more broadly, we provide formal definitions for and separately assess correlates of scavenging processes that differ subtly but are often used interchangeably in the anthropogenic mortality literature (scavenging, carcass persistence, and carcass removal).

Methods

Study area and study design

We surveyed for bird carcasses resulting from window collisions around buildings in Stillwater, Oklahoma, USA, a small urban area with a human population of 45,688 in the 2010 census and only 3 buildings exceeding 5 floors in height. The city of Stillwater covers roughly 85 km^2 and is located in the cross timbers ecoregion, a transitional area of grassland, shrubland, savannah, and woodland located at the interface of the eastern deciduous forests and the mixed grass and short-grass prairies of the Great Plains. The survey buildings included residences (n = 2; 1 single-family dwelling and 1 duplex house), academic and services buildings on the Oklahoma State University campus (n = 10), and commercial buildings in Stillwater (n = 3). Of these buildings, we surveyed 14 in 2015, 15 in 2016, and 13 in 2017 (residences were not surveyed in 2017). We slightly modified standardized survey methods (Hager and Cosentino 2014, Hager et al. 2017) to search for bird carcasses around each building 6 days/week between Apr and Oct in 2015 and 2016 and between Apr and May in 2017. We did not conduct full monitoring between Nov and Mar due to staffing limitations and because winter bird-window collision mortality is generally minimal compared to other seasons (O'Connell 2001, Hager et al. 2008, 2013, Borden et al. 2010; but see Breithaupt et al. 2013). However, we did monitor a subset of 3 buildings 1 day/week during winter of 2015-2016 and a subset of 5 buildings 2 days/week during winter of 2016-2017. Winter surveys were conducted only at on-campus buildings where we expected greater mortality due to putative collision risk correlates (e.g., large amounts and/or high proportions of glass).

All surveyors, including the authors, field technicians, and citizen scientists (i.e., volunteers that were OSU students and faculty or members of the Stillwater community), received training prior to conducting surveys. Training consisted of a brief project background; how, when, and where to survey; protocols for encountering dead, stunned, and experimentally placed birds; and an introduction to the project website, including pertinent data recording and submission materials. Upon discovery of an intact carcass during a survey, observers recorded the location and a description of the carcass (or species, if known), and took photographs from several angles. We similarly documented remains of partial carcasses, most of which consisted solely of feathers (i.e., feather piles) that had been plucked from the carcass by a scavenger. To avoid counting adventitiously lost feathers, we considered feather piles to be window-killed carcasses only if they consisted of ≥5 feathers in a circular area ~15 cm in diameter. We also recorded carcasses resulting from directly observed collision events (i.e., when an observer saw and/or heard a fatal bird collision occur); however, we did not count window smudges (e.g., feathers or other bird-related markings on the glass) because these can indicate non-fatal collisions. We collected carcasses and other remains using a plastic, sealable bag, and subsequently stored them in a freezer with identification tags containing a unique alphanumeric code. When we could not collect a carcass (e.g., because it was on an inaccessible ledge above ground level), we tracked the condition and location of the carcass to avoid double counting it on future surveys. Carcass retrieval and manipulation were covered under federal (U.S. Fish and Wildlife Service permit #MB05120C-0) and state (multiple permits over course of the study) scientific collecting permits; protocols were also approved by the OSU Institutional Animal Care and Use Committee (Animal Care and Use Protocol #AG-14-8).

Scavenging definitions

To be precise in meaning, for the remainder of this paper we operationally defined relevant terms that have not been specifically distinguished in similar studies of bird-window collisions or for any other anthropogenic sources of wildlife mortality, such as wildlife-vehicle collisions and bird and bat collisions with wind turbines. We defined “scavenging” as the first event where all or part of a carcass was consumed or otherwise taken from the area that would be searched in carcass surveys and “time to scavenging” as the length of time from initial carcass placement until this scavenging event. We defined “persistence” as the continued presence of an entire carcass or sufficient parts of the carcass with the potential to be detected on carcass surveys and “removal” as the point at which no carcass parts remained to be detected, either due to scavenging or decomposition (i.e., the end point of persistence). Although persistence and removal are related but separate phenomena, we use both “persistence time” and “time to removal” to refer to the length of time from carcass placement until the point at which no carcass parts remain to be detected. As an example of these definitions, when a carcass is entirely removed all at once, both scavenging and removal have simultaneously occurred, persistence has ended, and time to scavenging is the same as persistence time. When a carcass is only partially scavenged, then scavenging occurs before removal, persistence continues beyond scavenging, and time to scavenging is shorter than persistence time.

Scavenging trials

To assess the rate and correlates of scavenging, we placed carcasses at buildings used for carcass surveys and at some neighboring buildings due to occasional logistical constraints associated with placing carcasses and cameras. For all trials, we monitored carcasses with trail cameras (Browning Range Ops Series), and conducted daily carcass checks until they were removed. For a carcass that persisted >30 days, we continued monitoring at a reduced frequency (~2 checks/week) until the carcass was no longer detectable (i.e., had been removed). We did not retrieve any trial carcasses, and instead allowed them to be removed by scavengers or decay to the point that we could not detect them. Carcass placement times were constrained by the work schedule for our larger bird collision monitoring study; this prevented us from rigorously assessing how scavenging rates were influenced by time of carcass placement. Most carcasses (53 of 73 [73%]) were placed in the middle of the day (i.e., 1000-1500 h), 17 (23%) were placed 0800-1000 h or 1500-1700 h, and only 4 (5%) were placed 1700-0800 h. When possible, we used carcasses (n = 7) that were collected during carcass surveys in the previous 24 hours, but most carcasses had been stored in a freezer for up to several months after being collected during either carcass surveys (n= 54) or incidentally (n=12) at buildings that were not part of the study or from other mortality sources, such as vehicle collisions. For frozen carcasses, we selected intact carcasses from among those available and thawed them for 20-24 hours at room temperature before placement for scavenging trials. Trial carcasses (n = 73 total) comprised 21 species that occur in the study area and varied in size (range of lengths = 12-31 cm; range of weights = 9-150 g) and coloration (e.g., Yellow Warbler [*Setophaga petechia*], Northern Cardinal [*Cardinalis cardinalis*], and White-winged Dove [*Zenaida asiatica*]), but the most commonly used species were relatively similar in size, including Swainson's Thrush (*Catharus ustulatus*, n = 8), Cedar Waxwing (*Bombycilla cedrorum*, n = 8), and European Starling (*Sturnus vulgaris*, n = 8).

We started a new set of scavenging trials approximately every 6 weeks between Apr and Oct of 2015 and every 7 weeks between Apr of 2016 and Apr of 2017. Each set of trials consisted of placing between 4 and 8 carcasses across our entire study area, such that we placed 24 total carcasses in spring (Apr-May), 21 in summer (Jun-Aug), 16 in fall (Sep-Oct), and 12 in winter (Nov-Mar). The placement criteria were that each carcass must be: (1) ≤250 m from a current survey building and ≤2 m from any building, (2) ≥3 m from building egresses that experience large volumes of human foot traffic, and (3) ≥200 m (Euclidean distance) from other placed carcasses to avoid carcass swamping (i.e., placing more carcasses than the scavenger community is capable of detecting and/or removing [Smallwood et al. 2010]). Most carcasses placed simultaneously were actually much farther than 200 m from their nearest neighbor (mean = 828 m; range = 201-5565 m) based on Euclidean distances. Additionally, walking distance of the most direct route a scavenger could take between two carcasses was typically much greater than the Euclidean distance because of obstructions such as buildings. These criteria and concerns about camera theft limited the number of viable locations, such that some were used up to 3 times over the course of the study. However, we ensured spatiotemporal independence of scavenging trials by not reusing individual locations within 5 months and not using locations that were <50 m apart in consecutive trials. Overall, the 73 scavenger trials included 46 distinct carcass placement locations across 20 buildings.

To minimize theft, vandalism, and incidental image triggers, we secured cameras to a stable object (e.g., tree or metal pole) and aimed the lens toward a wall or similar obstruction so that the camera was not obvious (Fig 1.1a). We programmed trail cameras to take time-lapse pictures every 5 minutes from sunrise to sunset and 3 pictures (1 every 3 seconds) each

Figure 1.1. (a) Trail camera in security box attached to tree for monitoring the carcass of a female Northern Cardinal (*Cardinalis cardinalis*). (b) Swainson's Thrush (*Catharus ustulatus*) carcass placed in cultivated bed with wood chips for observer detection trial. For the actual trial, the carcass was ventrum down and the tag was not visible.

time motion was detected, with a forced timeout delay of 1 minute between trigger events. We mounted cameras ≤ 0.5 m above ground level and placed the carcass on the ground 0.5-1.5 m from the camera in line with the lens. If a carcass was moved beyond the viewable field of the camera between daily checks, we repositioned the carcass in the camera's view. After a carcass was removed (i.e., scavenged or decayed to a state where scavenging was no longer likely), we retrieved the camera and examined timestamped images to determine scavenger species, and when possible, the time of day that scavenging occurred. If the exact time of scavenging could not be determined using images, we estimated it as the midpoint between the last known time the carcass was entirely present and the first known time it was completely or partially absent. Although we observed the presence and activity of invertebrate scavengers (primarily orders Diptera, Hymenoptera, and Coleoptera), time of scavenging was recorded for vertebrate scavengers only. For scavenging events with known time of scavenging, we classified them as day (civil dawn to civil dusk) or night (civil dusk to civil dawn).

Observer detection trials

To assess the rate and correlates of observer detection, we used frozen carcasses obtained from carcass surveys with a small label affixed to the leg (Fig 1.1b). Although detection trials often temporally co-occurred with scavenging trials, we used different carcasses and locations for the two experiments. For each detection trial, we placed a labeled carcass in a survey area a short time before the carcass survey began (typically 0630-0730 h). Detection trials were conducted at all survey buildings and occurred in all non-winter months (Apr-Oct) between Apr 2015 and May 2017. We used 13 individuals of 7 species for 196 total detection trials, with the most commonly used species being House Finch (*Haemorhous* *mexicanus*, n = 55), Lincoln's Sparrow (*Melospiza lincolnii*, n = 44), and Grasshopper Sparrow (*Ammodramus savannarum*, n = 43). Because trial carcasses were generally small in size (mean length ~15 cm [range = 13-18 cm] and mean weight ~19 g [range = 12-31 g]) with drab coloration (i.e., brownish dorsum and whitish ventrum), our estimates likely represent minimum expected rates of observer detection (i.e., larger and/or more colorful carcasses should be more detectable). This approach of controlling for carcass appearance also provided the benefit of allowing us to isolate other correlates of observer detection (e.g., substrate and observer experience).

We used a random number generator (https://www.random.org/) in a stepwise fashion to select the days, buildings, and building façade sections for carcass placement trials. The number of trial carcasses placed for each observer depended largely on the number of surveys they conducted, such that we attempted to place ≥ 1 carcass for volunteers who conducted > 1 survey and placed ≥ 3 carcasses/month for full-time surveyors. We split observers into two proficiency groups: (1) experienced personnel, who regularly and frequently conducted carcass surveys and for whom we had ≥ 10 detection trials (n = 6; mean = 23.5 trials/observer; range = 10-56 trials), and (2) volunteers, who conducted surveys irregularly and infrequently and had < 10 detection trials (n = 24; mean = 2.3 trials/observer; range = 1-8 trials). We provided periodic reminders to surveyors that detection trials could occur at any time, but surveyors were always blind to the specific date and location of carcass placement. The exact location of carcass placement depended on the substrates available for the selected building façade section, because, as much as possible, we attempted to place carcasses equally on both natural substrates (n = 97; soil, mulch, grass, or other vegetation) and artificial substrates (n = 92; concrete, brick, gravel, or metal grate). We placed each carcass on its ventrum to hide the label and ≤ 2 m from a window (i.e., in an area that would be searched on a carcass survey).

Upon finding placed carcasses, surveyors took one photo of the carcass as they found it and collected the carcass. After daily carcass surveys were concluded (typically 0830-0930 h), we retrieved any carcasses not detected by observers. There were four potential outcomes for each placement trial: (1) detected (i.e., the surveyor found and collected the carcass), (2) not detected (i.e., the searcher failed to find the carcass, but it was present for us to retrieve), (3) not present (i.e., the surveyor did not detect the carcass and it was not present when we attempted to retrieve it, with the assumption being that it was also not present during the carcass survey), and (4) not surveyed (i.e., the surveyor did not conduct the survey). Outcomes in categories 3 and 4 (n = 5 and 2, respectively, of 196 total trials) were not included in analyses because they do not contribute to understanding the detection process and their small sample sizes were unlikely to influence analyses. Our assumption that category 3 carcasses were removed prior to surveys is likely valid in most cases because results from carcass categories 1 and 2 illustrate that we detected a high proportion of all carcasses available to be found (see Results). Because we immediately retrieved carcasses and stored them in the freezer, we were able to reuse some carcasses many times in observer detection trials.

Statistical analyses

We conducted analyses in R 3.3.3 (R Core Team 2017) with RStudio 1.0.136 (RStudio Team 2016) and calculated the raw mortality rate as the number of carcasses found/survey. Due to greater uncertainty regarding the mortality source for feather piles—

some of which could have included predation events unrelated to window collisions—we calculated mortality rates both including and excluding feather piles. Although we conducted carcass surveys and scavenging and observer detection trials at buildings that varied in type, size, surrounding vegetation, and surrounding extent of urban development, we did not analyze these types of variables in the following analyses because 1) we had relatively small samples of building types other than university campus buildings, 2) measurements of surrounding vegetation and landscape features would be statistically non-independent due to many of our buildings being in close proximity to one another, and 3) for observer detection trials specifically, most large-scale variables would be unlikely to effect the detectability of carcasses.

To determine daily persistence probability (*s*; the probability that any detectable portion of a carcass persists for 24 h) and its 95% confidence interval (CI) for scavenging trial carcasses, we used the function ‘persistence.prob’ in the R package ‘carcass’ (Korner-Nievergelt et al. 2015). We right-censored persistence times at 30 days, and because we performed near-daily searches, we assumed that persistence probability was constant over time. We estimated *s* for each season separately and for all seasons combined. To estimate observer detection probability (*f*; the probability that a carcass present in the study area is detected by an observer during a carcass survey) and its 95% CI based on detection trials, we used the function ‘search.efficiency’ in the R package ‘carcass’. We estimated *f* for all combinations of proficiency group, substrate, and season (excluding winter). We treated the estimated value of *f* as a minimum because experimental carcasses were likely less detectable on average than naturally occurring carcasses due to (1) being relatively small and drably colored, and (2) being placed ventrum down (most naturally occurring carcasses were dorsum down).

To calculate the probability that a bird carcass present in the study plot during the study period was detected, we used the estimated *s* and *f* (along with 95% CIs for both) in the function ‘pkorner’ in the R package ‘carcass’. We then used this calculated probability to adjust raw mortality rates by season. The search interval was 1 day for spring, summer, and fall estimates and 3.5 days for winter estimates. Because we did not conduct observer detection trials in winter, we used the *f* estimate averaged across the other three seasons for winter estimates. To evaluate potential predictor variables for time to first scavenging event and right-censored persistence time (i.e., time to removal), we used Cox proportional hazard regression (function ‘coxph’ in R package ‘survival’ [Therneau 2015]) with predictor variables including carcass size (species average mass [g] taken from Sibley [2014]), season, and scavenger species. Due to lack of convergence, we excluded carcasses that were not scavenged. We considered predictor variables to be important if the 95% CI of the exponentiated coefficient (hazard ratio) did not include 1. We did not formally analyze the time of day for when scavenging events occurred, but we used circular statistics to calculate a mean time of scavenging.

To assess the effect of carcass size, season, and scavenger species on whether or not any carcass remnants remained after the first scavenging event (i.e., whether persistence continued after scavenging), we used generalized linear models (GLM; function ‘glm’ in R) with binomial error distribution and a logit link. To evaluate factors influencing observer detection, we used linear models (LM; function ‘lm’ in R) with detection probability (*s*) as the dependent variable and predictor variables including season, substrate, and proficiency group. For both GLM and LM modeling, we ranked alternative models using Akaike's Information Criterion corrected for small sample sizes (ΔAICc; Burnham and Anderson 2002). We interpreted variables from models that had strong support (ΔAICc ≤ 2) and weak support (2 < ΔAICc ≤ 7), but we did not consider any models that were more complex versions of higher ranking nested models (i.e., models that contained uninformative variables; Richards 2008, Arnold 2010). For all regression and modeling analyses, the baseline categories on which quantitative comparisons were based included: fall (for season), cat (for scavenger species), artificial (for substrate), and experienced (for proficiency group).

Results

We conducted 6380 carcass surveys and found 359 bird carcasses (288 carcasses excluding feather piles) for a raw mortality rate of 0.056 carcasses/survey across all buildings and seasons (Appendix A: Table A1). At least 9 species scavenged 63 (86%) of the carcasses placed in scavenging trials, and the domestic cat (*Felis domesticus*) was the most common scavenger in all seasons and by far the most common scavenger overall (n = 25, 52% of known-species scavenging events) (Table 1.1; Fig 1.2). Other species that scavenged at least 3 carcasses included Virginia opossum (*Didelphis virginiana*), fox squirrel (*Sciurus niger*), and striped skunk (*Mephitis mephitis*). Species that we recorded interacting with a carcass sans scavenging it included human (*Homo sapiens*), nine-banded armadillo (*Dasypus novemcinctus*), and Great-tailed Grackle (*Quiscalus mexicanus*).

Table 1.1. Number of carcasses scavenged (and number of feather piles left) by season and scavenger during experimental scavenging trials conducted in Stillwater, Oklahoma, 2015-2017.

Scavenger species	**Spring**	**Summer**	**Fall**	**Winter**	**Total**
Domestic cat *Felis domesticus*	9 (4)	6 (5)	4 (2)	6 (0)	25 (11)
Virginia opossum *Didelphis virginiana*	3 (1)	4 (2)	2 (1)	1 (1)	10 (5)
Fox squirrel *Sciurus niger*	2 (0)	1 (0)	–	1 (0)	4 (0)
Striped skunk *Mephitis mephitis*	1 (1)	–	2 (0)	–	3 (1)
Common box turtle *Terrapene carolina*	–	1 (1)	1 (1)	–	2 (2)
American Crow *Corvus brachyrhynchos*	1 (1)	–	–	–	1 (1)
Domestic dog *Canis lupus familiaris*	1 (0)	–	–	–	1 (0)
Greater Roadrunner *Geococcyx californianus*	–	1 (1)	–	–	1 (1)
Raccoon *Procyon lotor*	–	–	1 (0)	–	1 (0)
Unknown scavenger	2 (2)	5 (2)	5 (0)	3 (0)	15 (4)
Not scavenged	5	3	1	1	10
All	24 (9)	21 (11)	16 (4)	12 (1)	73 (25)

Figure 1.2. Images captured by trail cameras monitoring placed carcasses. (a) Domestic cat (*Felis catus*) scavenging a Northern Cardinal (*Cardinalis cardinalis*) carcass. (b) Virginia opossum (*Didelphis virginiana*) about to scavenge a Cedar Waxwing (*Bombycilla cedrorum*) carcass.

For trials in which scavenging occurred (63 of 73 [86%] total trials), detectable remains persisted after the first scavenging event in 25 trials (40%), the scavenger species was unknown for 15 trials (24%), and the exact time of scavenging was unknown for 13 trials (21%). Most instances of unknown species or time were due to camera failure (e.g., the camera stopped recording images or the scavenger did not trigger motion detection). Among scavenging events with known times (n = 50), the circular mean time of scavenging was 0038 h, and 34 (68%) scavenging events occurred at night (Fig 1.3). Mean time to first scavenging was 2.7 days (n = 50; range = 0.0-12.0 days) for events with known times only and 3.3 days (n = 63; range = 0.0-19.9 days) when including events with estimated times. Mean persistence time was 3.1 days (n = 38; range = 0.0-19.9 days) for carcasses removed at scavenging and 13.7 days (n = 20; range = 2.7-41.8 days) for carcasses that persisted after scavenging. For carcasses that were not removed by a scavenger, mean persistence (i.e., the amount of time before decay left carcasses undetectable) was 40.6 days (n = 10; range = 14.0-75.9 days). Carcass daily persistence probability (*s*) was 0.91 across all buildings and seasons (Appendix A: Table A2). Across all observer detection trials, surveyors found 138 of 189 carcasses available to be found for a searcher efficiency (*f*) of 0.73 (Appendix A: Table A3). Based on the adjusted mortality rate (0.063 carcasses/survey), we estimate that 400 fatalities (321 fatalities excluding feather piles) occurred during monitoring (Appendix A: Table A2).

For the Cox proportional hazards analyses, time to first scavenging event differed among scavenger species, but the only significant deviation from the baseline (cats) was that time to scavenging was longer for unknown species (Appendix A: Table A4). Right-censored persistence time differed among seasons, and specifically, was longer in spring than in fall

(Appendix A: Table A5). For the GLM analysis of factors influencing whether detectable carcass remains persisted following scavenging, there was strong support for carcass size and season but not scavenger species (Table 1.2). The likelihood of detectable remains persisting increased with carcass size (β = 0.024, standard error [SE] = 0.010), and remains were more likely to persist after scavenging in spring (β = 1.510, SE = 0.838) and summer (β = 1.389, SE = 0.813) than in fall or winter. For the LM analysis of factors influencing observer detection, strong support was indicated for substrate and marginal support was indicated for proficiency group. However, no models ranked above the null model (Table 1.3).

Table 1.2. Model selection results for GLM analyses of factors influencing whether any carcass remains persist following an initial scavenging event during experimental scavenging trials conducted in Stillwater, Oklahoma, 2015-2017.

Model	***K***	**ΔAICc**	**ω_i**
Carcass size + Season	5	0.0	0.65
Carcass size	2	1.8	0.26
Season	4	4.2	0.08
Null	1	7.8	0.01
Carcass size + Scavenger species	11	10.6	< 0.01
Carcass size + Season + Scavenger species	14	12.8	< 0.01
Scavenger species	10	14.7	< 0.01
Season + Scavenger species	13	14.7	< 0.01

Notes: Factors included carcass size (average mass [g] for species), scavenger species (nine observed species and unknown), and season (spring, summer, fall, winter). *K*, number of parameters; ΔAICc, difference in value of Akaike's Information Criteria (corrected for small sample size) relative to best supported model; ω_i, Akaike weight of the model.

Table 1.3. Model selection results for LM analyses of factors influencing observer detection rates during experimental observer detection trials conducted in Stillwater, Oklahoma, 2015-2017.

