Bird-window collisions in the summer breeding season

Birds that reside in urban settings face numerous human-related threats to survival, including mortality from bird-window collisions (BWCs). Our current understanding of this issue has largely been driven by data collected during spring and fall migration, and patterns of collision mortality during the summer breeding season remain relatively unexplored. Data on BWCs during all phases of important bird activities, including reproduction, are necessary to inform full life cycle population modeling and population health assessments. We assessed BWCs during four breeding seasons (2009-2012) at a site in northwestern Illinois, USA, by comparing the abundance, richness, migratory class, and age of the species living around buildings to species mortally wounded by window collisions. We also systematically assessed the daily timing of BWCs throughout the breeding season. Bias associated with imperfect detection of carcasses was reduced by accounting for the effects of scavengers and carcass detection by field workers. We documented BWCs in 9 of 27 species breeding on site. Species abundance of bird carcasses was negatively related to the abundance of breeders. That is, mortality was highest for the least abundant migratory species and lowest for the most abundant Permanent Resident and Short-distance Migrant species. An exception was high mortality in one abundant Short-distance Migrant, the American Robin (*Turdus migratorius*; all hatch-year birds). Early in the breeding season, collision mortality was restricted to adults of Long-distance Migrants, whereas juveniles of all three migratory guilds (Long-distance and Short-distance Migrants and Permanent Residents) died at windows from late June through early August. Daily mortality for all species was highest at night and from sunrise - 1230 h and lowest between 1230 h - sunset. Generally, the species observed as carcasses matched birds considered a ‘high risk’ for BWCs, e.g., Ruby-throated Hummingbird (*Archilochus colubris*), and those considered ‘low risk’ were not observed as carcasses, e.g., Blue-gray Gnatcatcher (*Polioptila caerulea*). However, we found no carcasses of some high-risk species, such as Cedar Waxwing (*Bombycilla cedrorum*). Our results demonstrate that risk of BWCs during the breeding season does not necessarily

increase with abundance, but rather appears related to variation among species and age classes in reproductive behavior, flight speed, distance movements, and dispersal patterns. The major habitat types in the United States, such as desert scrub, closed canopy forest, and grasslands, favor unique assemblages of breeding bird communities, which should result in added variation in the species affected by window collisions.

Bird-window collisions in the summer breeding season

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ABSTRACT

Birds that reside in urban settings face numerous human-related threats to survival, including mortality from bird-window collisions (BWCs). Our current understanding of this issue has largely been driven by data collected during spring and fall migration, and patterns of collision mortality during the summer breeding season remain relatively unexplored. Data on BWCs during all phases of important bird activities, including reproduction, are necessary to inform full life cycle population modeling and population health assessments. We assessed BWCs during four breeding seasons (2009-2012) at a site in northwestern Illinois, USA, by comparing the abundance, richness, migratory class, and age of the species living around buildings to species mortally wounded by window collisions. We also systematically assessed the daily timing of BWCs throughout the breeding season. Bias associated with imperfect detection of carcasses was reduced by accounting for the effects of scavengers and carcass detection by field workers. We documented BWCs in 9 of 27 species breeding on site. Species abundance of bird carcasses was negatively related to the abundance of breeders. That is, mortality was highest for the least abundant migratory species and lowest for the most abundant Permanent Resident and Short-distance Migrant species. An exception was high mortality in one abundant Short-distance Migrant, the American Robin (*Turdus migratorius*; all hatch-year birds). Early in the breeding season, collision mortality was restricted to adults of Long-distance Migrants, whereas juveniles of all three migratory guilds (Long-distance and Short-distance Migrants and Permanent Residents) died at windows from late June through early August. Daily mortality for all species was highest at night and from sunrise - 1230 h and lowest between 1230 h - sunset. Generally, the species observed as carcasses matched birds considered a 'high risk' for BWCs, e.g., Ruby-throated Hummingbird (*Archilochus colubris*), and those considered 'low risk' were not observed as carcasses, e.g., Blue-gray Gnatcatcher (*Polioptila caerulea*). However, we found no carcasses of some high-risk species, such as Cedar Waxwing (*Bombycilla cedrorum*). Our results demonstrate that risk of BWCs during the breeding season does not necessarily increase with abundance, but rather appears related to variation among species and age classes in reproductive behavior, flight speed, distance movements, and dispersal patterns. The major habitat types in the United States, such as desert scrub, closed canopy forest, and grasslands, favor unique assemblages of breeding bird communities, which should result in added variation in the species affected by window collisions.