Model	***K***	**ΔAICc**	**ω_i**
Null	2	0.0	0.47
Substrate	3	0.8	0.32
Group	3	2.6	0.13
Group + Substrate	4	4.1	0.06
Season	4	7.6	0.01
Substrate + Season	5	10.8	< 0.01
Group + Season	5	12.8	< 0.01
Group + Substrate + Season	6	18.1	< 0.01

Notes: Factors included group (experienced, volunteer), season (spring, summer, fall, winter), and substrate (artificial, natural).

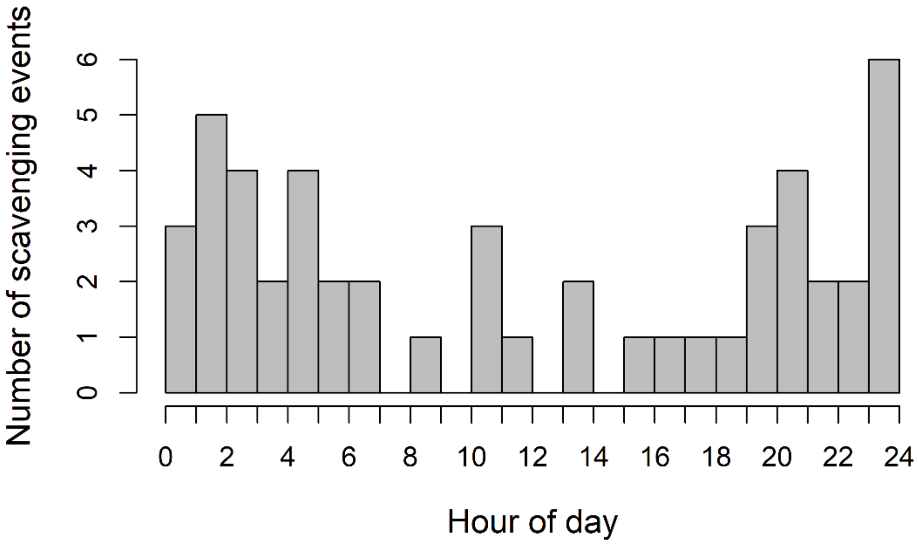

Figure 1.3. Frequency distribution of known-time scavenging events by hour of day (0 = 24 = midnight) during experimental scavenging trials conducted in Stillwater, Oklahoma, 2015-2017.

Discussion

For bird-window collisions, the largest source of avian collision mortality, we comprehensively examined correlates of mortality estimation biases over multiple seasons and years and included *a priori* analyses regarding correlates of observer detection and the effects of scavenger species on multiple components of the scavenging process. We also provide the first formal definition of these multiple scavenging processes that are often conflated in the literature on anthropogenic wildlife mortality, including: scavenging (an event where either all or part of a carcass is consumed), persistence (the presence of all or part of a carcass which could be detected), and removal (the point at which no carcass remains persist to be detected). We found that carcass persistence after scavenging was unrelated to the scavenger species and was more likely for larger carcasses and in spring and summer. Notably, scavenger species best predicted time to first scavenging, but season best predicted persistence time (i.e., time to carcass removal), a result that illustrates the need to consider and quantify these events separately. Finally, we found limited evidence that the substrate on which a carcass rests, and possibly surveyor experience, could influence carcass detection rates.

The suite of 9 scavenger species that we observed largely overlapped with previous bird-window collision studies that assessed scavenging—all of which have been conducted in North America (Hager et al. 2012, Kahle et al. 2016, Kummer et al. 2016)—but the relative frequency of scavenging by different species varied from previous research. Most notably, ours was the first study to document domestic cats as the most frequent scavenger; the most common scavengers in other studies included raccoon (*Procyon lotor*) in Illinois (Hager et al. 2012), striped skunk (*Mephitis mephitis*) in California (Kahle et al. 2016), and Black-billed

Magpie (*Pica hudsonia*) in Alberta (Kummer et al. 2016). Cats were the second most common scavenger in two earlier studies (Hager et al. 2012, Kummer et al. 2016). Species we observed that had been unreported previously as scavengers of window-killed bird carcasses—likely due to their geographic distributions not overlapping with locations of previous research in Alberta, coastal northern California, and northwestern Illinois—included Greater Roadrunner (*Geococcyx californius*) and common box turtle (*Terrapene carolina*). However, both of these species are known to scavenge carrion generally (Platt et al. 2009, Rogers et al. 2014).

We found no evidence for differences among scavenger species in the likelihood of carcass remains persisting after the initial scavenging event. These results contradict the suggestion by Hager et al. (2012) that some scavenger species are more likely to leave detectable carcass remains after scavenging, which if true, would have implications for estimating scavenger removal rates when surveyors count scavenged remains like feather piles. The lack of differences among scavengers in our study may have arisen due to the relatively small sample of scavenging events for most species (we recorded ≤2 scavenging events for 5 of 9 species). Kummer et al. (2016) found that the best predictors of carcass removal differed between cats and corvids, the two scavenger groups for which they had the largest samples, which indicates that the scavenging process as a whole does differ among scavengers. Similarly, we found some support for among-species differences in time to scavenging, but the only significant comparison was that time to scavenging was faster for cats than unknown species. Further replication and additional similar research in other locations and regions would provide greater insight into among-species variation in time to scavenging and persistence after scavenging.

Season and carcass size had no effect on time to first scavenging. The lack of effect of season is surprising because this factor has repeatedly been shown to influence both scavenging and removal (Rawlings and Horn 2010, Smallwood et al. 2010, Boves and Belthoff 2012, Hager et al. 2012, Villegas-Patraca et al. 2012, Kummer et al. 2016, Henrich et al. 2017), regardless of whether carcasses were left in place, frozen carcasses were thawed, or carcass substitutes (e.g., raw chicken breast) were used for scavenging trials. We did find an effect of season on persistence time, with carcasses persisting longer in spring than fall. Among window collision studies, this finding agrees with Kummer et al. (2016), but contrasts Rawlings and Horn (2010) and Hager et al. (2012) who found persistence to be shorter in spring. In our study, the longer persistence in spring and lack of a seasonal effect on time to scavenging may both be related to the mild winters and hot summers at our study site, which allow scavengers—including cats and opossums, the two most frequently observed scavengers—to be abundant and active year-round, similar to magpies in Alberta (Kummer et al. 2016) but in contrast to mammals in Illinois (Hager et al. 2012). Shorter persistence in fall may have occurred because our study area experiences warmer temperatures in fall (Sep-Oct daily high 20.4-32.6°C) than spring (Apr-May daily high 19.6-28.3°C), which may allow more rapid invertebrate and microbial decomposition (Devault et al. 2004, Santos et al. 2011).

The observed positive correlation between carcass size and persistence after scavenging matches findings from previous studies of anthropogenic mortality, including bird-window collisions (Ponce et al. 2010, Smallwood et al. 2010, Santos et al. 2011, Teixeira et al. 2013, Bracey et al. 2016; but see Kostecke et al. 2001, Bernardino et al. 2011, Paula et al. 2015). If carcasses are opportunistically scavenged as encountered, carcass size should only affect time to scavenging (in the sense of our definition, which is independent of whether the carcass is entirely removed) insofar as it affects carcass detectability. However, even assuming equal detectability of all carcasses by scavengers, carcass size should also affect persistence time (i.e., time to removal) because larger carcasses require greater time and effort to remove entirely. Indeed, we observed that larger carcasses were more likely to persist after scavenging, even though size had no effect on overall persistence time. A possible explanation for the similar persistence times across carcass sizes is that the size of our trial carcasses did not vary substantially. The largest trial carcass was ~150 g, a size matching the small or medium category for other similar studies that also considered larger carcasses, such as Ring-necked Pheasant (*Phasianus colchicus*; ~1000 g) and Red-legged Partridge (*Alectoris rufa*; ~500 g) (e.g., Ponce et al. 2010, Smallwood et al. 2010, Bernadino et al. 2011, Villegas-Patraca et al. 2012). Regardless of the explanation, this finding further illustrates that a full understanding of how scavengers detect and remove carcasses requires parsing apart the factors influencing the time to scavenging, whether or not any carcass remains persist after scavenging, and the time to complete carcass removal.

We recorded more than twice as many scavenging events at night as we did during the day. Hager et al. (2012) noted a similar pattern (2 diurnal and 6 nocturnal scavenging events) based on a smaller sample size of trials in Illinois, and Villegas-Patraca et al. (2012) reported that >80% of carcasses were removed between 1700 and 0700 h in Mexico. This concentration of scavenging activity at night is perhaps unsurprising given that 3 of the 4 species we most frequently observed scavenging bird carcasses (cat, opossum, skunk) are largely nocturnal. However, for most studies, precise scavenging times are either unreported (Kummer et al. 2016) or unknown (Rawlings and Horn 2010, Bracey et al. 2016). A general period of peak scavenging (i.e., day or night) may be ascribed when the scavenger community is known, but descriptions of scavenging frequency by species are often lacking. Thus, there is a dearth of knowledge and a need for further research regarding exact scavenging times and temporal peaks of scavenging activity.

The timing of peak scavenging relative to the timing of peak mortality has important implications for this study and for the accurate estimation of anthropogenic wildlife mortality. Based on concurrent research in our study area, > 60% of bird-window collisions occur between evening and early morning (1900 to 0900 h; unpublished data [see Chapter 2]); however, the distribution of collisions within this period is unknown. If most collisions occur early in this period (i.e., in the evening), then a larger proportion of carcasses would be expected to be scavenged before the subsequent morning's carcass survey than if most collisions occur late in this period (i.e., in the early morning). Notably, most bias estimators, including the one used in this study (Korner-Nievergelt et al. 2011), were developed for studies of wildlife collisions with wind turbines, which generally have search intervals > 1 day in length (Smallwood 2013). For these studies, it may be implicitly assumed that there is more than one peak in scavenging activity between carcass searches, and thus the relative timing of scavenging and mortality are unimportant. However, for studies such as ours with a search interval of 1 day, timing is more consequential. Specifically, if peak mortality occurs in the morning immediately prior to carcass surveys, there is little opportunity for scavengers to scavenge and remove carcasses, and these estimators may substantially overestimate the proportion of carcasses removed. Further research is needed to determine diel variation in mortality for different anthropogenic threats and to assess relative biases of different statistical estimators for studies with 1-day search intervals and varying temporal occurrence of peak scavenging and mortality.

Our observed values of mean time to scavenging (2.7-3.3 days) and mean persistence time (3.1-40.6 days) suggest that relatively few carcasses were removed between daily searches. However, the estimated daily persistence probability was 0.91, which indicates that even with daily searches, raw fatality counts would have underestimated mortality by ~9%. Previous studies have documented comparable carcass persistence, including 3.5 days survival time (Kummer et al. 2016), 4.3 days expected time to scavenging (Bracey et al. 2016), and 3.5-29.6 days survival time (Hager et al. 2012). Notably, the subtle differences among the terms scavenging, removal, and persistence/survival were not clearly distinguished in these studies, which limits cross-study comparisons and could lead to misapplication of bias estimates. The three studies of window collisions where trial carcasses were left in place for > 1 day (Hager et al. 2012, Bracey et al. 2016, Kummer et al. 2016) all acknowledged that scavenging did not always lead to complete carcass removal. Although Hager et al. (2012) separately recorded persistence time beyond initial scavenging, all three studies used the terms removal and scavenging interchangeably in presenting and discussing results. Failing to recognize and/or distinguish the difference between the initial scavenging event and complete carcass removal is also common for other anthropogenic mortality sources (e.g., Kostecke et al. 2001, Flint et al. 2010, Bernardino et al. 2011). Because removal may not coincide with scavenging for a large proportion of carcasses, we recommend that future studies follow the terminology used here and clearly distinguish between scavenging (an event where all or part of the carcass is taken by a scavenger) and removal (the end point of persistence, which may or may not coincide with scavenging).

Searcher efficiency was highest when experienced surveyors were searching on artificial substrates. Artificial substrates provided better visual contrast (less camouflage) with fewer obstructions than natural substrates. Among studies of other anthropogenic mortality sources that tested for effects of vegetation structure, searcher efficiency has similarly been shown to decrease in areas of dense vegetation (Morrison 2002, Rivera-Milán et al. 2004, Stevens et al. 2011, Boves and Belthoff 2012, Campedelli et al. 2014). Our overall estimated searcher efficiency ($f = 0.73$), despite likely representing a minimum value, exceeded estimates from window collision studies in Alberta (0.60; Wood 2014) and Minnesota (0.16; Bracey et al. 2016), as well as most previous estimates for observer detection trials for other anthropogenic mortality sources (e.g., Linz et al. 1991, Morrison 2002, Gehring et al. 2011, Campedelli et al. 2014). Our relatively high overall searcher efficiency is likely related to the study area's limited vegetation cover and large expanses of pavement and manicured lawn.

We found some evidence that experienced searchers were more efficient at detecting carcasses, a finding that corroborates some previous studies (Ponce et al. 2010, Bracey et al. 2016; but see Rivera-Milán et al. 2004) and likely reflects the well-developed search images of experienced observers relative to occasional volunteers. Contrary to expectations based on previous studies (Gehring et al. 2011, Boves and Belthoff 2012), we found no effect of season on searcher efficiency. However, unlike previous research, our survey areas exhibited minimal seasonal changes in vegetation cover, and further, we did not perform observer detection trials in winter when conditions influencing detectability may have differed more dramatically. Because we expected carcass size and color to affect detection (Smallwood 2013) and sought to isolate other potential detectability correlates, we used a limited number of species that were similar in appearance. We therefore cannot make conclusive statements based on our searcher detection trials about variability in detectability among carcass species. However, the longer persistence of larger carcasses in the scavenging trials does provide further evidence that detection may be biased toward larger species in studies where partially scavenged carcasses are included in fatality counts.

Conclusions

In assessing the effects of the scavenger community on carcass persistence, as well as correlates of observer detection, our research provides important insight into how these biases influence quantification of bird-window collision mortality. Furthermore, our approach of explicitly parsing apart carcass scavenging and removal events improves understanding of the scavenging process and provides a framework for future studies of both window collisions and other mortality sources that will make them more interpretable and comparable. Understanding the community of scavengers present in different spatiotemporal contexts, and how scavenging and removal rates differ among species, seasons, and locations, is a key area of future anthropogenic mortality research. Similarly, understanding factors influencing observer detection bias will help inform future study designs and observer training programs to best account for these factors. Further research is also needed to separately assess the correlates of scavenging and observer detection for different geographic locations, scavenger communities, and bird species, and to assess other potential correlates of scavenging and detection, such as local vegetation and surrounding features of the landscape at multiple spatial scales. A larger collective body of research on scavenging and observer detection biases would provide important site-specific information about mortality impacts and potential mitigation. Further, if conducted in a standardized fashion (e.g., with explicit definition of the scavenging terms defined here), this aggregate of research could be used to generate a data-informed range of bias correction factors, which could then be used to update and improve on previous large-scale estimates of bird-building collision mortality (e.g., Machtans et al. 2013; Loss et al. 2014) that largely relied on assumptions about these bias factors or used bias estimates from other mortality sources. Collectively, the current study, as well as these areas of future research will contribute to minimizing biases in estimating the magnitude and population impacts of bird-building collisions, and of anthropogenic sources of wildlife mortality more broadly.

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CHAPTER II

MULTI-SCALE TEMPORAL VARIATION IN BIRD-WINDOW COLLISIONS IN THE CENTRAL UNITED STATES

Abstract. Expansion of urbanization and infrastructure associated with human activities has numerous impacts on wildlife including causing wildlife-structure collisions. Collisions with building windows are a top mortality source for birds, but a lack of formal research into the timing of these collisions hampers efforts to predict them and mitigate effects on avian populations. In Stillwater, Oklahoma, USA, we investigated patterns of bird-window collisions at multiple temporal scales from within-day to among-season variation. We found that fatal and non-fatal collisions peaked during overnight and early morning hours and that these diel patterns were seasonally invariant. We also found that fatal collisions varied weekly, monthly, and seasonally, and that these temporal patterns were influenced by avian residency status. Unexpectedly, given past studies showing most collisions occur during fall migration, total mortality was highest in May and higher for resident than migrant individuals. However, mortality was greater for migrants than residents during spring and fall migration, and migrant mortality was greater in fall than spring. These findings, some of which contradict past descriptive research and "common knowledge" regarding this source of bird collision mortality,

have important implications for understanding the mechanisms by which birds collide and for improved timing of measures design to reduce collisions.

Introduction

As earth's human population grows, urbanization and the construction of infrastructure (e.g., buildings, roads, communication towers, and energy installations) are increasing. The effects of this expanding human footprint on wildlife and the terrestrial and aerial ecosystems they inhabit are largely negative (McKinney 2002, Chace and Walsh 2006, Lambertucci et al. 2015). Collisions of wildlife with human structures and vehicles are a major, increasing source of mortality associated with urbanization, particularly for volant animals like birds and bats (Calvert et al. 2013, Loss et al. 2015). Recognition of the increasing severity of wildlife collisions has led to growth in research evaluating the magnitude and effects of various collision sources, the factors driving collision rates, and the optimal approaches to reduce collisions in order to assist conservation efforts for affected species (Kunz et al. 2007, Bernardino et al. 2018).

For birds, collisions with buildings, particularly at windows and other glassy surfaces, represent the largest source of collision mortality in North America (Machtans et al. 2013, Loss et al. 2014). A large body of research now exists for this mortality source, including studies that: test approaches to deter collisions (Klem 2009, Rössler et al. 2015, Kahle et al. 2016); identify building-, vegetation-, and landscape-related correlates of collision rates (Gelb and Delacretaz 2009, Cusa et al. 2015, Hager et al. 2017); and quantify and identify correlates of biases influencing collision estimates (e.g., searcher detection and scavenger removal; Bracey et al. 2016, Kummer et al. 2016, Riding and Loss 2018). Understanding the timing of bird-window collisions—for example whether birds collide more frequently in migratory or non-migratory periods or in the morning or afternoon—is important for understanding mechanisms by which birds collide, the likelihood of population impacts (Boyce et al. 1999), and the optimal timing of management interventions. However, few studies have formally quantified the timing of bird-window collisions beyond anecdotal or descriptive accounts, and none have done so at the multiple scales at which this temporal variation appears to occur.

These multiple scales of temporal variation in bird-window collisions are expected based on avian and vegetation phenology, bird behaviors that vary across time, and human behaviors and activity patterns that influence vegetation and bird behavior. Indeed, evidence suggests that both diel (Klem 1989, Gelb and Delacretaz 2009, Nishi 2010, Hager and Craig 2014, Šumrada 2015, Aymí et al. 2017) and seasonal (Codoner 1995, Blem and Willis 1998, Borden et al. 2010, Hager et al. 2013, Bracey et al. 2016) collision patterns exist, as opposed to a random or uniform temporal distribution of collisions. Daily patterns are most likely driven by bird behaviors and activity schedules. Nearly all birds exhibit bimodal diel patterns in foraging and local movements, with the highest peak early in the day and a secondary peak in the evening (Robbins 1981, Bednekoff and Houston 1994). For migratory species, diel patterns of long-distance movements also exist, with some species migrating primarily during the day, and others, including those most vulnerable to window collisions (Loss et al. 2014), migrating primarily at night. Anthropogenic lighting can attract and disorient these nocturnally migrating birds, likely elevating collision risk during overnight and pre-dawn periods

(Van Doren et al. 2017). However, migrating birds are also prone to window collisions in daylight hours during local (e.g., foraging) flights (Hager et al. 2017). Descriptive accounts illustrate tentative diel patterns in collisions, such as most collisions appearing to occur between sunrise and noon during migration (Gelb and Delacretaz 2009, Šumrada 2015, Aymí et al. 2017) and between late morning and early afternoon in the breeding season (Hager and Craig 2014).

Seasonal collision patterns are likely influenced by avian life history strategies (e.g., year-round resident versus migratory; Blem and Willis 1998, Hager and Craig 2014); variation in weather, bird population sizes, and human provision of food at bird feeders near residences (Dunn 1993, Kummer and Bayne 2015, Van Doren and Horton 2018); and phenology of vegetation that provides food, concealment, and/or nesting substrates near buildings. Overall, collision mortality tends to be higher during migratory periods, especially in fall migration (Johnson and Hudson 1976, O'Connell 2001, Breithaupt et al. 2013, Bracey et al. 2016). Geography may mediate such patterns by influencing the magnitude and timing of migration peaks at different latitudes (Dokter et al. 2018). For example, seasonal peaks of collision rates for migratory species should occur later in spring and earlier in fall with increasing latitude.

To enhance understanding of factors driving bird collision timing and provide information to improve collision deterrence efforts, we conducted an analysis of multi-scale temporal variation in bird-building collisions in a small urban area in the U.S. Great Plains. This region is largely unstudied with respect to bird-window collisions. Further, small urban areas in largely rural landscapes, such as our study area, are understudied despite evidence that variation in and predictors of collisions in such settings differ from intensely urbanized regions (Hager et al. 2017). Using a multi-year, multi-season, systematic approach, we: (1) quantified diel (time-of-day) collision patterns across and within seasons by conducting morning, midday, and evening surveys, and (2) assessed monthly and seasonal (time-of-year) collision patterns, including in relation to avian residency status, based on carcass surveys from April through October. Based on the above preliminary evidence, and with respect to objective 1, we predicted collisions would occur most frequently during morning hours (i.e., most carcasses would be found during midday surveys) and that diel patterns would be seasonally invariant. With respect to objective 2, we predicted mortality would be highest in the fall and that migratory species would experience a greater frequency of collisions than resident species, especially during migration seasons.

Methods

Study area and study design

We searched for bird carcasses resulting from window collisions in Stillwater, Oklahoma, USA, a small urban area with a human population of 45,688 in the 2010 census. The study area lies in the cross timbers transitional ecoregion, where deciduous forests from the east mingle with grasslands from the west to create a mixture of prairie, savannah, and woodland. We selected survey buildings based on building size, amount of surrounding vegetation, and accessibility (see Hager et al. 2017), a continental study that included a subsample of our study buildings). Buildings varied in footprint area (200–8000 m^2) and height (6–27 m), but none were the high-rise skyscrapers typical of larger urban areas. In total we monitored 16 buildings, including residences (n = 2), buildings on the Oklahoma State University main campus (n = 11), and commercial off-campus structures (n = 3).

To serve as a baseline for assessing temporal variation in collisions, we conducted morning carcass surveys around all buildings ≥6 days/week during all non-winter months (Apr–Oct) in 2015 and 2016. We started these near-daily surveys between 0700–0900 h (all times Central), unless inclement weather or other extenuating circumstances (e.g., safety or volunteer availability) made this infeasible. During winter months (Nov–Mar), we did not conduct full-scale monitoring due to staffing limitations and because winter bird-window collision mortality is generally minimal compared to other seasons (O'Connell 2001, Hager et al. 2008, Hager et al. 2013, Borden et al. 2010, Schneider et al. 2018). We did monitor a subset of 4 buildings 1 day/week during winter of 2015–2016 and a subset of 5 buildings 2 days/week during winter of 2016–2017, but we excluded winter data from formal statistical analyses because the sampling interval differed substantially from other seasons.

To assess diel patterns, we also conducted midday (1200–1400 h) and evening (1700–1900 h) carcass surveys at a subset of the buildings monitored in the morning. To ensure an adequate sample size of collisions for diel analyses, these midday and evening surveys (hereafter referred to collectively as “extra surveys”) were conducted at non-randomly selected buildings or portions of buildings that we considered likely to experience the greatest number of collisions based on preliminary observations and putative correlates of mortality risk (e.g., large surface area of glass). We conducted these extra surveys in 2-week (2015) or 1-week (2016) bouts within seasons, totaling 5 bouts in spring (Apr–May), 3 in summer (Jun–Aug), and 3 in fall (Sep–Oct). During these bouts, extra surveys were conducted for each day that morning surveys were conducted (i.e., ≥6 days/week).

Data collection

Surveyors fell into two groups: experienced personnel who regularly and frequently conducted carcass surveys (including the authors, research technicians, and more experienced volunteer citizen scientists), and less experienced volunteer citizen scientists who conducted surveys irregularly and infrequently (we describe in the Discussion how this variation in survey experience could have influenced our results). Prior to participation, we required all surveyors to receive training on protocols for conducting surveys, collecting dead birds, and recording and entering data. During surveys, we walked slowly along the exterior perimeter of focal buildings, intensively searching a 2 m swath along walls with glass surfaces, such as windows. We entered three buildings to survey ledges below windows that could not be observed from outside. All surveys consisted of a single pass around each building or along each building segment, but we alternated the direction each building or segment was monitored daily (clockwise on even days, counter-clockwise on odd days).

The purpose of these surveys was to detect and accurately count carcasses of collision-killed birds; thus, we did not include smudges (e.g., feathers or other bird-related markings on glass surfaces), as these had ambiguous outcomes and could have led to double-counting some carcasses (e.g., one or more smudges in one location corresponding to a living or dead bird that moved to another location before being encountered). However, we did record non-fatal collisions, including those directly witnessed by the surveyor where the bird did not immediately die and/or flew away after experiencing no apparent harm, and stunned birds lying on the ground or in vegetation that had likely suffered a recent collision. Upon discovery of an intact carcass or stunned bird, surveyors took photographs and recorded the location and a description of the event (including species, if known). We similarly documented remains indicative of a carcass. In most cases, such remains consisted solely of feathers (i.e., a feather pile) that had been plucked from the carcass by a scavenger. To avoid counting adventitiously lost feathers, we defined a feather pile to consist of ≥ 5 feathers within a circular area approximately 15 cm in diameter. As some feather piles could have originated from sources other than window collisions (e.g., predation of live birds), counts of feather piles were excluded from some analyses (as described below). We collected carcasses and remains using a plastic, sealable bag, and subsequently stored them in a freezer with a unique alphanumeric identification code for each individual bird. When we could not collect a carcass (e.g., because it was on an inaccessible ledge above ground level), and at one building where carcasses were regularly left in place as part of a concurrent study, we tracked the condition and location of the carcass to avoid double counting it on future surveys. We collected carcasses under federal (U.S. Fish and Wildlife Service permit #MB05120C-0) and state (multiple permits over course of the study) scientific collecting permits with protocols approved by the OSU Institutional Animal Care and Use Committee (Animal Care and Use Protocol #AG-14-8). Other than attempting to photograph birds that collided for identification and documentation, we did not interact with live birds during surveys and were not required to obtain a separate Animal Care and Use Protocol. We followed published guidelines (Fair et al. 2010) for best practices to minimize potential negative impacts to live birds during our surveys.

We determined residency status of each individual bird observed in carcass surveys based on the date collision events were observed; the age of the bird, when determinable (e.g., hatch year birds are unlikely to be migrating in May and June); seasonal occurrence data from eBird (Sullivan et al. 2009); and a guide to arrival, migration, and departure dates for species in our study region (Oklahoma Bird Records Committee 2014). We categorized each carcass as: (1) resident, for individuals from non-migratory species and seasonally or partially resident species found outside of a migratory period; (2) migrant, for any individual determined to be on migration, including summer and winter residents during their migratory periods and passage migrants that occur in our study area only while migrating; (3) unknown, for individuals from species (including partial migrants) with significant overlap in timing for resident and migratory periods (e.g., American Robin [*Turdus migratorius*] during Apr and Oct); and (4) unidentified, for any bird remains that could not be identified to species, most of which were feather piles. The Lincoln’s Sparrow (*Melospiza lincolnii*), a species that is a winter resident of our study area but spends the summer far to the north and west, provides an example of how one species could have individuals classified into more than one residency status. Individuals observed during Apr–May and Sep–Oct were classified as migrants whereas individuals found during Nov–Mar were classified as residents.

Statistical analyses

For diel analyses, we did not include carcasses in counts if the building where we found the bird was not surveyed during the preceding period (e.g., we excluded data from a morning survey if the same building was not also surveyed the evening before). This was done to ensure we counted birds that collided only in the interval immediately preceding the survey. For monthly analyses, we included carcasses found during extra surveys because we assumed they would have been detected on subsequent morning surveys due to relatively low daily scavenging (0.09) and high surveyor detection (0.73) rates in our study area (Riding and Loss 2018).

We conducted all analyses in R 3.5.0 (R Core Team 2018) with RStudio 1.1.447 (RStudio Team 2016). Where noted below, we tested for overdispersion of data in regression models using the function 'dispersiontest' in R package 'AER'; these tests were conducted for global models without interaction terms that were fit using function 'glm'. To compare and rank models for diel and monthly analyses (see below), we used Akaike's Information Criterion corrected for small sample sizes (ΔAICc; Burnham and Anderson 2002). We interpreted variables from models that had strong support ($\Delta\text{AICc} \leq 2$) via conditional model averaging (function 'model.avg' in R package 'MuMIn'), but we did not consider any models that were more complex versions of higher ranking nested models (i.e., models that contained uninformative variables; Richards 2008, Arnold 2010).

To assess diel patterns, we treated individual surveys as replicates and separately analyzed two dependent variables (number of carcasses and number of non-fatal collisions) using zero-inflated Poisson (ZIP) regression (function ‘glmmTMB’ in R package ‘glmmTMB’ with ‘family = poisson’) because the models were not overdispersed but > 97% of these surveys resulted in a count of 0 carcasses. ZIP regression models are commonly used in cases of excess zero counts and have two parts: a logit model for predicting excess (structural) zeros and a Poisson model for predicting the count, which may or may not be zero (Lambert 1992). We included an offset for number of surveys (specific to each season and building combination) to account for varying sampling effort. Also, we modeled Year and Building as random effects (Brooks et al. 2017) because the substantial variation across levels of these variables was not of primary interest for our objectives. Notably, although inter-annual variation in collisions is likely to occur, our study was not long enough to conduct an analysis at this temporal scale. Additionally, although we included an analysis of bias-corrected fatality estimates for the monthly analysis, we were unable to do this for diel analysis—where individual surveys were treated as replicates—due to computational challenges of applying bias adjustments to the results of individual surveys. Potential predictors for both the logit and count components of the ZIP model included Season (categorical: spring, summer, fall), SurveyTime (survey start time in decimal format where, for example, 7.5 = 0730 hr), and the interaction Season*SurveyTime. However, when modeling the number of non-fatal collisions, we considered univariate logit models only because the algorithm often failed to converge with more than one variable in that model component. We modeled the continuous SurveyTime predictor rather than a categorical Period predictor (morning, midday, evening) because SurveyTime and Period (coded numerically: 1 = morning, 2 = midday, 3 = evening) were highly correlated (Pearson r = 0.99).

To assess monthly and seasonal patterns of fatal collisions we summed carcass counts for each month and residency class combination (i.e., month-residency class combinations treated as replicates) and separately analyzed three different dependent variables: (1) carcasses and feather piles, (2) carcasses only (i.e., excluding feather piles), and (3) counts adjusted for two major survey-related biases that cause raw counts to underestimate mortality: imperfect observer detection of carcasses and scavenger removal of carcasses between surveys (Riding and Loss 2018). Because only 7 of 28 (25%) month-residency class combinations had values of zero, we did not use zero-inflated regression; however, because data were overdispersed we employed a negative binomial distribution (function ‘glm.nb’ in R package ‘MASS’) with an offset for number of surveys to account for varying effort. For the analysis of bias-adjusted mortality estimates, we rounded values to the nearest integer because the negative binomial is a discrete probability distribution. Potential predictors included Month (coded categorically as 4 = April, 5 = May, etc.), Season (categorical: spring, summer, fall), and ResStatus (categorical: migrant, resident, unknown, unidentified). As Month and Season were conceptually and statistically correlated, we did not include both together in any models. We did not include interactions between ResStatus and other predictors because model algorithms failed to converge when we attempted to do so. For both diel and monthly analyses, the levels of categorical variables against which we made comparisons were fall (Season), April (Month), and migrant (ResStatus).

Results

Diel patterns

For diel analyses, we conducted 1438 surveys (442 morning, 494 midday, 502 evening) and tallied a total of 33 carcasses and 31 non-fatal collisions (Fig 2.1). Volunteers conducted 44 (10%) morning surveys, but all extra surveys were conducted by experienced personnel. We started very few surveys (n = 29; 2%) outside of our target time frames for each period, and all surveys started within ~60 min of either the beginning or end of the target frame. Further, the intervals between successive surveys at the same building were always ≥ 120 min.

For the diel analysis of fatal collisions, the AICc ranking of ZIP regression models resulted in 3 models in the confidence set (i.e., ΔAICc ≤ 2; Table 2.1). Among these confidence models, the logit component included SurveyTime or intercept-only models. Model averaging indicated that the number of structural zeros tended to increase with an increase in SurveyTime (i.e., more surveys with zero carcasses later in the day; β = 0.31, SE = 0.11); specifically, the odds of a survey resulting in a structural zero increased by a factor of 1.37 (the exponentiated coefficient of SurveyTime; i.e., *e*^0.31) for each hour later in the day. The count components from the confidence set included Season, intercept-only, and SurveyTime+Season models. Notably, the interaction term SurveyTime*Season did not appear in the confidence set, indicating that diel patterns of carcass counts did not vary by season. Based on model-averaged coefficients, the number of carcasses found during surveys used for the diel analyses was lower in summer relative to fall (β = -0.97, SE = 0.53) and decreased with an increase in SurveyTime (i.e., fewer carcasses later in the day; β = -0.21, SE = 0.06; Fig 2.1). However, the number of carcasses did not differ substantially between spring and fall (β = -0.07, SE = 0.45).

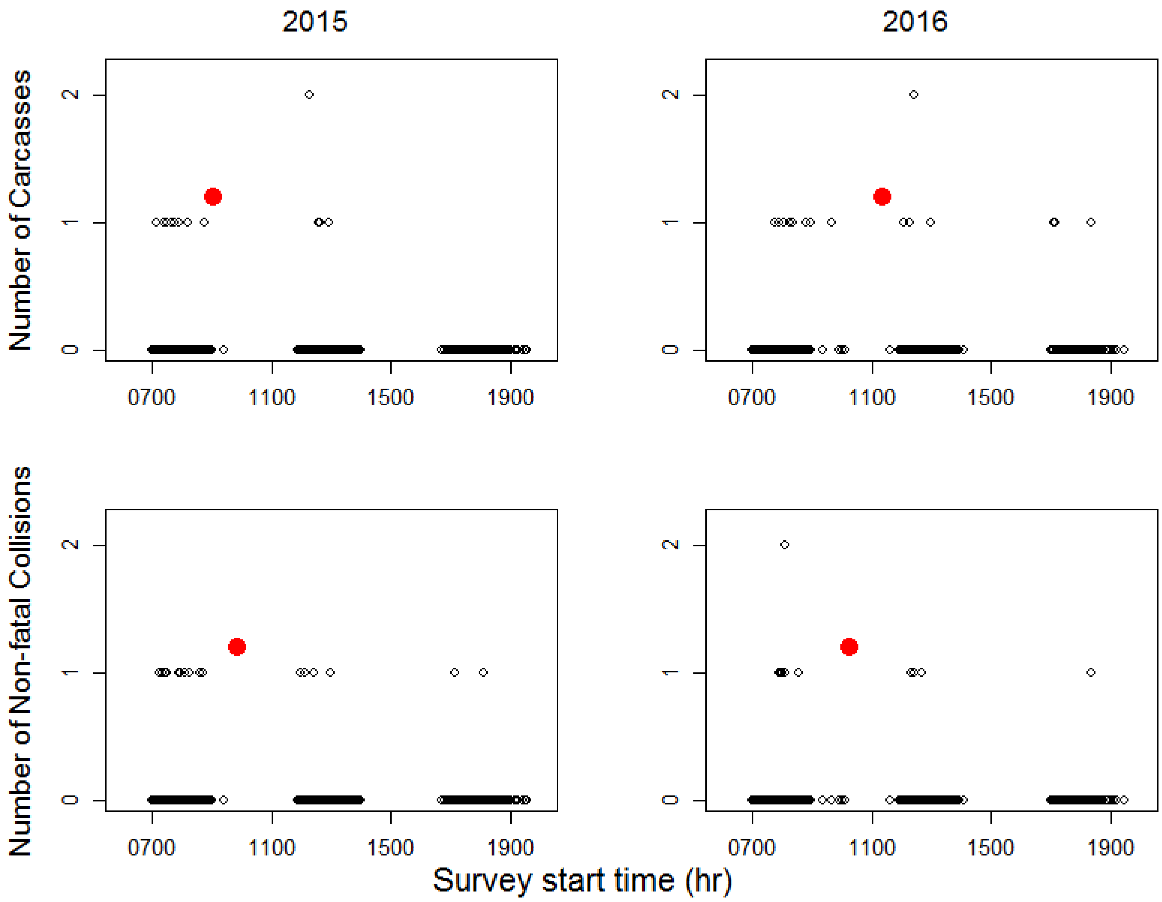

Figure 2.1. Number of carcasses or non-fatal collisions observed on surveys with different start times for 2015 and 2016. Red dots indicate annual mean start time of surveys with at least one carcass or non-fatal collision observed.

Table 2.1. Confidence set models (i.e., those with ΔAICc ≤ 2) resulting from full model selection comparison among candidate ZIP regression models that included factors potentially affecting numbers of bird carcasses found in morning, midday, and evening collision surveys. Weights are based solely on comparison of these models; full model selection results are shown in Appendix B: Table B3.

Logit model	Count model	K	ΔAICc	weight
SurveyTime	Season	7	0.0	0.49
SurveyTime	Null	5	1.0	0.30
Null	SurveyTime+Season	9	1.6	0.22

For the diel analysis of non-fatal collisions, the AICc ranking of ZIP regression models resulted in 2 confidence set models, among which the only predictor variable to appear in either the logit or count components was SurveyTime (Table 2.2). The top overall model had an intercept-only logit model with SurveyTime in the count model, while the other confidence set model had SurveyTime in the logit model and an intercept-only count model. This suggests that only SurveyTime was important to both the number of structural zeros and the number of non-fatal collisions, but it also suggests the influence of SurveyTime may be weak. As described in the methods, we were unable to test for an interaction between time of day and season for non-fatal collisions. Model averaging of the confidence set indicates that structural zeros increased with SurveyTime (i.e., more zeros later in the day; β = 0.31, SE = 0.09) and that the number of non-fatal collisions decreased with an increase in SurveyTime (i.e., fewer collisions later in the day; β = -0.25, SE = 0.06; Fig 2.1).

Table 2.2. Confidence set models (i.e., those with ΔAICc ≤ 2) resulting from full model selection comparison among candidate ZIP regression models that included factors potentially affecting numbers of non-fatal bird collisions found in morning, midday, and evening collision surveys. Weights are based solely on comparison of these models; full model selection results are shown in Appendix B: Table B2.

Logit model	Count model	K	ΔAICc	weight
Null	SurveyTime	5	0.0	0.69
SurveyTime	Null	5	1.6	0.31

Monthly/seasonal patterns

For the monthly analyses, we conducted 6631 surveys during non-winter months (Apr–Oct). We did not formally analyze winter data but we observed fewer carcasses (n=19) and feather piles (n=3) in winter months (Nov–Mar) than in other seasons (Table 3). Among non-winter surveys we found 275 carcasses and 66 feather piles, for a total count of 341 collision fatalities. Results based on all three different dependent variables (carcass counts including and excluding feather piles and bias-adjusted carcass counts) were nearly identical, with models ranked in the same relative order and estimated coefficients having the same sign and very minor estimated differences in effect sizes (see Appendix B: Tables B3-B4). Therefore, we present only results for the analysis of unadjusted total carcass counts (i.e., including feather piles).

In assessing predictors of monthly total carcass counts, there was only one confidence set model (Table 2.4), which contained the predictors ResStatus and Month. The estimated coefficients suggest that mortality was higher among resident individuals than migratory individuals (β = 0.55, SE = 0.18) and that the greatest numbers of monthly collisions occurred in May (β = 1.48, SE = 0.25), followed by Oct (β = 0.54, SE = 0.28) and Sep (β = 0.52, SE = 0.28). The high collision mortality for May was due to frequent collisions by both migrant and resident individuals during that month (Fig 2.2). The second highest unadjusted monthly total was in June, but when we adjusted for scavenger removal and searcher detection, June ranked slightly behind both Sep and Oct (Table 2.3). Although both the raw counts and bias-adjusted estimates of total bird mortality (Table 2.3) were greater for spring (Apr–May) than fall (Sep–Oct), migrant mortality was higher during fall than spring (Fig 2.2).

Table 2.3. Raw counts and seasonally-adjusted estimates of carcasses and feather piles by month based on carcass surveys in Stillwater, Oklahoma during Apr 2015 to Mar 2017.

Month	**Surveys**	**Carcasses**	**Feather piles**	**Total**	**Seasonal bias**	**Adjusted carcasses**	**Adj. total**	**Adj. per survey**
Jan	56	0	1	1	0.6800013	0	1.5	0.027
Feb	56	0	0	0	0.6800013	0	0	0.000
Mar	79	3	0	3	0.6800013	4.4*	4.4*	0.056*
Apr	982	24	5	29	0.8833435	27.2	32.8	0.033
May	1004	92	13	105	0.8833435	104.1	118.9	0.118
June	879	41	16	57	0.9051826	45.3	63.0	0.072
July	985	17	6	23	0.9051826	18.8	25.4	0.026
Aug	925	13	13	26	0.9051826	14.4	28.7	0.031
Sep	886	39	10	49	0.7583676	51.4	64.6	0.073
Oct	970	49	3	52	0.7583676	64.6	68.6	0.071
Nov	94	15	2	17	0.6800013	22.1*	25.0*	0.266*
Dec	65	1	0	1	0.6800013	1.5	1.5	0.023

* Adjusted numbers were overestimated for March and November because surveys in both months occurred more frequently than calculated in bias adjustments.

Table 2.4. Results of model selection for GLM analyses of factors affecting total carcass count by season for bird-window collision monitoring in Stillwater, Oklahoma, 2015-2017.

Parameters	**K**	**ΔAICc**	**weight**
Month+ResStatus	11	0.0	1
Season+ResStatus	7	23.2	<0.001
ResStatus	5	44.0	<0.001
Month	8	122.4	<0.001
Season	4	129.7	<0.001
Null	2	132.3	<0.001

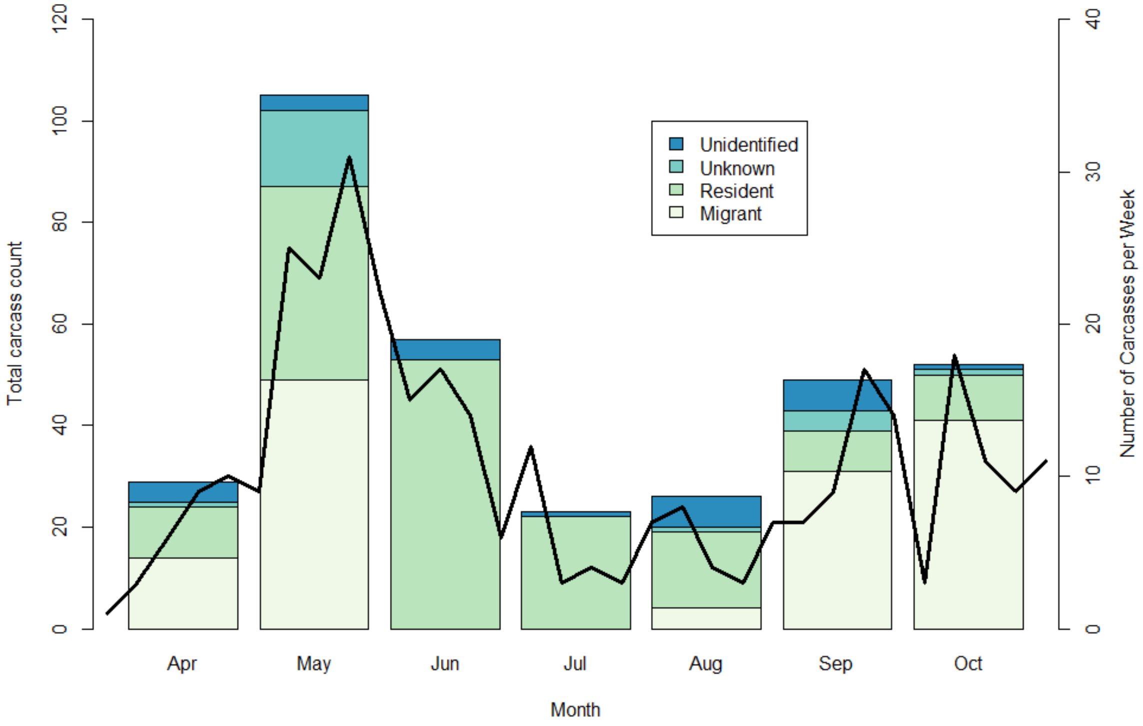

Figure 2.2. Monthly frequency of fatal collisions (including carcass counts and feather piles) by residency status of individual birds from collision monitoring in Stillwater, Oklahoma, 2015–2016. The black line indicates weekly fatal collisions detected (right-side y axis).