Keywords: Bird-window Collisions, Human Threats, Avian Mortality, Breeding Birds, Urban Ecology

INTRODUCTION

Birds that reside in urban settings face numerous human-related threats to survival, including mortality from bird-window collisions (’BWCs’; Fig. 1A). Knowledge of the drivers of BWCs is necessary to effectively manage urban ecosystems. Previous work demonstrates significant spatial variation in bird mortality resulting from window strikes. In particular, buildings with high window area and surrounding green space incur the greatest frequency of BWCs and are patchily distributed across the urban landscape (Bayne et al., 2012; Hager et al., 2013; Machtans et al., 2013; Loss et al., 2014). However, despite knowledge that bird behaviors differ across seasons, days, and species, we have an incomplete understanding of temporal and species-specific patterns of BWCs. This information is necessary to inform full life cycle population modeling and population health assessments, which would assist in conservation efforts aimed at reducing collision-related impacts (Loss et al., 2012).

Reference to Figure 1.

Collision mortality is reported to be highest during spring and fall migration relative to bird residency during winter and summer (Drewitt and Langston, 2008). However, this conclusion has been derived from studies that were conducted mainly during migration (Drewitt and Langston, 2008). A recent experiment employing a systematic sampling design for all seasons confirmed low mortality in winter, but suggested that collisions during the breeding season, i.e., June-early August, are similar in magnitude to spring and fall migration (Hager et al., 2013). In addition to variability across seasons, BWCs likely vary within a 24-h period due high levels of morning activity related to feeding and behavioral interactions within and among species (McNamara et al., 1987). In the breeding season, daily activities patterns would also be affected by high ambient temperatures resulting in low levels of activity during hot afternoons, and reproductive behaviors, such as dispersal of postfledging individuals (Whittaker and Marzluff, 2009), which may further influence risk of window strikes. A better understanding of the temporal patterns of mortality within the breeding season would clarify our current view of the threat posed by BWCs.

In addition to potential temporal dynamics of BWCs during the breeding season, the resident community during these months may determine the species, migratory guild, and ages of affected individuals. Short and Long-distance migrants, including birds of conservation concern, and hatch-year birds appear to experience the highest incidence of mortality (Hager et al., 2013; Loss et al., 2014). Moreover, it has been asserted that the abundance and richness of birds are the best predictors of BWCs (Klem, 1989). However, these conclusions deserve further scrutiny because, as stated earlier, little work has focusesd on mortality outside of spring and fall migration (Drewitt and Langston, 2008). Breeding bird communities may be composed of Short- and Long-distance Migrants, Permanent Resident species, and both adults and post-fledgling individuals (Blair, 1996). Thus, assessing whether BWCs are related to a species' migration strategy, age class, and abundance is ideally suited to the summer breeding season.

We addressed the need for a better understanding of summertime BWCs by documenting the temporal dynamics of and species affected by BWCs for a breeding bird community in northwestern Illinois, USA. This was evaluated during four summer seasons on a college campus composed of low-rise commercial buildings situated in moderate to high levels of green space. In 2009-2010, we used point count surveys to estimate the abundance, richness, migratory guild, and age class of the site's breeding birds, and compared these metrics to the species mortally wounded by window collisions. In 2011-2012, we completed systematic surveys at five intervals each day to assess how mortality was distributed throughout a 24-h period. Birds affected by window collisions in our study were then compared to vulnerability estimates for species in the United States (Loss et al., 2014). Bias associated with imperfect detection of carcasses was reduced in all summers by accounting for the effects of scavengers and carcass detection by field workers.

MATERIALS AND METHODS

Study site

We assessed BWCs at Augustana College in northwestern Illinois, USA, for nine weeks of each breeding season (June–early August) from 2009-2012. The campus was constructed within the bluffs of the Mississippi River (90 degrees 33' W, 41 degrees 30' N) and located in the *Eastern Tallgrass Prairie* Bird Conservation Region (Sauer et al., 2003). Bluff faces contained moderately disturbed deciduous hardwood forest ('wooded bluff faces'), and terraces above and below bluffs were similar in structure to grassland savanna with scattered woody trees and shrubs and an open understory of landscaped grass ('landscaped savanna'). Work was completed at four low-rise commercial buildings (range 3-5 stories): Westerlin Residence Hall, Hanson Hall of Science, Thomas Tredway Library, and Swenson Hall of Geosciences.