We were unable to formally test for an interaction of ResStatus with Month or Season, but such an interaction appears likely. Specifically, whereas migrant mortality surpassed resident mortality in spring and fall, nearly all collision fatalities in June and July were residents (and none were migrants), and total resident mortality was greater than total migrant mortality for all months combined (Fig 2.2). In addition to monthly patterns, we also observed week-to-week variation in collisions that, although generally coinciding with monthly trends (Fig 2.2), indicated that collision variation occurred at a temporal scale intermediate to diel and monthly variation. For example, summarizing total counts by week illustrated a small peak in collisions in early July and a relative lull in collisions in early Oct.

Discussion

In this multi-scale assessment of bird-window collision temporal patterns, our predictions related to the diel timing of collisions were only partly supported. We predicted more casualties during morning than other times of day, which should have resulted in the greatest number of carcasses on midday surveys and more non-fatal collisions during morning surveys than midday and evening surveys. However, the greatest numbers of both carcasses and non-fatal collisions were observed on morning surveys, indicating that more collisions occurred during overnight and early morning periods than mid-to-late morning and afternoon. As predicted, this diel pattern was consistent across seasons. Our predictions regarding monthly and seasonal patterns were also only partially supported. Unexpectedly, total collision mortality was highest in May and higher for resident than migrant individuals. However, as predicted, mortality was greater for migrants than residents in both spring and fall migration, and migrant mortality was greater in fall than spring.

We observed more carcasses and non-fatal collisions in the morning than in midday and evening surveys combined, even though we included fewer morning surveys in diel analyses. These estimated differences in mortality are likely conservative in that an even greater proportion of mortality than we observed likely occurs overnight and in the early morning. A concurrent study (Riding and Loss 2018) found that relatively inexperienced volunteers had slightly lower carcass detection rates (0.69) than experienced surveyors (0.76). Because roughly 10% of morning surveys were conducted by less-experienced volunteers and all midday or evening surveys were conducted by full-time technicians or the authors, we likely missed more carcasses on morning surveys. Additionally, most scavenging events (68%) were at night (Riding and Loss 2018), so bird carcasses from overnight collisions were the least likely to persist until the subsequent survey. Thus, underestimation of collision mortality in the preceding interval was almost certainly greater for morning surveys than for midday and evening surveys.

A prevailing hypothesis for why daytime bird-window collisions occur is that birds making local (e.g., foraging) movements fail to perceive a barrier when flying toward objects either on the other side of glass or reflected on a glassy surface (Machtans et al. 2013, Hager et al. 2017). Under this hypothesis, daytime collisions for both residents and migrating birds at stopover locations would be expected to occur most frequently when birds are most active, which is typically near dawn regardless of season. Our finding of the greatest number of collision fatalities on morning surveys circumstantially supports the above hypothesis and expectation, as do past descriptive studies of diel variation in bird-window collisions (Klem 1989, Gelb and Delacretaz 2009, Šumrada 2015, Aymí et al. 2017). However, our study design did not allow differentiation between nocturnal and early morning collisions, and a nontrivial proportion of carcasses detected on morning surveys likely represented collisions from the preceding overnight period. Nighttime collisions may occur at any structural component not easily detectable at night (i.e., they are not limited to glass surfaces), and can be exacerbated by artificial light emission that attracts and disorients migrating birds (Parkins et al. 2015, Ramirez et al. 2015). Nonetheless, the observation of more non-fatal collisions (including directly witnessed collisions) during morning than midday or evening surveys does strongly suggest that morning carcass counts included many collisions that occurred near or after dawn.

A potential limitation of our study regarding time-of-day analyses is the longer interval between evening and morning surveys than between other survey periods. Even if collisions occurred uniformly or randomly in time, we would find more carcasses during morning surveys due to the longer preceding time interval. However, as described above, the early morning peak observed for non-fatal collisions (Fig 2.1), which are less persistent than carcasses and therefore do not accumulate over time, suggests that collisions do not have a uniform or random temporal distribution and that a real peak in collision frequency occurs sometime shortly prior to when we conducted morning surveys. Further research is needed to identify the exact timing of collisions, including during overnight periods, and this could be accomplished with carcass surveys conducted at different times of night or remote detection methods, such as video cameras, motion-triggered still cameras, microphones that record sounds of impact, and glass-mounted pressure sensors that detect vibrations from collision impacts.

We predicted diel collision patterns would not vary seasonally because the bimodal activity pattern of birds (i.e., primary peak near sunrise and secondary peak before sunset) is relatively invariant seasonally. Hager and Cosentino (2014) provide excellent guidelines for conducting bird-window collision surveys, but their recommendation to conduct surveys in mid-to-late afternoon is based on summer monitoring that found mortality to peak between late morning and early afternoon in Illinois, USA (Hager and Craig 2014). We suspect differences in diel patterns between that study and ours are related to geographic variation and/or seasonal sampling coverage, as our larger sample of surveys included spring and fall migration in addition to summer. Although many collision-prone species migrate nocturnally, the diel collision peak for migrants could still occur in early morning because nocturnally-migrating birds often set-down into stopover habitats during early morning (Diehl et al. 2003, Coppack et al. 2008) and may be most susceptible to collisions at this time. Summer collisions likely include resident individuals that collide during foraging and other short-distance movements on breeding grounds, unpaired (i.e., “floater”) individuals moving across territories, and birds dispersing between locations of successive breeding attempts. Although there could be subtle seasonal variation in diel collision patterns that we failed to detect, the majority of collisions across seasons appear to occur near or before dawn (see also Aymí et al. 2017, Gelb and Delacretaz 2009, Klem 1989, Šumrada 2015). In combination with the previous study showing that scavenging peaks overnight, we suggest that conducting daily collision surveys in the morning should result in the least biased mortality estimates, especially in urbanized areas where humans (e.g., cleaning crews) remove carcasses in the early morning. As noted by Hager and Cosentino (2014), further research is needed to identify how the optimal survey time is influenced by factors such as geography, the bird community, and human and animal scavengers.

We expected more collisions in fall than other seasons because bird populations in North America are larger after summer breeding and include higher proportions of young birds that have less experience with flight, migration, and human structures. Also, numerous studies have found the greatest window collision mortality in fall (Agudelo-Álvarez et al. 2010, Borden et al. 2010, Bracey et al. 2016, Hager et al. 2013, Kahle et al. 2016, Klem 1989, Kummer and Bayne 2015, Zink and Eckles 2010, Low et al. 2017). Contrary to expectation, both total carcass counts and bias-adjusted estimates were highest in May and higher in spring than fall. However, this pattern was driven by the relatively large number of resident birds that collided in May. When considering migrating individuals only, we found slightly more collisions in fall than spring—despite the greatest single-month total occurring in May—a finding more in line with past studies. Notably, two other studies that found a large proportion of resident colliders (Blem and Willis 1998, Breithaupt et al. 2013) also documented a seasonal pattern less skewed toward fall. Another explanation for the large amount of spring mortality, and for the peak of migrant mortality in May, is that some long-distance migrants follow elliptical migration paths where migration routes in fall are farther east than in spring (Cooper et al. 2017, La Sorte et al. 2014), such that in central North America, numbers of some species are greatest during spring migration. This explanation is supported by our observation of some elliptical migrants colliding during spring but not fall (e.g., Swainson's Thrush [*Catharus ustulatus*]). Our study adds further nuance to the understanding of seasonal variation in bird collisions and exemplifies the need to study bird-window collisions in a wider array of geographic contexts to allow region-relevant management recommendations.

Our predictions regarding avian residency status were only partly supported; more migrants than non-migrants were indeed killed during migration, but across the entire period of Apr–Oct, more residents collided. This latter result was unexpected given that previous studies have almost universally reported higher mortality among migrants (Aymí et al. 2017, Gelb and Delacretaz 2009, Hager et al. 2017, O'Connell 2001, Sabo et al. 2016, Wittig et al. 2017, Agudelo-Álvarez et al. 2010, Keyes and Sexton 2014), although most only sampled during migratory periods. Even with our individual-based residency designations, we may have slightly underestimated migrant mortality because all individuals of some migratory species were classified as unknown due to overlapping resident and migratory periods. However, even if all unknown individuals were migrating, there were too few birds in this category (22 of 341 [7%] total carcasses) to change our conclusions regarding the migrant-resident comparisons. Anecdotally, many spring and summer carcasses were recently fledged juveniles (n=26 [25%] in May; n=17 [30%] in June), clearly indicating that some collision victims were indeed not migrating, and therefore, that the high number of resident collisions is not an artifact of our classification system. Moreover, we observed many collisions in June, when very few species, except shorebirds (order Charadriiformes) and small numbers of some tyrant flycatchers (family Tyrannidae), are migrating through our study area (Oklahoma Bird Records Committee 2014). It is possible, however, that some resident individuals were undergoing post-breeding dispersal at the time of collision, as evidenced by a small late-June peak of Tufted Titmouse (*Baeolophus bicolor*) and Carolina Chickadee (*Poecile carolinensis*) collision victims with brood patches (unpublished data).

Other seasonally variable factors, especially weather, likely contributed to the seasonal and monthly collision variation that we observed. Studies conducted to date show no clear, consistent weather-related predictors of bird-building collisions (Evans Ogden 2002, Keyes and Sexton 2014), but formal analyses are lacking, and weather has been a contributing factor in several major bird-building collision events (Brewer and Ellis 1958, Maehr et al. 1983, Wang et al. 2011, Ramirez et al. 2015). Regular weather conditions such as precipitation, cloud cover, and the presence and/or strength of headwinds or tailwinds—as well as more extreme weather events like intense storms—are known to influence the timing and magnitude of bird migration (Van Doren and Horton 2018), and are thus likely to influence collision risk. Some of these factors (e.g., low cloud ceilings) may have especially strong effects on nocturnal migrants by exacerbating effects of nocturnal lighting and driving birds into areas of greater collision risk. When considering the week-to-week variation we observed within seasons, the fine-scale peaks and lulls in collisions may respectively reflect weather conditions that favor or disfavor bird migration (e.g., strong tailwinds or headwinds, respectively) and/or elevate or reduce collision risk for migrating birds (e.g., low cloud ceilings or clear skies, respectively). A complementary explanation for weekly variation is the varying migration phenologies of different bird groups; for example, the fall collision peaks in late Sep and mid-Oct may reflect the migration peaks for wood warblers (family Parulidae) and sparrows (family Passerellidae), respectively, in our study region. Further research is needed to investigate correlations between weather and collisions at various temporal scales, and analyses such as ours that document multi-scale temporal variation in collisions are a step toward this improved understanding.

In conclusion, we documented multi-scale temporal variation in bird-building collisions, including diel, monthly, and seasonal patterns, some of which contradict past descriptive research and "common knowledge" regarding bird-building collisions. This information is crucial for improving understanding of the mechanisms by which birds collide and for efficiently targeting collision reduction measures in time. For example, contrary to past research, we found strong evidence that both fatal and non-fatal collisions peak overnight and/or during early morning hours. This pattern—which has previously been shown for bird collisions with skyscrapers in major cities, but not for smaller buildings in smaller cities—indicates that any temporary efforts to deter collisions (e.g., closing blinds, raising movable screens, emitting sonic deterrents; Kahle et al. 2016, Swaddle and Ingrassia 2017) will likely be most effective during these time periods. This pattern also suggests collision reductions may be achievable by enacting lights out programs at smaller buildings and in smaller cities than for which this method has traditionally been prescribed.

We also found collisions to vary monthly and weekly with the unexpected pattern that more resident than migrant birds collided from Apr to Oct and that collisions peaked in May. At these longer temporal scales, weather and other seasonal changes likely drive collision variation, thus predictions of collision risk based on weather and date may allow better focusing of collision deterrence efforts. Our results can also inform sampling protocols for future studies of bird-window collision. Specifically, our findings of the greatest number of carcasses on early morning surveys, as well as the relatively high amount of spring collision mortality, indicate that studies seeking to capture a larger and/or more accurate representation of birds killed should consider sampling during early morning and in both spring and fall migration. Finally, future research could include multi-year monitoring to detect any long-term collision trends that may occur in relation to factors such as avian population trends, urbanization and land cover change, and long-term changes in bird distributions and weather in association with climate change.

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CHAPTER III

FINE-SCALE AND SPECIES-SPECIFIC SPATIAL VARIATION IN BIRD-WINDOW COLLISIONS IN THE CENTRAL UNITED STATES

Abstract. Continuing urbanization exposes more wildlife to the dangers of urban environments, including collisions with glass surfaces (i.e., windows). Bird-window collisions are a major source of direct anthropogenic mortality, but spatial correlates have previously been studied only at larger scales and/or for all species combined. In Stillwater, Oklahoma, USA, we assessed the relationship between bias-adjusted mortality frequency and several putative spatial correlates (including structural, vegetative, and land cover variables) at the scale of individual building façades during spring, summer, and fall and for eight frequently colliding species. Façade structure, particularly the proportion of glass on the façade surface, was important to collisions across seasons and species. Other important correlates when seasons and species were combined included façade height, length, and structure. Species-specific results were more variable, and some species even had opposing relationships with important correlates. Given the overall importance of glass proportion and the variation in other correlates among seasons and species, general mitigation efforts should focus on

minimizing glass exposure but specific conservation goals may require further evaluation of correlates relevant to target species.

Introduction

Urbanization is increasing rapidly, with urban land cover expected to triple globally from 2000 to 2030 (Seto et al. 2012). Urbanization restructures biotic communities because tolerance to urban development is variable among species, and urban landscapes are variable with regard to abiotic conditions (e.g., temperature), vegetation cover, and human-built features (Faeth et al. 2005, Fischer et al. 2015, Oliveira Hagen et al. 2017). Even urban-avoiding species sometimes traverse urban landscapes during migration or other major movements, which means many species interact at least briefly with urban environments (Pennington et al. 2008, Seewagen et al. 2010, Homayoun and Blair 2016). Birds in urban settings, including migratory species that otherwise spend little time in heavily developed areas, are vulnerable to building collision mortality, a major conservation issue that has increasingly been the focus of scientific, management, policy, and public attention (Avery 1979, Erickson et al. 2005, Klem 2015, Seewagen and Sheppard 2017). Such collisions largely occur at windows and cause an estimated 365 to 988 million bird fatalities annually in the United States (Loss et al. 2014).

Bird responses to the spatial heterogeneity of resources (e.g., food and cover) and the built environment (e.g., buildings) occur at multiple scales and influence spatial variation in movements, habitat use, and thus bird-window collision risk (Hager et al.

2017). At broad scales, factors like proximity to water and extent of urbanization may affect the attraction of birds to the general area surrounding a building. At fine scales, features of buildings (e.g., building height, adjacent vegetation) and individual building façades (e.g., façade shape, proportion covered by windows) likely influence collision risk for birds already present near buildings. Previous studies of bird-window collisions have focused on collision correlates operating at the scale of entire buildings or broader (O'Connell 2001, Hager et al. 2008, 2013, 2017, Gelb and Delacretaz 2009, Klem et al. 2009, Borden et al. 2010, Bayne et al. 2012, Cusa et al. 2015, Ocampo-Peñuela et al. 2016), even though limited descriptive research indicates collision risk can vary among façades within a single building (Cusa et al. 2015, Kahle et al. 2016). The few studies that have considered effects of façade-level characteristics (Klem et al. 2004, Borden et al. 2010, Bracey 2011, Cusa et al. 2015) have focused on a single factor (e.g., façade aspect) or used the term façade ambiguously, where it was unclear if the term described a specific section of a building or an entire building. Furthermore, even in studies that spanned multiple seasons, season-specific assessments of collision risk factors have not been conducted.

Regardless of scale, important correlates of window collision risk likely vary among bird species—because species differentially use resources, select habitat, and respond to the urban built environment—which likely contributes to the known variation in window collision risk in association with taxonomy and life history traits (Loss et al. 2014, Sabo et al. 2016, Wittig et al. 2017, Nichols et al. 2018). Indeed, a study in Toronto, Canada found that feeding guild and habitat preference of a species affected landscape-level correlates of window collision risk, such that collision risk for species breeding in forested areas correlated with the amount of greenspace around buildings while collision risk for open woodland-inhabiting species was correlated with urban cover (Cusa et al. 2015). Other than this example from one major city, assessments of species-specific correlates of window collisions are lacking. Thus, in addition to the need for formal research into building façade-level collision correlates, there is also a need to investigate species-specific correlates of collision risk, especially in rural and small urban areas.

Façade-scale and species-specific assessments would be useful for informing management efforts to reduce bird-window collisions, such as considering collision risk in pre-construction building designs and mitigating collisions at existing buildings (e.g., by adding screens, cords, UV tape or paint, or patterned adhesive films; Klem and Saenger 2013, Rössler et al. 2015, Menacho-Odio 2018). Because mitigation across an entire building or multiple buildings may be cost-prohibitive, and in some cases unwarranted given evidence that collisions do not occur uniformly across all building façades, both fine-scale and species-specific understanding of spatial collision correlates could help target management efforts in which only specific portions of buildings are treated. Given the lack of formal analyses regarding fine-scale, species-specific correlates of bird-window collisions, our objective was to assess how bird-window collision rates in a small urban area in the central United States are influenced by façade-level variables, both within and across seasons and bird species. We addressed this objective by conducting near-daily surveys of 16 buildings in spring, summer, and fall to document specific collision locations and then relating façade-specific collision rates to eight potential predictor variables similar to factors that have been shown to influence collisions at coarser scales (e.g., building size, area of glass, and nearby vegetation).

Methods

Study area & study design

We surveyed for bird carcasses at 16 buildings in Stillwater, Oklahoma, USA, a small urban area with a human population of ~46,000 and with the vast majority of buildings consisting of residences or small (< 5 stories in height) office-type structures. Stillwater is in the cross timbers transitional ecoregion of the south-central United States, where deciduous forests from the east mingle with grasslands from the west to create a mixture of prairie, savannah, and woodland. We used a stratified approach to select survey buildings based on building size and amount of surrounding vegetation (Hager et al. 2017), but building selection was not completely random as we were constrained by building accessibility. The surveyed buildings included detached residences (n = 2), commercial off-campus-structures (n = 3), and classroom, office, and athletics buildings (n = 11) on the Oklahoma State University (OSU) main campus. We surveyed ≥ 6 days/week at all buildings during 1 Apr to 31 Oct in 2015-2016 and at 14 buildings (excluding the 2 residences) during 1 Apr to 31 May in 2017. For seasonal delineations, we considered spring to be Apr-May, summer to be Jun-Aug, and fall to be Sep-Oct.

Collision locations

Carcass surveys consisted of a single observer walking slowly along the exterior perimeter of a focal building, intensively searching a 2 m swath along all windowed walls. We also entered three buildings to survey ledges below windows that could not be observed from the outside. We alternated the direction that building perimeters were surveyed on a daily basis (clockwise on even days, counter-clockwise on odd days) to minimize detection effects related to the angle and direction from which an observer could approach a carcass (e.g., obstacles, shading). Upon discovery of an intact carcass, we took photographs and recorded the location and a description of the carcass. We similarly documented remains indicative of a carcass, which usually consisted solely of feathers (i.e., feather pile) that had been plucked from the carcass by a scavenger. To avoid counting adventitiously lost feathers, we only counted feather piles that consisted of ≥5 feathers within a circular area ~15 cm in diameter.

To avoid counting a single carcass more than once, we collected bird remains using a plastic, sealable bag, and subsequently stored them in a freezer with unique alphanumeric identification codes. When we could not collect a carcass (e.g., because it was on an inaccessible ledge above ground level), and at one building where carcasses were regularly left as found as part of a concurrent study of scavenger removal, we tracked the carcass condition and location to avoid double counting it on future surveys. We collected carcasses under federal (permit #MB05120C-0) and state (multiple permits over the study) scientific collecting permits, and protocols were approved by the OSU Institutional Animal Care and Use Committee (Animal Care and Use Protocol #AG-14-8).

We used written observer descriptions to record locations for carcasses and non-fatal collisions in Google Earth Pro 7.3.2 (Google; Mountain View, California), which allowed location accuracy to within ~2 m. When written location descriptions were ambiguous, we followed up within 1 day to have the observer who detected the carcass clarify the precise location by marking it on a map. We imported these collision locations to ArcGIS 10.2.1 (ESRI; Redlands, California) to generate and analyze spatial data. To generate façade-specific carcass counts, we spatially joined carcass locations, both including and excluding feather piles, to polygons representing the 2-m wide search area for each façade. We repeated this for each season (spring, summer, and fall) and for each species with ≥15 collision observations.

Façade variables

We defined a façade as a distinct section of a building (i.e., typically bounded by corners) that was qualitatively homogenous and exhibited minimal variation in measurable traits (e.g., height). We characterized eight façade-level variables, including façade height (m), façade length (m), façade type, distance to trees (m), three land cover variables, and proportion of the façade consisting of glass. We used digital photographs taken with a Panasonic DMC-ZS1 camera and analyzed in ImageJ 1.48 (Schneider et al. 2012) to measure the height, length, area, and glass-covered area of each surveyed building façade. We took photographs perpendicular to the center of each façade at a height of ~2 m and from as far away as possible (range: 5-75 m) while still capturing the façade with minimal obstacles. To serve as a known-dimension reference for calibrating measurements of façades and windows in photographs, we directly measured (i.e., with a measuring tape) ≥ 1 reference object (e.g., width of single window pane) at ~2 m height that was 1) clearly visible in the photograph, 2) near the center of the façade, and 3) occurred at multiple heights or along the length of the façade. Tall, long, or curved façades became non-orthogonal near the edges in photographs of the entire façade. To avoid biased measurements using these distorted portions of images, we used the known-length reference objects to adjust measurements incrementally away from the façade center. For very long façades, we took two photographs, each perpendicular to the façade at locations approximately 1/4th and 3/4th of the way along the façade's total length, and we then combined area estimates generated for each half of the façade.

Figure 3.1. Façade type examples from one building at Oklahoma State University (OS03 – Noble Research Center) monitored for bird-window collisions 2015-2017. A) Aerial view showing façade search areas as yellow polygons; façade perimeters with no search area were not monitored because they lacked windows. Façade types (described in text) included B) convex rounds, C) porticos, D) flats, E) alcoves, and F) concave corners.