Scavenger study

We minimized bias associated with imperfect detection of carcasses by using a sampling design that was informed by estimates of carcass persistence before removal by scavengers and decomposers and detection by field workers (Hager et al., 2012, 2013). Persistence or survival of whole and partial, i.e., feather piles (Fig. 1B), carcasses was monitored at four campus buildings (Hanson Hall of Science, Swenson Hall of Geosciences, Thomas Tredway Library, and Olin Center for Education Technology) during a 7-d study period (2-8 June 2010). Two of eight whole, intact bird carcasses were randomly placed below different facades of each building [see Hager et al. (2012) for details on carcass placement and daily monitoring]. Each carcass was a different species ranging in size from Tennessee Warbler [*Oreothlypis peregrina*; 9 g, Sealy (1985)] to Brown Thrasher [*Toxostoma rufum*; 70 g, Cavitt and Haas (2000)].

Reference to Figure 1.

Carcass surveys

In 2009 and 2010, we completed carcass surveys at intervals of 1-3 days at Hanson Hall of Science, Swenson Hall of Geosciences, and Thomas Tredway Library. During each survey, a trained fieldworker walked a complete transect around a building's footprint within a 2-m buffer. This buffer accommodated the perpendicular distance from external walls at which most carcasses are located (95 percent CI = 93-127 cm; N = 51 carcasses; SBH, unpubl. data). A bird carcass consisted of a full body, partial carcass, or feather pile (Hager et al., 2012). We assumed high average detection probability of bird carcasses (0.88, SE = 0.01) based on Hager et al. (2013).

In 2011 and 2012, we assessed the daily pattern of BWCs by sampling carcasses for four consecutive days per week at Hanson Hall of Science, Swenson Hall of Geosciences, and Westerlin Residence Hall, which was included because of construction activities that prevented access to Thomas Tredway Library. Within each day-building combination, five surveys were completed at sunrise, 0900 h (CDT), 1230 h, 1600 h, and one hour prior to sunset. We assumed that a carcass found during a survey died in the interval between that time and the previous survey. A 'clean-up survey' was conducted at sunset the day before the first sunrise survey for each sampling week. This survey removed all carcasses that accumulated between survey-weeks, which may have otherwise introduced detection bias on the first day of weekly sampling.

Carcasses and corresponding identification tags were placed in zip-lock plastic bags and later identified to species in the laboratory. Birds were classified as adult or juvenile based on plumage, degree of cranial pneumatization, and, in hummingbirds, pattern of bill serration (Pyle, 1997). We consulted Fair et al. (2010) for recommendations related to collecting procedures of bird carcasses.

Point count surveys

We used 50-m radius point counts of 5-min duration to characterize the breeding avian community in 2009 and 2010 (Johnson, 2008; Hager et al., 2013). One point count circle each was established in wooded bluff face and landscaped savanna, which were the two dominant habitat types present on campus. Count circle edges were within 50-125 m of each of the three study buildings. We completed two surveys/week in June and July during appropriate weather conditions and within 4 h after sunrise (Bled et al., 2013).

We identified and counted all birds seen and heard during each survey. Unfortunately, we could not distinguish birds of various age classes, which precluded an evaluation of how BWCs varied among adults and juveniles living near buildings. For each season, abundance was the maximum number of individuals counted (Johnson, 2008), and species richness was the total number of species observed. The following species, guilds, and taxonomic groups were excluded from analyses: birds flying over the site, migratory flocks, waterfowl, and raptors (Kalinowski and Johnson, 2010; Hager et al., 2013). We followed the recommendations of Fair et al. (2010) in reducing impacts to birds resulting from investigator presence during point count surveys.

We consulted the North American Ornithological Atlas Committee (2012) to classify levels of each species' breeding behaviors, which were documented opportunistically during point counts and at other times throughout the season. Species classified above the 'observed' level were considered part of the site's breeding community.

Data analysis

For the carcass detection study, we estimated mean survival times (t) for complete and partial (i.e., feather piles) carcasses at each building using the exponential model $r = e^{-d/t}$, where r is the probability of survival for d = 1 day (Huso, 2011; Hager et al., 2012).

We used a Fisher's Exact Test to examine differences in the number of BWCs among species considered Short-distance Migrant, Long-distance Migrant, and Permanent Resident.

To determine whether species abundance was related to susceptibility to collisions, we used a generalized linear model, specifying a Poisson distribution with a log link function. We included abundance and year as predictors of carcass counts, but did not retain year as it was not significant. One species, the American Robin (*Turdus migratorius*), was omitted from this analysis because its inclusion resulted in an inadequate fit (Goodness of fit: Pearson X^2=73.6, P = 0.013).

We used a general linear model to evaluate the relationship between BWCs and time-of-day. We standardized the carcass data, i.e., number carcasses/survey, to account for slight differences in effort—due to inclement weather that prevented some surveys from being conducted—among weeks and years. Time-of-day and year were included as predictors of the number of carcasses detected per survey; year was not significant and was removed from the final model.

RESULTS

Scavenger assessment

During the 7-day scavenger study, the probability of daily carcass survival was high (0.8) and average carcass persistence at buildings was 6.25 days. A scavenger removed one carcass within 24 h after initial placement. Within 5 days, decomposers gradually transformed the remaining seven carcasses into feather piles, which remained detectable and persisted until the end of the study (Fig. 1B).

Reference to Figure 1.

Bird density and mortality

In 2009 and 2010, we documented BWCs in 9 of 27 breeding species (Fig. 2). An additional four species were collected as carcasses, but not observed during point counts, including Belted Kingfisher (*Megaceryle alcyon*), Yellow-billed Cuckoo (*Coccyzus americanus*), Baltimore Oriole (*Icterus galbula*), and Indigo Bunting (*Passerina cyanea*). Indeed, there was habitat available for these species to breed on site, but the fact that they were never documented during point counts and that no breeding behavior was observed suggests a low probability of breeding. There was no significant difference in the number of carcass species vs. non-carcass species (N = carcass, non-carcass) among Short-distance Migrants (1, 9), Long-distance Migrants (4, 3), and Permanent Residents (4, 6) (Fisher's Exact Test, $P = 0.15$).

Reference to Figure 2.

Bird abundance was correlated negatively with BWCs ($P = 0.003$; Fig. 2). That is, BWCs were highest in the least abundant species, which tended to be Long-distance Migrants, e.g., Ruby-throated Hummingbird (*Archilochus colubris*), and lowest in species observed with high abundance values, e.g., House Sparrow (*Passer domesticus*), Chipping Sparrow (*Spizella passerina*), and American Goldfinch (*Spinus tristis*). Indeed, the American Robin had the highest values each year for abundance and mortality. However, removing this species from the data set improved model fit and allowed us to complete the analysis for all other species.

We determined the age classes of 24 carcasses, which were 67 percent juveniles and 33 percent adults (Fig. 3). Juveniles were documented from the third week in June to the end of July, and were principally composed of Short-distance Migrants ($N = 10$; all American Robins) followed equally in sample sizes by Long-distance Migrants ($N = 2$ Ruby-throated Hummingbirds and $N = 1$ Gray Catbird, *Dumetella carolinensis*) and Permanent Residents ($N = 1$ each of Black-capped Chickadee, *Poecile atricapillus*, Northern Cardinal, *Cardinalis cardinalis*, and House Finch, *Carpodacus mexicanus*) (Fig. 3A). Adults (all Long-distance Migrants) were affected by window collisions only at the beginning of the breeding season (Fig. 3B); species (N) included Yellow-billed Cuckoo (1), Ruby-throated Hummingbird (2), Eastern Wood-Pewee, *Contopus virens* (1), Red-eyed Vireo, *Vireo olivaceus* (1), Gray Catbird (1), Indigo Bunting (1), and Baltimore Oriole (1).

Reference to Figure 3.

Daily patterns of mortality

BWCs in the breeding seasons of 2011 and 2012 were correlated negatively with time throughout a 24-h period ($r^2 = 0.46$, $F_{1,8} = 6.79$, $P = 0.031$), and nearly all birds died at night and between sunrise and 1600 h (Fig. 4). Carcass species documented in these seasons included: American Robin, Ruby-throated Hummingbird, Black-capped Chickadee, and four carcass species that were not observed in 2009 and 2010: Northern Flicker (*Colaptes auratus*), Ovenbird (*Seiurus aurocapilla*), White-breasted Nuthatch (*Sitta carolinensis*), and House Sparrow (*Passer domesticus*).

Reference to Figure 4.