Façade type included five categories (Fig 3.1): 1) alcove, where the façade, usually in conjunction with the adjoining façades, formed an indentation/concavity in the building outline when viewed on a horizontal plane (i.e., from above); 2) portico, where the façade formed an indentation/concavity in the building surface along a vertical plane resulting in a covered walkway or patio near ground level; 3) concave corner, where two short (≤ 5 m) façades united to form a small indentation in the building outline; 4) convex round, where the façade curved without any well-defined corners to form a protrusion in the building outline (note that a concave round would be considered an alcove); and 5) flat, where the façade formed a plane, perhaps with some small protrusions or indentations (typically ornamentations).

We calculated the remaining variables (land cover and distance to trees) using spatial data layers provided by the department of Geospatial Systems at Oklahoma State University (OSUGS), which included: georectified aerial imagery, points of individual tree bole locations, and polygons of some land cover types (buildings, parking lots, sidewalks, lawns, and flower beds). These data were limited to the main OSU campus, except for the aerial imagery, which covered the entire study area. For off-campus buildings, we used the aerial imagery (spatial resolution varied between 0.05 to 1.00 m, but was mostly < 0.25 m) and ground-truthing to digitize locations of individual tree locations. For the entire study area, we used aerial imagery to digitize cover classes that, spatially or categorically, were not included in the OSUGS land cover layer. We aggregated land cover into three cover classes: impervious (e.g., asphalt and concrete), lawn (short, maintained turf grasses), and flowerbeds (including hedges and shrubs). Because most façade search areas lacked tree canopy coverage and tree canopy did little to describe the cover at ground level, we did not consider it when classifying land cover. We calculated the proportion of each 2-m wide façade search area polygon overlapped by each cover class. We calculated distance to trees as the mean distance to the 3 trees nearest each façade polygon (trees within the polygon had a distance of 0 m). We used multiple trees, rather than only the nearest tree, to better characterize the proximity of tall vegetation generally.

Statistical analyses

We adjusted carcass counts to account for two major survey related biases that cause raw counts to underestimate mortality: scavenger removal of carcasses between surveys and imperfect observer detection of carcasses that remain present for surveys (Riding and Loss 2018). Although we assumed that a carcass location corresponded to a collision at the nearest façade, the source and location of mortality for feather piles had greater uncertainty. That is, a feather pile could represent a predator-killed bird or a window-killed bird that a scavenger moved away from the collision site before consuming. Therefore, we conducted analyses of counts across all species both including and excluding feather piles.

We conducted statistical analyses in R 3.5.2 (R Core Team 2018) with RStudio 1.1.463 (RStudio Team 2016). We treated individual façades as replicates to assess the importance of façade-level variables in explaining bias-adjusted carcass counts at each façade. Because response variables were continuous with a large number of zeros (i.e., we observed zero carcasses at many façades over the course of the entire study), we used a compound Poisson-gamma mixed model (function ‘cpglmm’ in package ‘cpglm’;

Zhang 2013), a type of Tweedie distribution model that handles continuous, zero-inflated data without treating the zero and non-zero values separately (Lecomte et al. 2013). We specified a random effect for building because façades nested within buildings were not completely independent of each other. Because numbers of surveys (even within the same building) often varied as a result of some buildings or façades being inaccessible due to construction or other activities, we standardized for effort by specifying an offset term for number of surveys at each façade (analyses for individual seasons included numbers of surveys for that season only). We conducted univariate correlation analyses among all possible pairs of numeric predictor variables, and we did not use impervious cover and lawn cover together in models because they were strongly correlated ($r > 0.7$).

When assessing bias-adjusted carcass counts across species, 3 of 4 façades at building OS12 appeared to be outliers for spring, summer, and multi-season models (Appendix C: Fig C1), but not for fall or species-specific models. Therefore, we performed these analyses including and excluding that building to assess effects on model selection results. We did this rather than simply excluding OS12 from analyses because it was responsible for 35% ($n = 154$) of all carcass observations across seasons, and its exclusion would have greatly reduced replication of collisions for our study. Ultimately, we assessed predictor variables against 16 total response variables: 3 multi-season all-species models (including building OS12 and feather piles, excluding OS12, and excluding feather piles); 5 seasonal models (spring including and excluding OS12, summer including and excluding OS12, and fall including OS12); and 8 species-specific models across seasons (all including OS12).

Response variables for all models were bias-adjusted carcass counts, but for brevity, we hereafter refer to them primarily as "collisions". To derive important predictor variables for each response variable, we used a 3-step model selection procedure with Akaike's Information Criterion corrected for small sample size (ΔAICc; Burnham and Anderson 2002). We used this 3-step process rather than an automated approach (e.g., stepwise selection) because these typically result in a single model, whereas we were interested in comparing among several potentially competitive models. First, we compared ΔAICc values for a null model and 8 single-variable models (i.e., the eight façade variables individually). The 3 top-ranked single-variable models (i.e., lowest ΔAICc) were used to construct 17 two-variable models (i.e., all possible additive combinations that included variables from the top 3 single-variable models), unless impervious cover or lawn cover was a top-ranked variable, in which case there were only 15 or 16 two-variable models. Second, we compared ΔAICc values among the null model, top-ranked single variable models, and 15 to 17 two-variable models. The 3 top-ranked models from this second comparison were used in combination with other variables appearing in the 10 top-ranked models to make three sets of two- to five-variable additive models that had not already been assessed. Third, we compared ΔAICc values among the null model, the 5 top-ranked models from step 2, and 6 to 9 additional multivariate models generated in step 2.

We interpreted models that were strongly supported (i.e., ΔAICc < 2) in the third model selection step only. When multiple models had strong support in this final model selection step, we combined them for interpretation using conditional model averaging (function 'model.avg' in R package 'MuMIn'). We did not consider any models for interpretation that were more complex versions of higher ranking nested models (i.e., models that contained uninformative variables; Richards 2008, Arnold 2010). For the single categorical variable (façade type), the baseline category used for comparisons was 'alcove'. We considered estimated coefficients of other categories to be meaningfully different if the standard error (SE) was less than the absolute value of the estimated coefficient. Finally, façade type could not be included in fall and species-specific models (with one exception) because at least one façade type experienced no collision mortality causing ill-defined estimates with SEs that were orders of magnitude larger.

Results

From Apr 2015 to May 2017, we conducted 6190 total surveys (2270 spring, 2340 summer, 1580 fall) and recorded 63 bird species as casualties of window collisions, including 418 carcasses (214 spring, 104 summer, 100 fall) of which 71 were feather piles (25 spring, 35 summer, 11 fall). Among 235 façades at 16 buildings (range: 4-41 façades per building), we recorded collisions at 88 façades across 14 buildings (spring: 57 façades at 13 buildings; summer: 41 façades at 13 buildings; fall: 38 façades at 11 buildings).

Barring two exceptions, modeling results including and excluding the likely outlier building (OS12) were nearly identical, with models ranked in the same relative order and estimated coefficients having the same sign and very minor estimated differences in effect sizes. The first exception was in both multi-season and spring models where excluding OS12 caused the round façade type to have a meaningful negative effect size. In other words, rounds experienced a decrease in number of collisions compared to alcoves when we excluded OS12 but not when we included OS12. The second exception was that façade length was present in the strongly supported summer model including OS12 but absent when we excluded OS12. Across all seasons and species, modeling results including and excluding feather piles were likewise similar. Further, because most feather piles could not be identified to species, they were rarely included in species-specific modeling. Because we have noted these relatively slight differences here, results presented and discussed below include both OS12 and feather piles.

Table 3.1. Akaike's Information Criterion (ΔAICc) ranking for multi-season, all-species models assessing relationships between façade variables and bias-adjusted counts of bird carcasses based on window collision mortality surveys in Stillwater, Oklahoma, 2015-2017. Number of parameters (K) and weights (ω_i) are also given. Potential predictor variables included proportion of façade surface covered by glass (Glass), façade height (Height), façade length (Length), façade type (Type), mean tree distance (Tree), and land cover by flowerbeds (Flower), impervious surfaces (Imperv), and lawns (Lawn).

Variables	**ΔAICc**	**K**	**ω_i**
Glass, Height, Length, Type	0.0	10	0.940
Glass, Height, Length	5.6	6	0.058
Glass, Height	14.2	5	<0.001
Glass, Length, Type	15.3	9	<0.001
Glass, Length	29.6	5	<0.001
Glass, Type	37.0	8	<0.001
Glass	43.1	4	<0.001
Null	72.6	3	<0.001

Total collision mortality

For collisions including all seasons and species, only one model received strong support (Table 3.1). Among façade types, alcoves experienced more collision mortality than corners (β = -1.07, SE = 0.50), flats (β = -0.99, SE = 0.27), and porticos (β = -0.97, SE = 0.42) but did not differ meaningfully from rounds (β = -0.23, SE = 0.42; see above exception when OS12 was excluded). Also, collisions increased with increasing glass proportion (β = 3.01, SE = 0.41), façade height (β = 0.10, SE = 0.02), and façade length (β = 0.02, SE = 0.01). Notably, these variables all represented aspects of façade size or structure, and no vegetation or land cover variables were represented in the top model for the multi-season, all-species analysis.

Table 3.2. Comparison of relationships for variables from strongly supported models for four different collision response variables (bias-adjusted seasonal carcass counts across all species) based on bird-window collision monitoring in Stillwater, Oklahoma, 2015-2017. Potential predictor variables include proportion of façade surface covered by glass (Glass), façade height (Height), façade length (Length), façade type (Type), mean tree distance (Tree), and land cover by flowerbeds (Flower), impervious surfaces (Imperv), and lawn (Lawn). Positive and negative coefficients are indicated by + and –, respectively; predictor variables not appearing in top models are indicated by 0. When more than one model was strongly supported, inference was based on averaged coefficients. For façade type, the type with the highest mortality is indicated and ‘na’ indicates that façade type could not be included in modeling.

Response variable	**Models**	**Glass**	**Height**	**Length**	**Type**	**Tree**	**Flower**	**Imperv**	**Lawn**
Multi-season	1	+	+	+	alcove	0	0	0	0
Spring	1	+	+	+	alcove	0	0	0	0
Summer	1	+	+	+	0	0	0	0	+
Fall	2	+	+	0	na	+	0	0	+

Table 3.3. Comparison of relationships for variables from strongly supported models for nine different collision response variables (species-specific bias-adjusted carcass counts across all seasons) based on bird-window collision monitoring in Stillwater, Oklahoma, 2015-2017. Potential predictor variables include proportion of façade surface covered by glass (Glass), façade height (Height), façade length (Length), façade type (Type), mean tree distance (Tree), and land cover by flowerbeds (Flower), impervious surfaces (Imperv), and lawn (Lawn). Positive and negative coefficients are indicated by + and –, respectively; predictor variables not appearing in top models are indicated by 0. When more than one model was strongly supported, inference was based on averaged coefficients.

Species	Models	Glass	Height	Length	Tree	Flower	Imperv	Lawn
All species	1	+	+	+	0	0	0	0
Lincoln's Sparrow	2	+	0	0	+	–	0	0
Mourning Dove	1	+	+	0	0	0	0	0
Swainson's Thrush	1	+	+	0	0	0	0	0
European Starling	3	+	+	+	0	–	0	0
House Finch	2	+	+	+	+	0	–	0
Painted Bunting	2	+	+	+	0	–	+	0
American Robin	2	0	0	+	0	0	–	+
Indigo Bunting	1	+	+	0	0	0	0	0

Seasonal collision mortality

For spring collisions, only one model received strong support (Appendix C: Table C1), and it included the exact same variables (with similar coefficients and SEs) as the multi-season model (i.e., façade proportion glass, height, length, and type). Given that we observed more fatal collisions in spring than in summer and fall combined, it follows that spring results closely mirror multi-season results. For summer collisions, there was only one strongly supported model (Appendix C: Table C2), which differed slightly from the top multi-season model in having façade type replaced by lawn cover as an important variable. Collisions increased with increasing glass proportion ($\beta = 2.76$, SE = 0.49), façade height ($\beta = 0.11$, SE = 0.02), façade length ($\beta = 0.01$, SE < 0.01), and lawn cover (β = 0.86, SE = 0.29). For fall collisions, there were two strongly supported models (Appendix C: Table C3), with collisions positively related to glass proportion (β = 3.92, SE = 0.61), façade height (β = 0.09, SE = 0.03), mean tree distance (β = 0.04, SE = 0.01), and lawn cover (β = 0.66, SE = 0.42). In summary (Table 3.2), structural aspects of a façade (especially height and proportion covered by glass) seemed more strongly correlated with seasonal collisions than did vegetative and land cover variables.

Species-specific collision mortality

In decreasing order of frequency and representing 47% of our total mortality, the eight species with sufficient observations (n ≥ 15) of collision mortality to model individually were Lincoln's Sparrow (*Melospiza lincolnii*; n = 41), Mourning Dove (*Zenaida macroura*; n = 29), Swainson's Thrush (*Catharus ustulatus*; n = 28), European Starling (*Sturnus vulgaris*; n = 27), House Finch (*Haemorhous mexicanus*; n = 21), Painted Bunting (*Passerina ciris*; n = 19), American Robin (*Turdus migratorius*; n = 17), and Indigo Bunting (*Passerina cyanea*; n = 15). Overall, species-specific models showed more variation in collision correlates than did season-specific modeling, with vegetative and land cover variables appearing in more supported models (Table 3.3).

For Lincoln's Sparrow, there were two strongly supported models (Appendix C: Table C4) that indicated collisions increased with increasing proportion of glass (β = 3.04, SE = 0.61) and mean tree distance (β = 0.02, SE = 0.01) and decreasing cover by flowerbeds (β = -2.10, SE = 1.78). This was only one of two species for which façade height was not in a strongly supported model. The other such species was American Robin, which had two strongly supported models (Appendix C: Table C5) indicating collisions increased with increasing façade length (β = 0.03, SE = 0.01) and lawn cover (β = 1.42, SE = 0.70) and decreasing impervious cover (β = -1.49, SE = 0.71). The robin was the only species for which glass proportion was not included in a strongly supported model.

The only species for which façade type could be modeled was Mourning Dove, but type did not appear in the single strongly supported model (Appendix C: Table C6). Mourning Dove collisions were positively related to façade height (β = 0.17, SE = 0.06) and proportion of glass (β = 3.11, SE = 1.17). Two other species had a single strongly supported model (Appendix C: Tables C7-C8) that similarly contained only positive effects of façade height and glass proportion: Swainson's Thrush (height: β = 0.22, SE = 0.05; glass: β = 6.59, SE = 1.28) and Indigo Bunting (height: β = 0.17, SE = 0.06; glass: β = 3.11, SE = 1.17).

Collisions for the remaining three species were all positively related to façade structural features and negatively related to either impervious cover or flowerbed cover. Based on three strongly supported models (Appendix C: Table C9), European Starling collisions were positively affected by façade height (β = 0.14, SE = 0.07), façade length (β = 0.03, SE = 0.02), and glass proportion (β = 2.62, SE = 1.75), and negatively affected by flowerbed cover (β = -30.00, SE = 16.19). From two strongly supported models (Appendix C: Table C10), House Finch collisions were positively related to façade height (β = 0.25, SE = 0.09), façade length (β = 0.04, SE = 0.02), glass proportion (β = 5.01, SE = 2.28), and mean tree distance (β = 0.10, SE = 0.06), and negatively related to impervious cover (β = -3.47, SE = 1.44). Also from two strongly supported models, Painted Bunting collisions (Appendix C: Table C11) were positively related with façade height (β = 0.21, SE = 0.05), façade length (β = 0.02, SE = 0.01), glass proportion (β = 3.72, SE = 1.10), and impervious cover (β = 1.55, SE = 0.75), and negatively related with flowerbed cover (β = -6.80, SE = 6.98).

Discussion

Total collision mortality

We assessed the influence of fine-scale (i.e., façade-level) building structural and vegetation variables on spatial patterning of fatal bird-window collisions in a small urban area of the central U.S. to better understand the collision process and inform collision deterrence practices that could be targeted within individual buildings. The proportion of glass on the façade surface was the predictor variable supported in the greatest number of collision models, including the model for all species and seasons, the all-species spring, summer, and fall models, and the multi-season models for seven of the eight species. In other words, more collisions occurred at façades with a larger proportion of glass, a general result that corroborates previous studies wherein the amount or proportion of glass across entire buildings positively correlated with collisions (e.g., Klem et al. 2009, Borden et al. 2010, Hager et al. 2013, Keyes and Sexton 2014, Cusa et al. 2015, Barton et al. 2017, Schneider et al. 2018), but this is the first clear confirmation that such a relationship also occurs at the scale of individual building façades.

Although more glass certainly contributes to elevated bird collision risk, unaccounted for conflating factors may have contributed somewhat to the apparent importance of glass proportion in our study. For example, glass proportion is likely correlated with both the proximity and contiguousness of glass areas; in other words, windows tend to be closer together and glass has larger contiguous area when glass proportion is greater, and these properties may make it more difficult for birds to perceive the glass. Also, glass proportion is likely to be positively correlated with the amount and/or intensity of light emitted at night (i.e., more light emitted from façades with more window area; Parkins et al. 2015). This light pollution may attract and confuse nocturnally migrating birds, increasing collisions at buildings (Evans Ogden 2002, Gauthreaux and Belser 2006, Haupt and Schillemeit 2011, Keyes and Sexton 2014).

Next to glass proportion, the most frequently supported variables represented aspects of façade size (e.g., height and length). This follows previous studies in finding more collisions or higher collision risk at larger buildings (Machtans et al. 2013, Loss et al. 2014, Hager et al. 2017), but again, this finding had yet to be confirmed at the finer façade scale. Large façades provide more area for collisions relative to smaller façades with the same proportion of glass. In combination with the overwhelming importance of glass proportion, our results therefore suggest that large façades with high proportions of glass likely pose the greatest collision risk to birds. Thus, collision deterrence efforts may need to focus on larger façades independent of building size.

In addition to the structural variables discussed above, façade type also appeared in the model for total collisions, with greater mortality at alcoves than other façade types. Building and façade shape have never been formally assessed in relation to window collisions, and this finding could reflect how the tunnel-like nature of alcoves, especially deep alcoves with tall façades, may “trap” birds. Such entrapment may be exacerbated by unique lighting, reflection, and/or see-through effects that occur in deeper alcoves with decreased penetration by natural light, and trapped birds may be at greater risk of subsequent collision if the end of the alcove has a large proportion of glass that appears to provide a safe exit. Porticos are similarly tunnel-like but had much lower collision rates. The relatively low mortality at porticos may arise from birds more easily recognizing the horizontal exit paths associated with this façade type as opposed to the vertical exit path associated with alcoves, and this differential perception may in turn be related to birds in flight generally having larger visual fields laterally than above the head (Martin 2012).

Equally notable is that vegetative and land cover variables did not appear in the multi-season, all-species model. This result was somewhat unexpected given that such variables have previously been correlated with collisions at broader scales (Klem et al. 2009, Borden et al. 2010, Hager et al. 2013, Kummer et al. 2016, Elmhurst and Grady 2017) and at other types of glass structures (Sierro and Schmid 2001, Barton et al. 2017). However, these variables were not entirely unimportant, as they appeared in several seasonal and species-specific models. In fact, the lack of such variables in this model may partially arise from opposing season- or species-specific effects (e.g., opposite relationships of House Finch and Painted Bunting with impervious cover) that cancel each other out when seasons and species are aggregated. This potential lack of influence on total collisions by vegetative and land cover variables at the façade scale is certainly an area that requires further investigation; specifically, studies should be conducted in other regions and should assess other vegetation and land cover types to determine if and when these factors affect collisions at the façade scale.

Seasonal collision mortality

Seasonal analyses of collisions generated results that differed slightly from the multi-season all-species analysis, except for the spring analysis which documented the exact same collision correlates as the overall analysis, an intuitive finding given that the greatest number of collisions occurred during spring. Summer and fall analyses did not support the predictive importance of some structural variables (façade type and length) that were supported in the overall analysis; however, additional collision correlates were also revealed for these seasons (lawn cover and tree distance). These results indicate that collision correlates differ seasonally, a finding that is heretofore undocumented for the issue of bird-window collisions, and which suggests that results of past studies, which analyzed data across all seasons or from a single season only, should not necessarily be extrapolated to individual seasons. Fall migration is often assumed to be the most critical period for window collisions, because collision frequency or mortality is often reported to be greater in fall than any other season (Zink and Eckles 2010, Kummer and Bayne 2015, Bracey et al. 2016). However, collision mortality in seasons other than fall may be underappreciated, and may in some cases even exceed fall mortality (Dunn 1993, Gómez-Moreno et al. 2018, Schneider et al. 2018, Riding et al. *in review*). Thus, identification and consideration of season-specific collision correlates will be important to consider in areas where substantial mortality occurs in seasons other than fall.

As seasonal assessment of bird-building collision correlates is novel, we list two caveats related to our study that could limit the generalizability of our findings. First, results from this same study area, and based on the same collision data, suggest that patterns of temporal variation in collisions likely differ geographically. Specifically, our study area experiences an unusually high number of bird-building collisions during spring, although temporal patterns more closely mirror other study sites when considering migrating individuals only (i.e., greater collision mortality of migrating individuals in fall than spring; Riding et al. *in review*). Thus, the factors driving spatial variation in collisions may also be unique to our study area, and caution should be exercised when extrapolating season-specific results (as well as our overall and species-specific results) to other geographic regions or study areas that are urbanized to a greater or lesser degree. Second, seasonal results may be confounded by species-specific results because our study area experiences substantial seasonal variation in the species composition of collision casualties (Riding et al. *in prep*). That is, these seasonal results may be at least partly influenced by which species were present (and colliding) in addition to seasonal changes that influence collision risk factors (e.g., latitude of sun at sunrise, vegetative growth, availability of plant and insect food sources near buildings, and patterns of when and how frequently buildings are illuminated with artificial night lighting). However, regardless of these caveats, we hypothesize that seasonal variation in collision correlates is widespread, even if the nature of such seasonal variations differs from those observed in this study.

Species-specific collision mortality

Species-specific analyses showed highly variable collision correlates among species. For example, although glass proportion and façade height appeared in the models for most (but not all) individual species, all other variables only appeared in top models for 1 to 4 of the 8 species assessed. Moreover, for impervious cover, the direction of the effect differed among species (positive for American Robin and House Finch, negative for Painted Bunting). Although these 8 species represent nearly half of the collision mortality we observed, they comprised only 13% of species observed as collision casualties. Even pairs of species with close taxonomic relationships and similar life history traits (American Robin and Swainson's Thrush; Painted Bunting and Indigo Bunting) had differing results, which suggests it may be difficult to extrapolate findings from one species to another. Like the season-specific analyses, our finding of among-species variation in collision correlates indicates that analyses including all species may overlook important species-specific collision risk factors; however, the same caveat regarding potential conflating between season- and species-specific patterns also exists for this analysis.