Species vulnerability

Eleven of 17 carcass species observed in all four breeding seasons (2009-2012) were recently listed by Loss et al. (2014) as being highly vulnerable to striking windows in the United States (Table 1). Of these, we found that Ruby-throated Hummingbirds and Gray Catbirds died in the greatest numbers and in at least two of the breeding seasons. However, two species of the breeding community, Cedar Waxwings

(*Bombycilla cedrorum*) and Blue Jays, considered vulnerable to BWCs were never found as carcasses. Generally, bird groups estimated to be at high risk and low risk for window collisions corresponded to the bird groups we observed as carcasses (Table 2). For example, Hummingbirds and Swifts and Kingfishers are listed as high-risk groups, which we documented with carcasses from Ruby-throated Hummingbird and Belted Kingfisher. Inconsistent with published vulnerability estimates (Loss et al., 2014) were observations of no mortality in high-risk groups, e.g., Waxwings, and documented mortality in low-risk groups, e.g., Flycatchers and Vireos.

Highly Vulnerable Species[a]	***N* Carcasses**	***N* Breeding Seasons**
Ruby-throated Hummingbird	6	3
Gray Catbird	3	2
House Finch	1	1
Northern Cardinal	1	1
Downy Woodpecker	1	1
Black-capped Chickadee	1	1
Northern Flicker[b]	1	1
White-breasted Nuthatch[b]	1	1
Ovenbird[b]	1	1
Cedar Waxwing	0	0
Bluejay	0	0

[a] Based on Table 4 of Loss et al. (2014)

[b] Carcass found in either 2011 or 2012 when estimating daily mortality, but not during the previous two summers when community composition was assessed.

Table 1. Number of carcasses and number of breeding seasons in which carcasses were found of species estimated as being highly vulnerable to window collisions. Data were collected from 2009-2012 in northwestern Illinois, USA.

DISCUSSION

To better understand summer-time BWCs, we used a systematic sampling protocol to assess whether abundance, richness, migratory guild, and age class of a breeding community in Illinois influenced which species were affected by BWCs. In addition, we assessed how mortality varied throughout a 24 h period within breeding seasons. In the scavenger study, carcasses persisted for over 6 days, which when combined with high search detection probability (Hager et al., 2013), reduced bias associated with imperfect detection of carcasses.

Our results suggest that number of BWCs during the breeding season does not necessarily increase with abundance. For example, the incidence of mortality was high for only one abundant species, the American Robin. Considering the remaining 26 breeding species at this site, collision mortality was inversely related to species' abundance and unaffected by migration strategy. Moreover, a relatively small percentage (roughly 30 percent) of the breeding species were affected by window collisions. These results are consistent with other studies conducted during migration and winter that species' abundance may not be related to the magnitude of collision mortality and relatively few species living around buildings die from hitting windows (Hager et al., 2008, 2013).

Early in the breeding season, collision mortality was restricted to adults of Long-distance Migrants, whereas juveniles of all three migratory guilds (Long-distance and Short-distance Migrants and Permanent Residents) died at windows from late June through early August. Mortality differences among age classes would be expected to reflect the timing at which individuals were present on site: adult mortality prior to successful reproduction and post-fledging mortality after juveniles enter the population. However, adults generally remain within breeding territories near buildings throughout the entire season and, if collision risk is simply related to abundance, then we should have observed adult mortality more consistently throughout the summer. The mechanism driving mortality differences in age and migratory class is unknown, and because we could not differentiate age classes during point counts, we don't know whether differences in species or age class abundance drove differences in mortality.

Alternatively, BWCs are hypothesized to be influenced by flight behavior and temporal variation in