Only one previous study, which focused on the building scale, attempted to assess structural and vegetative correlates of bird-window collisions for individual species (Cusa et al. 2015). This study, which aggregated species-specific results into feeding and habitat guilds for ease of interpretation, showed for example, that foliage gleaners from forested habitats were more likely to collide at buildings surrounded by a greater extent of urban greenery. While we did not formally group species by life history traits (e.g., feeding guild, migratory strategy), those that we assessed (1 species in Columbiformes: Family Columbidae; 7 species in Passeriformes: Families Turdidae, Sturnidae, Passerellidae, Fringillidae, and Cardinalidae) represented modest diversity in taxonomy, as well as various life history strategies for diet, breeding habitat, urban adaptivity, and foraging and migration strategies.

The above life history variation that we captured across the 8 species assessed likely explains some of the among-species differences in collision correlates. The most disparate species-level results were for American Robin and Painted Bunting, which shared only 1 of 7 strongly supported variables with the same direction of relationship (increased collisions at longer façades). Robin collisions were negatively related to impervious cover (e.g., concrete) and positively related to lawn cover, whereas Painted bunting collisions were positively related to impervious cover and negatively related to flowerbed cover. These differences may be related to varying foraging strategies and/or the types of activity birds were engaged in prior to colliding. Robins frequently forage on lawns and adapt well to urban settings, making them likely to forage on a lawn (but not on concrete) near a building. If startled into flight by a perceived predator (e.g., human [*Homo sapiens*] or dog [*Canis lupus familiaris*]), a robin may occasionally flee toward a building, perhaps even directly at a window if it is misperceived as an opening in the building (Ros et al. 2017). Painted Buntings often forage on the ground (albeit in taller grasses than those used in lawns), but are likely to be present in highly urbanized areas during migration or dispersal only. The positive relationship between bunting collisions and impervious cover may arise if buntings become confused (e.g., in alcoves – see above) when they stop in highly developed areas during migration. The negative relationship between bunting collisions and flowerbed cover may occur because migrating buntings are more capable of finding shelter, and perhaps avoiding confusion, when there is extensive, low-growing, non-lawn vegetation. In order to enact species-specific management, further research may be needed to elucidate mechanisms of the collision process related to different bird species and life history traits.

Conclusions

Our novel façade-level results, along with past research focusing on bird collision correlates at building, landscape, and regional scales, are informative for efforts to make buildings more bird-friendly by refining collision deterrence efforts and architectural and landscape designs. At the façade-level, bird window collisions seem to be most strongly driven by the proportion of glass covering a façade. Façade size (i.e., height and length) and type also positively influenced number of collisions. Therefore, collision deterrence efforts should be targeted toward large, alcove-like façades covered by a large proportion of glass, and building designers should consider reducing and/or avoiding the use of such design features whenever possible. However, season- and species-specific results suggest that management approaches can be even further refined if the goal is to mitigate collisions during a particular season or for a particular bird species. Future studies also should bear in mind the temporal nuances of collision correlates in both collecting and interpreting data, to ensure that seasonally appropriate data is used for mitigation efforts. An especially fruitful research avenue would be before-after bird collision monitoring studies that test deterrence methods based on collision correlates at multiple scales (e.g., installing anti-collision films on glass surfaces); such research would help refine and validate recommendations regarding the best approaches to reduce bird-building collisions.

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CHAPTER IV

EFFECTS OF NIGHT-TIME LIGHTING ON BIRD-BUILDING COLLISIONS

Abstract. Artificial light at night (ALAN), which has severe effects on the physiology of many plants and animals, is increasing concomitantly with expanding urbanization. ALAN can exacerbate bird collisions with human structures, a major source of avian mortality, by attracting and entrapping nocturnally migrating birds. Much previous work was conducted at non-building structures (e.g., communication towers and wind turbines), so little is known about how ALAN affects bird-building collisions, especially in small urban areas. In Stillwater, Oklahoma, USA, we measured nocturnal irradiance using a spectrometer to characterize light and generate a lightscape (i.e., map of lighting intensity) to compare against a map of mortality intensity. Nocturnal irradiance spectra were often similar to emittance spectra of artificial light types known to be nearby. However, we did not find a spatial correlation between light intensity and collision mortality intensity. We discuss some potentially confounding factors in our study and directions for future research.

Introduction

Urban areas are experiencing unprecedented growth, in both land area and human population, that is projected to continue worldwide (United Nations 2014) and is leading to profound effects on the environment, including a global increase in the spatial extent and intensity of artificial illumination (Kyba et al. 2017a, Koen et al. 2018). Nocturnal emission of artificial lighting, often termed light pollution or artificial light at night (ALAN), has severe biological and ecological impacts; it has been shown to alter the physiology, behavior, reproduction, and survival of invertebrates, vertebrates, and plants (Rich and Longcore 2006, Gaston et al. 2017, Owens and Lewis 2018). In birds specifically, ALAN can affect physiology (e.g., stress and hormones; de Jong et al. 2016, Ouyang et al. 2017, Dominoni et al. 2018) with cascading effects on reproductive phenology (Kempenaers et al. 2010, Dominoni et al. 2013), the onset of daily activities (Miller 2006, Dominoni et al. 2014), and migratory behaviors, such as timing and orientation (Evans et al. 2007, Watson et al. 2016, La Sorte et al. 2017, Van Doren et al. 2017).

Continued urbanization is also exacerbating the prevalence of bird-building collisions, a major source of direct anthropogenic mortality for birds in North America and globally (Klem 2009, Calvert et al. 2013, Loss et al. 2014). Bird collisions at buildings and other structures (e.g., communication towers) primarily occur when a bird's ability to perceive or avoid an obstacle, such as glass surfaces on buildings, is impaired. ALAN can increase the risk of collision, particularly for nocturnally migrating species (Kemper 1996, Gehring et al. 2009, Longcore et al. 2013), by increasing this impairment and causing light entrapment. Entrapment occurs when birds are attracted to and confused by lighting, especially when visibility is poor (e.g., precipitation and/or low clouds; Evans Ogden 2002, Ramirez et al. 2015). Light-entrapped birds experience increased collision risk with nearby structures as they make looping flights around bright light sources, while birds that avoid collision but remain entrapped may exhaust themselves to the point of dropping to the ground (Evans Ogden 1996, Van Doren et al. 2017). These exhausted birds may be subject to predation or to later collisions with buildings or vehicles when they attempt to forage or re-initiate migratory flights.

The effects of ALAN on bird-building collisions likely vary with a variety of factors, including season, bird species, and type and intensity of lighting. The spectral qualities (i.e., color) of light are thought to differentially affect bird flight behavior and therefore collisions at human structures (Evans et al. 2007, Marquenie et al. 2013, Rebke et al. 2019). Filtering LEDs, which have become more abundant in outdoor lighting, is thought to be one way to reduce light pollution for a targeted species or taxonomic group without completely removing lights required for human safety (Longcore et al. 2018). However, the color of light has not been investigated in the context of building collisions, specifically, so it is unknown how spectral qualities may influence collisions in urban areas.

Large, bright lights, such as searchlights, spotlights, and flood lights at sports stadiums and outdoor recreational fields, have greater potential to entrap nocturnally migrating birds (Jones and Francis 2003, Gauthreaux and Belser 2006, Gehring et al. 2009). This effect may be exacerbated when low cloud ceilings increase reflected ALAN and drive migrating birds closer to the ground and the area of the lights’ influence (Morris et al. 2003, Kerlinger et al. 2010), but bright lighting, weather, and the interaction between them has not yet been studied in bird-building collisions. Small, low-wattage lights may not individually affect the behavior of birds migrating overhead, but collectively, they may increase collision risk for both resident and migratory species (Parkins et al. 2015). In addition to the constant exterior illumination required for safety reasons at many public and private non-residential buildings, interior lights in many buildings emanate out through windows. This low-level but widespread lighting may induce earlier onset of daily foraging, singing, and territoriality behaviors, including during nocturnal periods (Dominoni et al. 2014, de Jong et al. 2016) and may increase the frequency of bird-building collisions, particularly because 1) acitivity may be clustered in the areas of increased light immediately around buildings and 2) avian perception of windows may be reduced when illumination is emanating from inside the buildings.

Although ALAN appears to increase bird-building collisions, very little peer-reviewed research has been conducted on the issue and past studies have been relatively descriptive and focused in large metropolitan areas (Evans Ogden 2002, The Field Museum 2002, Parkins et al. 2015). Lighting in smaller urban areas surrounded by relatively undeveloped landscapes may affect bird-building collisions differently than contiguous lighting that covers a much larger spatial extent. Therefore, we assessed the relationship between ALAN and bird-building collisions in a small urban area in the U.S. Great Plains. Our first objective was to characterize the spectral qualities of ALAN around buildings generally and at building façades of low and high collision incidence specifically. We predicted that ambient light spectrograms would correlate with local light sources and that irradiance values would generally be higher (i.e., brighter lighting) at locations with high collision frequency. Our second objective was to compare lighting intensity measurements with a major light source (stadium flood lights) on and off. We predicted that light intensity would increase when the flood lights were engaged. Our third objective was to assess the spatial relationship between ALAN intensity and collision intensity. We predicted that areas of greater ALAN intensity would be more likely to impair and entrap birds, leading to greater collision mortality.

Methods

Study area and study design

We surveyed for bird carcasses at 16 buildings in Stillwater, Oklahoma, USA, a small urban area with a human population of ~46,000 and with the vast majority of buildings consisting of residences and small office-type structures <5 stories in height. Stillwater is in the cross timbers transitional ecoregion of the southcentral United States, where deciduous forests from the east mingle with grasslands from the west to create a mixture of prairie, savannah, and woodland. We used a stratified approach to select survey buildings based on building size and amount of surrounding vegetation (Hager et al. 2017), but building selection was not completely random as we were constrained by building accessibility. The surveyed buildings included detached residences (n = 2), commercial off-campus-structures (n = 3), and classroom, office, and athletics buildings (n = 11) on the Oklahoma State University main campus. We surveyed ≥6 days/week at all buildings during 1 Apr to 31 Oct in 2015-2016 and at 14 buildings (excluding the 2 residences) during 1 Apr to 31 May in 2017. For seasonal delineations, we considered spring to be Apr-May, summer to be Jun-Aug, and fall to be Sep-Oct.

Initial selection of light measurement locations was systematic, with points placed ~10 m away from a survey building and spaced ~70 m apart around the building perimeter. However, there were four factors that caused us to adjust the location and spacing of measurement points. First, we took light measurements only at portions of buildings monitored for bird collisions, and accounting for unmonitored portions of buildings sometimes resulted in longer distances between points. Second, we shortened distances between points (sometimes to as little as ~12 m) when visual assessment suggested substantial fine-scale variation in light intensity, for example, in association with different lighting characteristics on adjacent facades that formed a building corner. Third, at two buildings, we could not place points on one side due to construction activities or the proximity of a neighboring building < 10 m away. Finally, we added seven points (two near survey buildings, five in a linear transect moving away from the stadium) to increase data for comparing light intensity with the flood lights on and off (Fig 4.1).

We measured light around monitored buildings during Aug to Oct 2017 and May 2018. Although temporal variation in lighting intensity may have occurred between the non-overlapping periods when we collected collision and lighting data, we assumed that nocturnal light levels were relatively constant across our study period (Apr 2015-May 2018), except when the flood lights at the football stadium were on. We did not measure light at the two residences because we did not detect any carcasses at residences, residences were isolated from other survey buildings, and viable measurement locations around residences were limited due to proximity of neighboring buildings and property access issues.

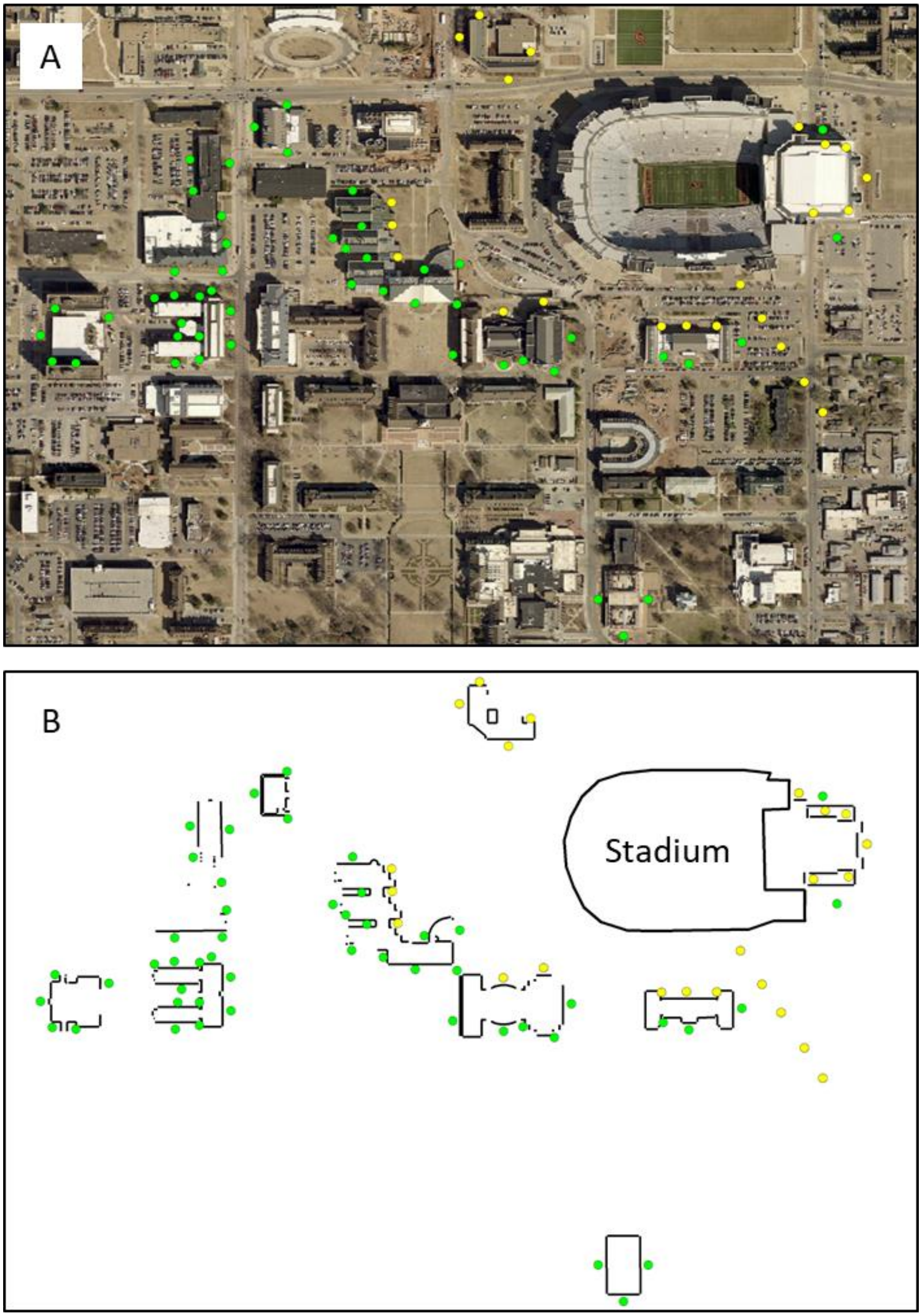

Figure 4.1. Locations (green dots) on the Oklahoma State University campus core at which nocturnal light was measured. Yellow dots indicate where measurements were taken with stadium lights off and on. A) Aerial view showing context with all structures. B) Simplified map showing the stadium and sections of buildings monitored for window collisions.

Mortality data

Carcass surveys consisted of a single observer walking slowly along the exterior perimeter of a focal building, intensively searching a 2-m wide swath along all windowed walls. We also entered three buildings to survey ledges below windows that could not be observed from the outside. We alternated the direction that building perimeters were surveyed on a daily basis (clockwise on even days, counter-clockwise on odd days) to minimize detection effects related to the angle and direction from which an observer approached a carcass (e.g., obstacles and shading). Upon discovery of an intact carcass, we took photographs and recorded the location and a description of the carcass. We similarly documented remains indicative of a carcass, which usually consisted solely of feathers (i.e., feather pile) that had been plucked from the carcass by a scavenger. However, due to greater uncertainty concerning the source and location of mortality for feather piles, we excluded them from analyses.

To avoid counting a single carcass more than once, we collected bird remains using a plastic, sealable bag, and subsequently stored them in a freezer with unique alphanumeric identification codes. When we could not collect a carcass (e.g., because it was on an inaccessible ledge above ground level), and at one building where carcasses were regularly left as found as part of a concurrent study of scavenger removal, we tracked the carcass condition and location to avoid double counting it on future surveys. We collected carcasses under federal (permit #MB05120C-0) and state (multiple permits over the study) scientific collecting permits, and protocols were approved by the OSU Institutional Animal Care and Use Committee (Animal Care and Use Protocol #AG-14-8).

We used written observer descriptions to record locations for carcasses and non-fatal collisions in Google Earth Pro 7.3.2 (Google; Mountain View, California), which allowed location accuracy to within ~2 m. When written location descriptions were ambiguous, the observer who detected the carcass clarified the precise location by marking it on a map. We imported these locations to ArcGIS 10.2.1 (ESRI; Redlands, California) to generate and analyze spatial data. We used georectified aerial imagery and polygons of some land cover types (e.g., buildings) provided by the department of Geospatial Systems at Oklahoma State University (OSUGS) to generate lines representing the midline of the 2-m wide search area for each building façade. We snapped carcass location points to this midline (which moved their location ≤ 1 m), then spatially joined the points to the line to derive façade-specific carcass counts. To match OSUGS data, we projected all data layers to NAD_1983_HARN_StatePlane_Oklahoma_North_FIPS_3501_Feet.

Lighting data

For humans, electromagnetic radiation occurs as visible light when the wavelength is 400-700 nm, but birds have expanded visual coverage into the UV range (300-400 nm; Hart and Hunt 2007, Martin 2012). The OSU standards for outdoor lighting require either LED (default is 4000k CCT) or incandescent lights, depending on the location and fixture type (Oklahoma State University 2018). The football stadium has 72 metal halide lamps in each of six racks (432 total lamps) along its upper rim, and the same light type in smaller racks at other athletic fields (e.g., baseball and intramural fields; *personal communication*, J. Tanner, Engineering Tech, OSU Athletic Department). LED lights emit a narrow peak near 450 nm and a much broader peak that maximizes around 600 nm, metal halide lights exhibit multiple short peaks from ~380 to ~630 nm with one (or two) tall, narrow peak(s) at ~580 nm, and incandescent (tungsten/halogen) lights steadily increase in radiated intensity from short to long wavelengths (Behar-Cohen et al. 2011, Bará and Escofet 2018, Bouroussis and Topalis 2018). The City of Stillwater has high pressure sodium (72%) or metal halide (24%) lamps in most street lighting (*personal communication*, G. Roach, Engineering Technologist, City of Stillwater), but off-campus buildings were variable in their lighting. High pressure sodium emittance is greatest from ~560 to ~ 630 nm, often with multiple distinct peaks within that range (Behar-Cohen et al. 2011, Bouroussis and Topalis 2018).

Among the various methods of quantifying visible light, irradiance is the most frequently used in photobiology (Johnsen 2011). Irradiance is the number of photons that hit a surface of a certain size over a period of time and has units of photons/sec/cm^2/nm where nm is distance on the electromagnetic spectrum (i.e., spectral irradiance; Johnsen 2011). This can be converted to, and is often recorded by popular software as, Watts/m^2/nm (or Watts/m^2 with known spectral distance, usually 0.5 nm). Vector irradiance is directional (the direction the sensor faces matters) and is often used to determine general illumination (Johnsen 2011). To measure light intensity, we recorded vector irradiance (Watts/m^2) at night (from evening civil twilight to ~3 hours thereafter) using a cosine-corrected sensor attached directly to the body of a BLUE-Wave VIS portable spectrometer (StellarNet Inc., Tampa, Florida, USA). The spectrometer was connected via USB cable to a laptop running SpectraWiz software (StellarNet Inc.), which recorded values every 0.5 nm along the spectrum visible to birds (350-700 nm; 350 nm was the minimum range for this spectrometer). We calibrated measurements at each point with a dark reference measurement that entailed covering the sensor with a black foam cube. For each reading, the spectrometer was held steady by hand at shoulder height (~1.5 m; two individuals of roughly equal height held the spectrometer during measurements) until fluctuations became minimal. We set the integration time to 1 sec averaged across 3 scans. This integration time is longer than typical diurnal light recordings (e.g., Goller et al. 2018) but did not cause oversaturation because of the decreased ambient light intensity at night. Additionally, we wore dark, non-reflective clothing and kept the sensor field of view unobstructed by equipment and personnel during measurements.

At each location, we twice repeated five directional readings (10 total measurements), which consisted of horizontal readings in each of the four cardinal directions, as well as an upward-pointing vertical reading (Moore et al. 2012). We averaged the 10 readings at each 0.5 nm increment to derive a general spectrogram of general illumination (Moore et al. 2012), then summed those averages to a single value of ambient light intensity. We had to revisit several points on warmer evenings because a preliminary inspection of lighting data indicated that the spectrometer did not perform accurately in cooler temperatures (< ~10 °C).

For comparing light intensity between periods when the stadium flood lights were on and off, we measured light twice at points < 300 m from and with an unobstructed view of the stadium. In addition, we took two readings of sixth direction, where the sensor was directed toward an imaginary point centered over the football field just above the rim of the football stadium. We averaged the two readings for this sixth direction at each point but did not combine them with any other readings. We took the on and off measurements as close together in time as possible (on average ~2 days between measurements) to minimize variation from other light sources (e.g., changes in moon phase and lighting from neighboring buildings). However, we provide reasoning below (see Discussion) for why changes in moon phase probably did not contribute variation to our lighting measurements. We were unable to take measurements at three locations when stadium flood lights were on because our sampling schedule coincided with a football game and those locations were occupied by tailgaters.

Data analyses

Except where noted, we conducted analyses in R 3.5.2 (R Core Team 2018) with RStudio 1.1.463 (RStudio Team 2016). We adjusted carcass counts to account for two major biases that cause raw counts to underestimate mortality: scavenger removal of carcasses between surveys and imperfect observer detection of carcasses that remain present for surveys (Riding and Loss 2018). We also standardized the adjusted counts by façade-specific search effort because the number of surveys, even among façades at the same building, often varied as a result of inaccessibility due to construction or other activities. To assess spatial clustering of mortality events, we conducted Kernel Density analysis (KD; ArcGIS Spatial Analyst toolbox), which calculates a magnitude-per-unit area value using a kernel function to smooth surfaces. Our input for KD analyses included an output cell size of 1 m, search radius of 5 m, and bias-adjusted estimates of bird carcasses per survey for population. This generated a KD raster that we reclassified into a mortality intensity raster with eight classes where, excluding zeros, each successive class doubled in range (e.g., class 1: 0.001-0.149; class 2: 0.150-0.298). Because the KD raster was heavily skewed with zero values, this classification method allowed for some cells in each class while retaining a frequency distribution similar to the KD raster. We determined building façades of high collision incidence (hereafter "hot spots") and low collision incidence (hereafter "cold spots") based on KD values and important correlates of collision revealed in a concurrent study of the spatial patterning of bird-building collisions (Riding et al. *in prep*).

To characterize light recorded around survey buildings (objective 1), we examined a spectrogram averaged across light measurement points and compared it to known spectra for common artificial light sources. Because the buildings on OSU campus core were more likely to have consistent lighting types and placement, we also assessed averaged spectrograms for on-campus (n = 10) and off-campus buildings (n = 4) separately. We included one campus building (OS18) in the off-campus group because it was at the edge of campus with few nearby buildings but near typical street lighting, and therefore was more similar to the context of off-campus buildings. Also, we examined spectrograms from the nearest light measurement location for six hot spots (four on-campus) and six cold spots (five on-campus).

To compare lighting intensity between individual points when stadium flood lights were on and off (objective 2), we used two data sets: 1) summed values averaged across the cardinal directions and up (i.e., ambient light as a whole for the point), and 2) summed values for the sixth (stadium) direction (i.e., vector irradiance emanating from the direction of the stadium). We performed each of the following on both data sets. First, we used a paired Wilcoxon signed rank test (function 'wilcox.test' with 'paired = T') because the aggregated light values for each point were not normally distributed. To visualize the relationship between light values at single points with stadium lights on versus off, we examined paired plots (function ‘paired.plotProfiles’ in package ‘PairedData’). Also, to assess if distance from stadium was an important factor in light measurements, we used linear models (function ‘lm’) with two response variables: light intensity with stadium lights on and difference in light intensity between stadium lights on and off. For each response variable, we compared an intercept-only model against a model with distance to the stadium as an explanatory variable using Akaike’s Information Criterion corrected for small sample size (ΔAICc; Burnham and Anderson 2002).

We used inverse distance weighting (IDW; ArcGIS Spatial Analyst toolbox) to interpolate a raster of light intensity (i.e., "lightscape"; Bennie et al. 2014) based on summed light measurements, excluding measurements taken when the stadium lights were on. We used the above-described light intensity value for each measurement location with output cell size at 1.8 m, power at 2, search radius as ‘variable’ (6 points), and with building footprints as barrier polylines to prevent light measurements from contributing to interpolated values at locations where those light sources would not reach. To ensure that areas next to buildings (i.e., where carcasses were located) were not interpolated as areas of no light data, we intentionally distorted the barrier polylines to make them slightly smaller than the actual building footprints. We reclassified the output lightscape raster with 8 classes based on quantile breaks. Finally, we extracted the values from the reclassified lightscape (IDW) and mortality intensity (KD) rasters to the individual carcass points snapped to search area midlines.

To examine the relationship between ALAN intensity and collision intensity (objective 3), we used the extracted IDW value as the predictor variable and the extracted KD value as the response variable in a geographically weighted regression (GWR;

ArcGIS Spatial Statistics toolbox) with a fixed kernel. Although GWR accounts for non-independence due to spatial autocorrelation, it can produce spurious correlations, particularly with small samples (Páez et al. 2011). Therefore, as a general method to validate the GWR results, we used the same explanatory and response variables in a generalized linear model (GLM; function 'glm') with a Poisson distribution, and compared it with an intercept-only model using ΔAICc.

Results

From Apr 2015 to May 2017, we conducted 6069 building collision surveys and detected 322 carcasses. Adjusting for observer detection and scavenger removal biases resulted in an estimate of 362 total carcasses (0.06 carcasses/survey) across the entire study period. From Aug 2017 to May 2018, we recorded 126 sets of night-time lighting measurements, including 23 pairs of measurements with the stadium lights on and off. We had to discard 16 measurements (10 stadium lights off, 6 on) due to anomalous readings that appeared to be related to the spectrometer malfunctioning during cooler temperatures (< ~10 °C), which left us with 14 paired measurements (i.e., stadium lights on/off) and 93 measurements when stadium lights were off.

Regarding objective 1 (characterizing light) for the spectrogram averaged across all locations, irradiance increased across the lower end of the spectrum (350 to 450 nm) with a maximum peak at ~460 nm and a relative plateau from 480 to 700 nm (Fig 4.2A). This was not an exact match for any commonly used lights, but the LED and incandescent lighting types on campus could have combined to form the observed irradiance peak near 450 nm and the plateau at longer wavelengths. The same basic pattern was present in the spectrogram for on-campus buildings (Fig 4.2B), but off-campus buildings tended to have darker exteriors (Fig 4.2C) with a maximum peak at ~360 nm, a steady decline to ~510 nm, and remained low thereafter with a few minor peaks 540-620 nm. The minor peaks roughly correspond to expected peaks for high-pressure sodium lights. Some of the hot spots did exhibit spectral signatures similar to LED lights (Fig 4.3B) or combinations of LED and high pressure sodium lights (Figs 4.3A, C), but other hot spots (Figs 4.3D-F) and all cold spots (Fig 4.4) were relatively dark (i.e., low irradiance intensity) with no obvious light-type spectral patterns.

Regarding objective 2, results for both data sets were very similar, so only the first is presented and discussed below. Light intensity values did not differ significantly when stadium lights were on versus off (Wilcoxon V = 56, p = 0.86). There was no consistent shift in light values, with some individual locations becoming brighter and others darker when stadium lights were on (Fig 4.5). The null model outperformed the model with distance to stadium as a predictor whether the response variable was light intensity with stadium lights on (ΔAICc = 1.0) or difference in light intensity with stadium lights on and off (ΔAICc = 5.1), both suggesting that distance to stadium had little impact on light intensity when stadium lights were on.

In comparing ALAN intensity to mortality intensity (objective 3), the GWR global adjusted $r^2 = 0.49$, but all local r^2 values were < 0.02 except for one building (OS11) where $r^2 = \sim 0.50$ for five points, suggesting that light intensity was a poor correlate of mortality intensity across the study area. The GLM validated this result, as the effect size was negative and relatively small (β = -0.05, SE = 0.01), even though the model with the predictor performed much better than the null model (ΔAICc = 14.7).

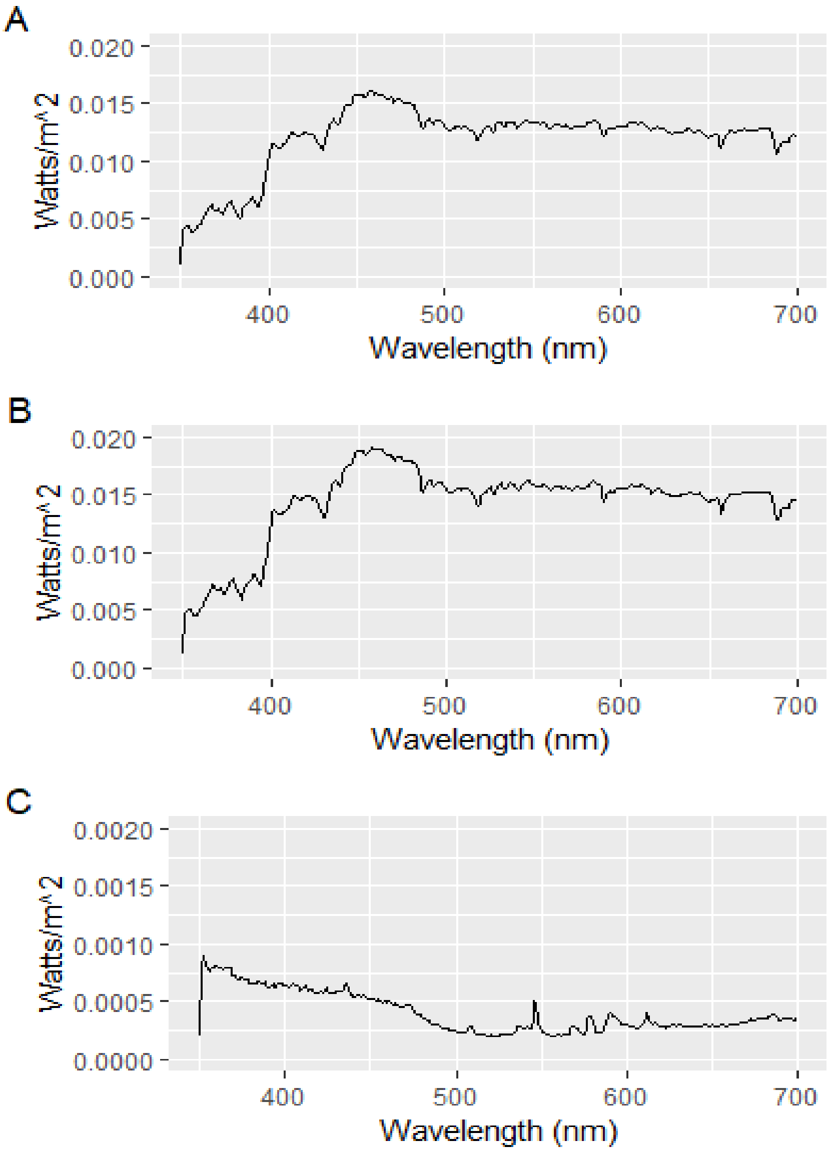

Figure 4.2. Spectrograms of nocturnal irradiance (Watts/m^2) averaged every 1 nm and measured from Aug 2017 to May 2018 around buildings monitored for bird-window collisions in Stillwater, Oklahoma, USA, separated as A) all buildings (n =14), B) buildings at Oklahoma State University (n = 10), and C) off-campus buildings (n = 4). Note that the y-axis of C has a different scale than A and B.

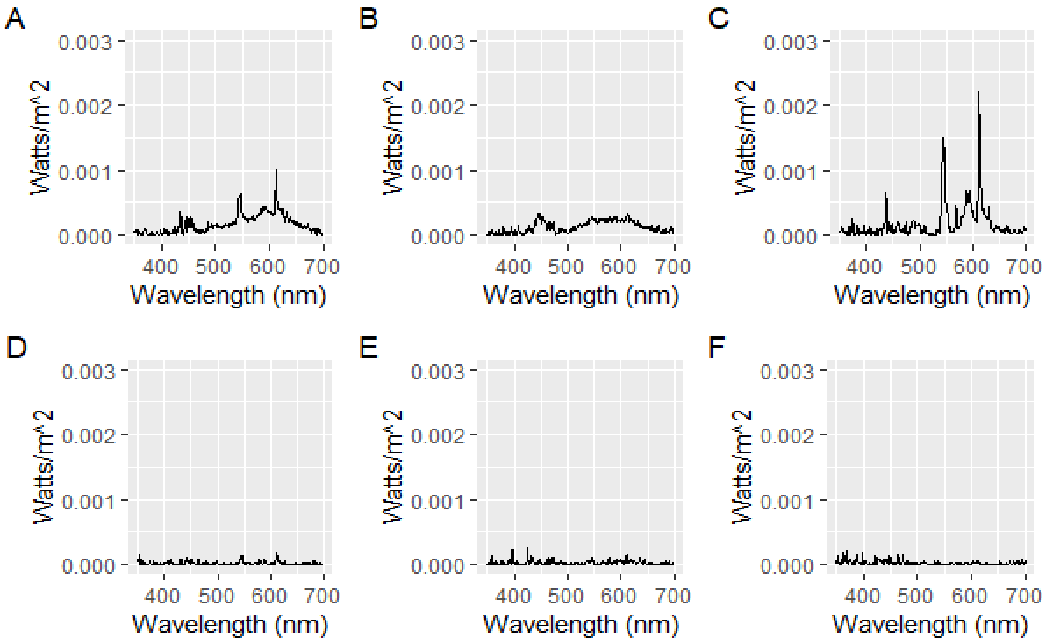

Figure 4.3. Spectrograms of nocturnal irradiance (averaged every 1 nm) measured from Aug 2017 to May 2018 at six locations with high bird-building collision incidence (hot spots) in Stillwater, Oklahoma, USA.

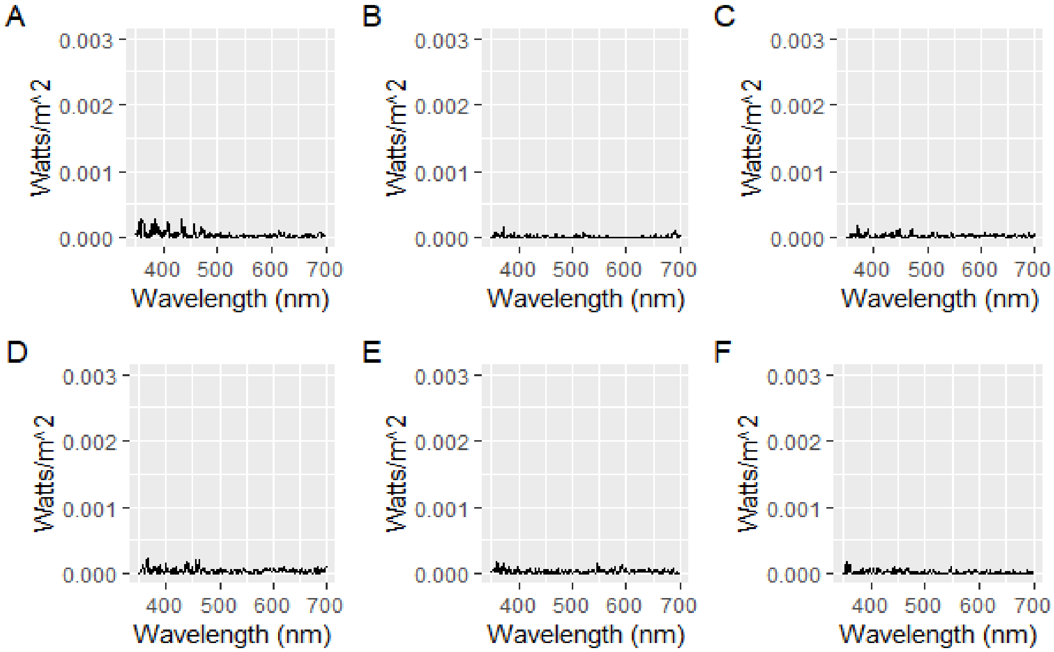

Figure 4.4. Spectrograms of nocturnal irradiance (averaged every 1 nm) measured from Aug 2017 to May 2018 at six locations with low bird-building collision incidence (cold spots) in Stillwater, Oklahoma, USA.

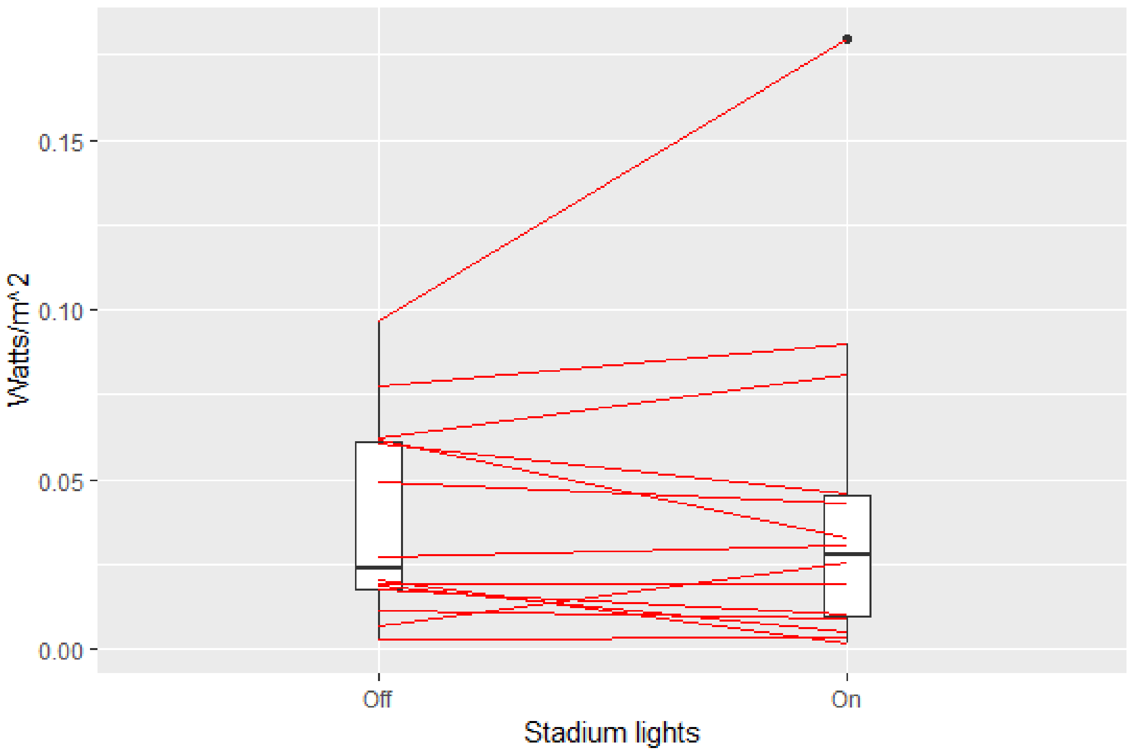

Figure 4.5. Paired boxplots (stadium floodlights off/on) of aggregated nocturnal irradiance measured from Aug 2017 to May 2018 around buildings monitored for bird-window collisions in Stillwater, Oklahoma, USA. Red lines show changes in irradiance value for individual locations.

Discussion

This was the first study of bird-window collisions to investigate ambient light generally, rather than focus on light emanating from within buildings (e.g., Parkins et al. 2015). Spectrograms of light appeared to be combinations of the most common nearby light sources, but many locations were poorly lit with no recognizable spectral signatures. Surprisingly, we found that nearby stadium flood lights had no consistent effect on irradiance measurements and ALAN intensity did not correlate well with collision mortality intensity. One of the few studies to quantitatively assess the effects of ALAN on building collisions (Parkins et al. 2015), did find a relationship between collision frequency and building lighting, but they could not disentangle the effects of lighting from other building characteristics (e.g., glass coverage). Below, we discuss a variety of factors that potentially contributed to our unexpected findings.

The apparent lack of change in irradiance when stadium lights were on versus when they were off likely relates both to the nature of the light source and of environmental conditions during periods when lighting data were collected. Regarding the light source, the stadium flood lights were angled downward to illuminate the field, such that most of the radiant energy was absorbed inside the stadium or reflected up at an angle that would be unlikely to increase light at ground level adjacent to the stadium. Increased irradiance may only be expected during periods when a low cloud ceiling is present, but most (23 of 28 [82%]) paired measurements were taken when skies were clear. In general, cloud-related variables correlate positively to various measures of ALAN (Kyba et al. 2011, Puschnig et al. 2014, Hänel et al. 2018). Anecdotally, we witnessed several hundred birds temporarily experience light entrapment by circling the banks of flood lights above the stadium on the evening of 23 Sep 2017. This was a clear night during peak fall migration for some species (e.g., Parulidae), so we surmise that the number of birds becoming light-entrapped could have been much higher had a low cloud ceiling been present. Future research should consider implications for bird-building collisions related to ALAN variation associated with varying cloud cover conditions, especially cloud altitude, given that the effects of ALAN on migratory behavior have been shown to be influenced by cloud cover and altitude (Cochran and Graber 1958, Bolshakov et al. 2013).

Most of our lighting data were collected during fall 2017, a time period when we were not conducting collision monitoring. Due to addition (or, less frequently, removal) of lights and changes in lighting schedules in urban areas, there is likely spatiotemporal heterogeneity in urban light emission. Thus, the lighting data we recorded may not have been entirely representative of ALAN intensity during the periods we observed collision fatalities. This mismatch could be alleviated in future studies by ensuring temporal overlap of data collection and could include recording lighting data multiple times during the study to assess temporal changes in ALAN.

The daily temporal pattern of collision mortality could be another factor leading to the apparent lack of correlation between lighting and collisions. In a concurrent study (see Chapter 2 [Riding et al. *in review*]), we found that most collisions occurred during the night or early morning (i.e., within ~2 hours of sunrise). We were not able to tease apart the proportion of nocturnal collisions, but we expect it was non-trivial. There were likewise a number of fatal and non-fatal collisions that occurred during morning twilight or shortly after sunrise, when ALAN would be less influential. However, some of those near-dawn collisions may have been triggered by ALAN causing light entrapment during the previous night. Therefore, we suspect that ALAN could be related to most but not all of the collision mortality we recorded, which would again perpetuate some mismatch in the lighting and mortality data. Future research should strive to collect lighting data during the same daily period during which most lighting-related collisions occur and to exclude mortality events that likely lacked a direct link to ALAN.

A factor that we did not account for in our lighting measurements was moonlight. Lunar phase is known to affect lunar albedo (i.e., the moon's contribution to downwelling irradiance; Palmer and Johnsen 2015), but we think that moonlight had no appreciable effects on our lighting measurements for at least five complementary reasons. First, the moon was below the horizon during lighting measurements for 65% (72 of 110) of the points when we recorded measurements (lunar altitude determined from http://www.mooncalc.org). Second, cloud cover interrupted lunar luminescence for 18% (7 of 38) of the points for which the moon was above the horizon. Third, the proximity of measurement locations to buildings obstructed direct moonlight for an additional, but unrecorded number of measurements (*personal observation*). Fourth, 81% (25 of 31) of measurements for which the moon was above the horizon and not covered by clouds occurred when the lunar disc was < 50% illuminated, a condition wherein the normalized lunar brightness at 500 nm is < 20% that of a full moon (Palmer and Johnsen 2015). Fifth, the maximum illuminance of the moon in ideal conditions (i.e., full moon at zenith in clear atmosphere) is < 0.5 lux (Kyba et al. 2017b). For comparison, bright sunlight produces > 10,000 lux (direct sunlight may be as high as 100,000 lux; Li et al. 2005, Kandilli and Ulgen 2008), the interior lighting of buildings averages 200-500 lux (US General Services Administration 2019), and a standard 60 Watt light bulb produces about 800 lumens, which amounts to 80 lux when projected onto 10 m^2. Thus, even though moonlight may influence bird behavior at night, including during migration and in association with collision risk (Verheijen 1981, Pyle et al. 1993, Kanda et al. 2016), the infrequency of direct moonlight (< 32 of 110 [< 29%] points) and the relatively small contribution to total illuminance in a lighted urban area both likely prevented moonlight from contributing meaningfully to our measurements of irradiance.

Another important consideration that we did not directly address here is how light is perceived by birds and whether our characterization of light was more representative of light perception by birds than other coarse human-based measurements may be. The general mechanisms of phototransduction, signal transmission, and visual processing are similar across mammals and birds (Vallortigara 2004), and human perception may be a valid proxy for avian vision for some purposes (Seddon et al. 2010). However, human perception does not adequately mimic bird perception for most purposes (Eaton 2005, Martin 2012), and avian vision should be considered in a species-specific context because several visual aspects exhibit wide phylogenetic variation (Moore et al. 2012, Ödeen and Håstad 2013, Lind et al. 2014, Kelber et al. 2017). Therefore, simplified measures of light (e.g., the value we summed across the spectrum) may not be appropriate in evaluating collision-related perception across all bird species, and may in part explain why we failed to find a relationship between ALAN intensity and mortality intensity. Species-specific perception models (Fernández-Juricic 2016) should be considered for future research on the effects of ALAN.

Finally, the spatial scale of our study may have been too fine to address the effects of ALAN. The two primary hypothesized effects of ALAN on bird-building collisions (impairment and entrapment) may have sufficiently long temporal effects to increase collision risk across a broader spatial area as birds move toward and away from the immediate vicinity of bright lights. Furthermore, the effects of ALAN caused collectively by numerous low-wattage lights will be decentralized and widespread. The fine-scale spatial clustering of fatal collisions that we observed (see Chapter 3 [Riding et al. *in prep*]) may have been more correlated to structural (e.g., building height), vegetative (e.g., proximity of trees), or land cover characteristics often associated with bird-building collision (Klem et al. 2009, Cusa et al. 2015, Hager et al. 2017). Additionally, the method of light measurement, which would relate to both scale and relevance to perception, may have been important.

Despite the lack of evidence in this study, ALAN may pose a threat to birds by increasing their exposure to building collisions, especially for nocturnal migrants. Future studies may be informed and refined by our experiences and conclusions, namely, increased consideration of weather (especially cloud altitude), temporally matching lighting and collision data, species-specific perception modeling, and appropriate spatial scaling.

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APPENDICES

Appendix A: includes five supplemental tables for Chapter 1.

Appendix B: includes four supplemental tables for Chapter 2.

Appendix C: includes supplement material (one figure, 11 tables) for Chapter 3.

Appendix A: Table A1. Number of surveys and raw carcass counts with mortality rates (carcasses/survey) by season in Stillwater, Oklahoma, 2015-2017.

Season	Surveys	Total Carcasses (Mortality rate)	Total Carcasses, no feather piles (Mortality rate)
Spring	2115	157 (0.074)	136 (0.064)
Summer	2222	94 (0.042)	59 (0.027)
Fall	1769	93 (0.053)	81 (0.046)
Winter	274	15 (0.055)	12 (0.044)
All	6380	359 (0.056)	288 (0.045)

Appendix A: Table A2. Daily persistence probability (*s*) of carcasses, estimated mortality rates (carcasses/survey), and adjusted mortality counts for bird-window collisions in Stillwater, Oklahoma, 2015-2017. Numbers in parentheses were calculated with feather piles excluded.

Season	*s*	Estimated mortality rate	Adjusted mortality estimate
Spring	0.935	0.081 (0.070)	170.3 (147.5)
Summer	0.931	0.046 (0.029)	102.5 (64.4)
Fall	0.822	0.067 (0.058)	118.7 (103.4)
Winter	0.888	0.076 (0.061)	20.9 (16.7)
All [1]	0.913	0.063 (0.050)	400.4 (321.2)

1. Calculated from all seasons combined, not a summation.

Appendix A: Table A3. Number of trial carcasses detected by observers and estimated searcher efficiency (*f*) by substrate and proficiency group during experimental observer detection trials conducted in Stillwater, Oklahoma, 2015-2017.

Group	Substrate	n	Number detected	*f*
Experienced	Artificial	60	53	0.883
Experienced	Natural	78	50	0.641
Volunteers	Artificial	32	21	0.656
Volunteers	Natural	19	14	0.737
All	All	189	138	0.730

Appendix A: Table A4. Cox proportional hazard coefficients and exponentiated coefficients with 95% confidence interval for factors influencing time to scavenging (i.e., first scavenging occurrence, regardless of whether all carcass remains are removed) during experimental scavenger removal trials in Stillwater, Oklahoma, 2015-2017.

Factor	Coefficient	Exp(coef)	Lower 95% CI	Upper 95% CI
Carcass size	0.008	1.008	0.999	1.017
Season-Spring	-0.797	0.451	0.197	1.031
Season-Summer	-0.508	0.602	0.268	1.349
Season-Winter	-0.389	0.678	0.284	1.620
Scavenger-Crow	0.770	2.160	0.268	17.430
Scavenger-Dog	-0.953	0.386	0.047	3.167
Scavenger-Opossum	0.450	1.569	0.683	3.606
Scavenger-Raccoon	-0.943	0.389	0.049	3.016
Scavenger-Roadrunner	-2.084	0.124	0.015	1.051
Scavenger-Skunk	-0.464	0.629	0.172	2.296
Scavenger-Squirrel	0.341	1.407	0.436	4.536
Scavenger-Turtle	0.301	1.352	0.304	6.012
Scavenger-Unknown	-0.769	0.463	0.216	0.9948

Appendix A: Table A5. Cox proportional hazard coefficients and exponentiated coefficients with 95% confidence interval for factors influencing carcass persistence time (i.e., time until all carcass remains are removed) during experimental scavenger removal trials conducted in Stillwater, Oklahoma, 2015-2017.

Factor	Coefficient	Exp(coef)	Lower 95% CI	Upper 95% CI
Carcass size	-0.008	0.991	0.980	1.002
Season-Spring	-1.208	0.299	0.117	0.762
Season-Summer	-0.623	0.536	0.220	1.308
Season-Winter	-0.759	0.468	0.197	1.113
Scavenger-Crow	0.214	1.239	0.155	9.916
Scavenger-Dog	-0.477	0.621	0.077	5.009
Scavenger-Opossum	-0.161	0.852	0.353	2.056
Scavenger-Raccoon	0.168	1.183	0.147	9.496
Scavenger-Roadrunner	-1.610	0.200	0.024	1.634
Scavenger-Skunk	0.093	1.097	0.305	3.950
Scavenger-Squirrel	1.017	2.766	0.879	8.707
Scavenger-Turtle	0.637	1.892	0.230	15.571
Scavenger-Unknown	-0.457	0.633	0.266	1.507

Appendix B: Table B1. Full selection results for zero-inflated Poisson regression models that included factors potentially affecting numbers of bird carcasses found in morning, midday, and evening collision surveys. As described in the text, models were excluded from consideration if they were more complex versions of higher ranking models.

Logit model	**Count model**	**K**	**ΔAICc**	**Weight**	**Excluded?**
SurveyTime	Season	7	0.0	0.195	No
SurveyTime	Null	5	1.0	0.119	No
SurveyTime*Season	Null	9	1.3	0.104	Yes
SurveyTime+Season	Null	7	1.4	0.094	Yes
Null	SurveyTime+Season	7	1.6	0.087	No
SurveyTime	SurveyTime+Season	8	2.0	0.073	Yes
Season	SurveyTime	7	2.4	0.059	No
Null	SurveyTime	5	2.5	0.056	No
SurveyTime	SurveyTime	6	3.0	0.044	Yes
SurveyTime*Season	SurveyTime	10	3.2	0.039	Yes
SurveyTime+Season	Season	9	3.4	0.036	Yes
SurveyTime+Season	SurveyTime	8	3.5	0.034	Yes
SurveyTime*Season	Season	11	4.3	0.023	Yes
SurveyTime+Season	SurveyTime+Season	10	5.4	0.013	Yes
Null	SurveyTime*Season	9	5.4	0.013	Yes
SurveyTime	SurveyTime*Season	10	5.9	0.010	Yes
Null	Season	6	17.1	<0.001	No
Season	Null	6	17.9	<0.001	No
Null	Null	4	18.1	<0.001	No
Season	Season	8	19.6	<0.001	Yes

Appendix B: Table B2. Full selection results for zero-inflated Poisson regression models that included factors potentially affecting numbers of non-fatal bird collisions found in morning, midday, and evening collision surveys. As described in the text, models were excluded from consideration if they were more complex versions of higher ranking models.

Logit model	**Count model**	**K**	**ΔAICc**	**Weight**	**Excluded?**
Null	SurveyTime	5	0.0	0.435	No
SurveyTime	Null	5	1.6	0.191	No
SurveyTime	SurveyTime	6	2.0	0.159	Yes
Season	SurveyTime	7	2.9	0.102	Yes
Null	SurveyTime+Season	7	3.4	0.080	Yes
SurveyTime	SurveyTime+Season	8	5.4	0.029	Yes
SurveyTime	SurveyTime*Season	10	9.4	0.004	Yes
Null	Null	4	20.1	<0.001	No
Season	Null	6	23.1	<0.001	Yes
Null	Season	6	23.5	<0.001	Yes

Appendix B: Table B3. Full selection results for negative binomial regression models that included factors potentially affecting (a) monthly counts of total carcasses, (b) monthly counts of carcasses excluding feather piles, and (c) bias-adjusted monthly counts of total carcasses. As described in the text, models were excluded from consideration if they were more complex versions of higher ranking models.

(a)

Variables	**K**	**ΔAICc**	**Weight**	**Excluded?**
ResStatus+Month	11	0.0	1	No
ResStatus+Season	7	23.2	<0.001	No
ResStatus	5	44.0	<0.001	No
Month	8	122.4	<0.001	No
Season	4	12.97	<0.001	No
Null	2	132.3	<0.001	No

(b)

Variables	**K**	**ΔAICc**	**Weight**	**Excluded?**
ResStatus+Month	11	0.0	1	No
ResStatus+Season	7	26.9	<0.001	No
ResStatus	5	49.4	<0.001	No
Month	8	164.9	<0.001	No
Season	4	169.3	<0.001	No
Null	2	174.9	<0.001	No

(c)

Variables	**K**	**ΔAICc**	**Weight**	**Excluded?**
ResStatus+Month	11	0.0	1	No
ResStatus+Season	7	6563.7	<0.001	No
ResStatus	5	10834.6	<0.001	No
Month	8	25519.3	<0.001	No
Season	4	27927.2	<0.001	No
Null	2	29658.7	<0.001	No

Appendix B: Table B4. Negative binomial model coefficients and standard errors for factors potentially affecting (a) monthly counts of total carcasses, (b) monthly counts of carcasses excluding feather piles, and (c) bias-adjusted monthly counts of total carcasses.

(a)

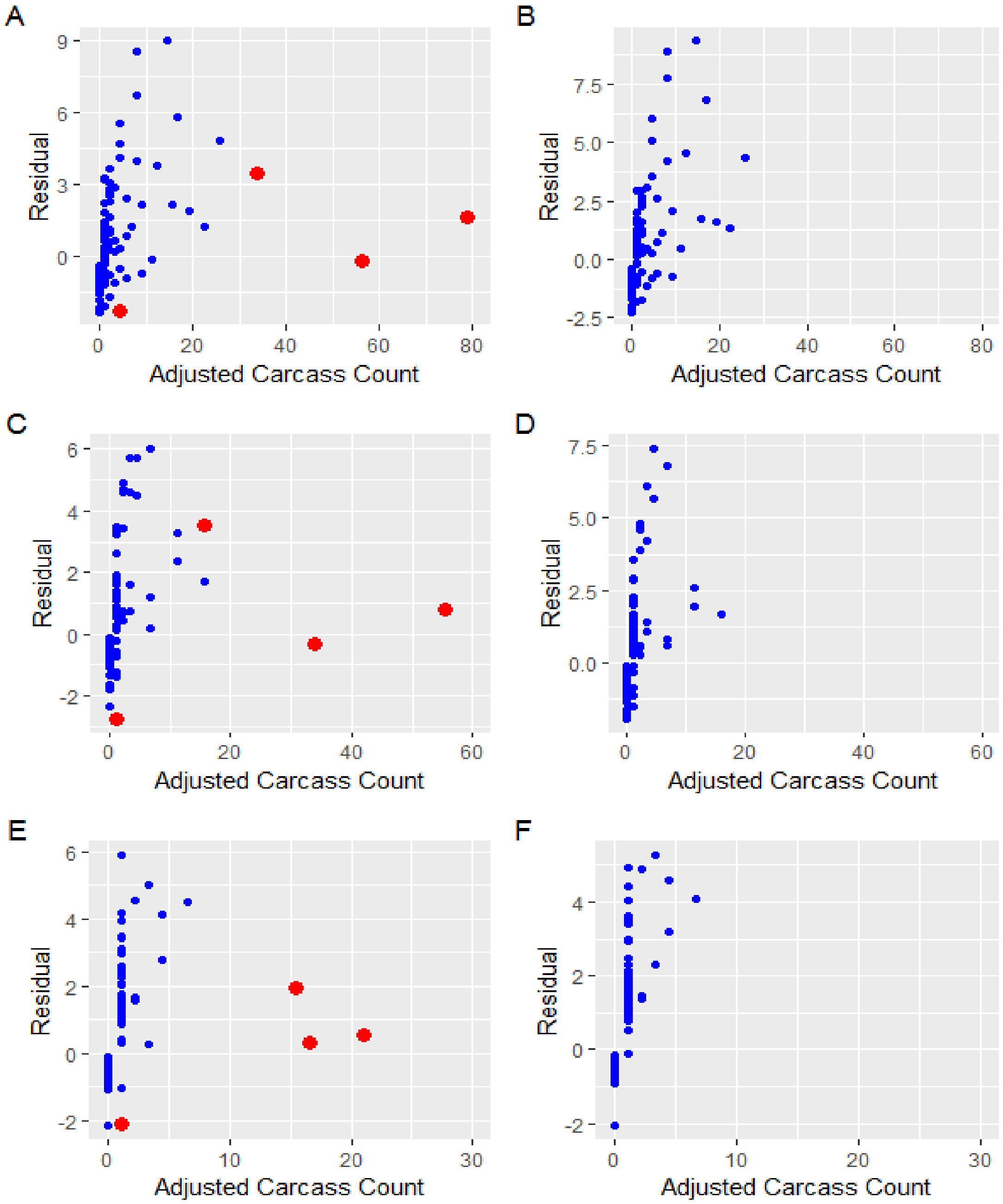
Factor	Coefficient	Standard Error
Intercept	2.37	0.21
Status-Resident	0.55	0.18
Status-Unknown	-2.03	0.20
Status-Unidentified	-1.37	0.19
Month5	1.48	0.25
Month6	0.18	0.26
Month7	-0.72	0.27
Month8	-0.03	0.26
Month9	0.52	0.28
Month10	0.54	0.28

(b)

Factor	Coefficient	Standard Error
Intercept	2.23	0.23
Status-Resident	0.25	0.18
Status-Unknown	-2.15	0.21
Status-Unidentified	-3.36	0.27
Month5	1.74	0.27
Month6	0.40	0.29
Month7	-0.55	0.30
Month8	-0.29	0.30
Month9	0.77	0.28
Month10	0.63	0.28

(c)

Factor	Coefficient	Standard Error
Intercept	2.35	0.02
Status-Resident	0.24	0.02
Status-Unknown	-2.21	0.02
Status-Unidentified	-3.58	0.02
Month5	1.80	0.02
Month6	0.39	0.02
Month7	-0.55	0.03
Month8	-0.31	0.03
Month9	0.96	0.02
Month10	0.75	0.02



Appendix C: Figure C1. Residuals plotted against dependent variables (adjusted carcass counts) for multi-season (A & B), spring (C & D), and summer models (E & F). For plots A, C, and E, n = 235 and the 4 façades of building OS12 are highlighted in red. For plots B, D, and F, n = 231 and building OS12 is excluded.

Appendix C: Table C1. Results for spring models of relationship between façade variables and bias-adjusted carcass counts based on Akaike's Information Criterion (ΔAICc).

Variables	**ΔAICc**	**K**	**ω_i**
Glass, Height, Length, Type	0.0	10	1.000
Glass, Height, Length	89.4	6	<0.001
Glass, Length, Type	96.0	9	<0.001
Glass, Height, Type	96.4	9	<0.001
Glass, Height	100.6	5	<0.001
Height, Length, Type	107.5	9	<0.001
Length, Type	116.9	8	<0.001
Glass, Length	118.5	5	<0.001
Glass, Type	123.3	8	<0.001
Height, Length	125.4	5	<0.001
Null	147.6	3	<0.001

Appendix C: Table C2. Results for summer models of relationship between façade variables and bias-adjusted carcass counts based on Akaike's Information Criterion (ΔAICc).

Variables	**ΔAICc**	**K**	**ω_i**
Glass, Height, Length, Lawn	0.0	7	1.000
Glass, Height, Length	5.6	6	<0.001
Glass, Height, Lawn	6.7	6	<0.001
Glass, Height	8.3	5	<0.001
Glass, Length, Type, Lawn	15.8	10	<0.001
Glass, Length, Lawn	19.8	6	<0.001
Glass, Length, Type	22.7	9	<0.001
Glass, Length	28.6	5	<0.001
Glass, Type, Lawn	28.7	9	<0.001
Glass, Type	30.6	8	<0.001
Glass, Lawn	33.7	5	<0.001
Height, Length	34.3	5	<0.001
Null	50.9	3	<0.001

Appendix C: Table C3. Results for fall models of relationship between façade variables and bias-adjusted carcass counts based on Akaike's Information Criterion (ΔAICc).

Variables	**ΔAICc**	**K**	**ω_i**
Glass, Height, Tree, Lawn	0.0	7	0.456
Glass, Height, Tree	0.2	6	0.415
Glass, Tree, Lawn	4.0	6	0.061
Glass, Tree	5.0	5	0.037
Glass, Height, Lawn	7.3	6	0.012
Glass, Height	7.4	5	0.011
Glass, Lawn	9.1	5	0.005
Glass, Length	9.4	5	0.004
Null	36.3	3	<0.001

Appendix C: Table C4. Results for Lincoln’s Sparrow models of relationship between façade variables and bias-adjusted carcass counts based on Akaike’s Information Criterion (ΔAICc).

Variables	**ΔAICc**	**K**	**ω_i**
Glass, Tree, Flower	0.0	6	0.55
Glass, Tree	0.4	5	0.45
Glass, Length, Flower	44.3	9	<0.001
Glass, Flower	45.1	5	<0.001
Glass	45.3	4	<0.001
Null	61.7	3	<0.001

Appendix C: Table C5. Results for American Robin models of relationship between façade variables and bias-adjusted carcass counts based on Akaike’s Information Criterion (ΔAICc).

Variables	**ΔAICc**	**K**	**ω_i**
Length, Impervious	0.0	5	0.432
Length, Lawn	0.6	5	0.318
Tree, Impervious	2.7	5	0.113
Length	2.7	4	0.110
Null	5.5	3	0.027

Appendix C: Table C6. Results for Mourning Dove models of relationship between façade variables and bias-adjusted carcass counts based on Akaike's Information Criterion (ΔAICc).

Variables	**ΔAICc**	**K**	**ω_i**
Glass, Height, Length	0.0	6	0.817
Glass, Height, Impervious	5.4	6	0.055
Glass, Height	6.3	5	0.035
Glass, Length	6.4	5	0.034
Height, Length, Impervious	7.0	6	0.025
Height, Length	7.1	5	0.024
Length, Impervious	8.8	5	0.010
Null	16.8	3	<0.001

Appendix C: Table C7. Results for Swainson's Thrush models of relationship between façade variables and bias-adjusted carcass counts based on Akaike's Information Criterion (ΔAICc).

Variables	**ΔAICc**	**K**	**ω_i**
Glass, Height	0.0	5	0.993
Glass, Length	11.7	5	0.003
Glass, Lawn	12.5	5	0.002
Glass	12.6	4	0.002
Null	29.1	3	<0.001

Appendix C: Table C8. Results for Indigo Bunting models of relationship between façade variables and bias-adjusted carcass counts based on Akaike's Information Criterion (ΔAICc).

Variables	**ΔAICc**	**K**	**ω_i**
Glass, Height	0.0	5	0.946
Glass, Lawn	7.1	5	0.027
Glass	7.7	4	0.020
Null	9.9	3	<0.001

Appendix C: Table C9. Results for European Starling models of relationship between façade variables and bias-adjusted carcass counts based on Akaike's Information Criterion (ΔAICc).

Variables	**ΔAICc**	**K**	**ω_i**
Glass, Height	0.0	5	0.415
Height	0.4	4	0.347
Length, Flower	1.2	5	0.224
Null	6.8	3	0.014

Appendix C: Table C10. Results for House Finch models of relationship between façade variables and bias-adjusted carcass counts based on Akaike's Information Criterion (ΔAICc).

Variables	ΔAICc	K	ωi
Glass, Height, Length, Tree, Impervious	0.0	8	0.506
Glass, Height, Length, Impervious	1.1	7	0.295
Glass, Height, Impervious	3.6	6	0.083
Glass, Height	4.8	5	0.046
Height, Length, Tree, Impervious	5.1	7	0.040
Height, Length, Impervious	6.7	6	0.017
Height	8.4	4	0.008
Length, Impervious	9.3	5	0.005
Null	21.8	3	<0.001

Appendix C: Table C11. Results for Painted Bunting models of relationship between façade variables and bias-adjusted carcass counts based on Akaike's Information Criterion (ΔAICc).

Variables	ΔAICc	K	ωi
Glass, Height, Impervious	0.0	6	0.452
Glass, Height, Length, Flower	1.7	7	0.192
Glass, Height, Length	2.6	6	0.121
Glass, Height, Flower	2.6	6	0.121
Glass, Height	2.9	5	0.105
Height, Impervious	10.0	5	0.003
Height, Length, Flower	10.3	6	0.003
Height, Flower	10.9	5	0.002
Height, Length	12.4	5	<0.001
Height	13.0	4	<0.001
Null	43.0	3	<0.001

VITA

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