Bird Group Vulnerability	Residual	Risk	Carcasses Found	Carcasses Not found
Hummingbirds and swifts	1.52	33.2	Ruby-throated Hummingbird	Chimney Swift
Kingfishers	0.56	3.6	Belted Kingfisher	–
Waxwings	0.55	3.6	–	Cedar Waxwing
Warblers	0.54	3.4	Ovenbird[a]	–
Nuthatches, tits, and creeper	0.50	3.1	Black-capped Chickadee White-breasted Nuthatch[a]	–
Cuckoos	0.46	2.9	Yellow-billed Cuckoo	–
Mimic Thrushes	0.41	2.6	Gray Catbird	–
Cardinaline Finches	0.36	2.3	Indigo Bunting, Northern Cardinal	–
Thrushes	0.25	1.8	American Robin	–
Cardueline Finches	0.23	1.7	House Finch	American Goldfinch
Woodpeckers	0.15	1.4	Downy Woodpecker, Northern Flicker[a]	Red-bellied Woodpecker
Doves and pigeons	0.08	1.2	–	Mourning Dove, Rock Pigeon
House Sparrow	-0.15	1.4	House Sparrow[a]	–
Wrens	-0.20	1.6	–	House Wren, Carolina Wren
Flycatchers	-0.41	2.6	Eastern Wood-Pewee	Eastern Phoebe
Vireos	-0.55	3.6	Red-eyed Vireo	–
Starling	-0.56	3.6	–	–
Blackbirds, meadowlarks, and orioles	-0.64	4.4	Baltimore Oriole	Common Grackle, Brown-headed Cowbird
Gnatcatchers	-1.68	48.1	–	Blue-gray Gnatcatcher

[a] Carcass found in either 2011 or 2012 when estimating daily mortality, but not during the previous two summers when community composition was assessed.

Table 2. Comparison between building collision vulnerability for bird groups and species within respective groups that were documented or not documented as carcasses during the breeding seasons 2009-2012, northwestern Illinois, USA. Vulnerability estimates based on Loss et al. (2014). According to Loss et al. (2014) "Risk values indicate the factor by which a species has a greater chance (for positive residuals) or a smaller chance (for negative residuals) of mortality compared with a species with average risk."

mobility, i.e., flight speed, distance moved, and dispersal patterns (Klem, 1989). From the perspective of adults, risk of hitting windows may be highest early in the breeding season as individuals engage in high velocity social interactions, such as chases, that are used, among other behaviors, for territory establishment and defense. Following territory settlement, reproductive behavior transitions to brooding of eggs and nestlings resulting in reduced mobility and a decrease in collision risk. Generally, the start of the breeding season in the upper Midwest is staggered among the different migratory guilds. Territorial behavior for Permanent Residents, such as the Downy Woodpecker, and Short-distance Migrants, such as the American Robin, generally begins in February and April, respectively. Thus, the time frame of our field work failed to capture intense territorial behaviors for Permanent Residents and Short-distance Migrants, and instead coincided with reduced mobility and no collisions. In contrast, adults of Long-distance Migrants, such as the Ruby-throated Hummingbird, would have been engaging in aggressive, territorial behavior (Robinson et al., 1996) at the start of our summer field seasons, i.e., early June, and therefore observations of relatively high mortality.

Differences in interspecific collision mortality among juveniles may be related to post-fledging dispersal movements, which varies among migratory guilds, foraging requirements, and habitat preferences (Whittaker and Marzluff, 2009; Ausprey and Rodewald, 2013). For example, Whittaker and Marzluff (2009) found that high speed and long distance dispersal movements were associated with migrating species, such as the American Robin, and selection for highly mobile individuals may be a response to ephemeral food sources, i.e., fruiting trees and shrubs and invertebrate concentration. Thus, juvenile robins with high levels of dispersal mobility should die at high rates, which is what we observed. In contrast, previous work has also demonstrated that juveniles of resident grainivorous species have low levels of dispersal mobility and are constrained to residential patches with bird feeders and preferred habitat (Whittaker and Marzluff, 2009; Ausprey and Rodewald, 2013). Indeed, we observed little to no mortality in juveniles of seed eating resident (as well as migrant) species, i.e., juveniles with lower expected dispersal mobility.

We found that the daily timing of collision mortality was highest at night, in the morning, and early afternoon hours. Bird mortality at night is known to occur when nocturnal migrants are attracted to lighted structures (Gauthreaux et al., 2006). Once entrapped by the light's influence, individuals may die from collisions with buildings and with other birds and from exhaustion. This may explain our observation of an Ovenbird (a nocturnal migrant that does not breed on campus) carcass in early June. For breeding species, recent research has demonstrated behavioral and physiologic effects of light-at-night in urban landscapes (Dominoni et al., 2013). Light-at-night may advance activity levels in urban birds causing them to engage in social behaviors, e.g., territorial disputes, in the predawn hours, which could increase collision risk. Alternatively, our survey design may have caused us to wrongly ascribe nighttime mortality to collisions occurring shortly after sunrise. We assumed that a carcass found during a particular survey time represented a mortality event in the interval between that time and the previous survey. Unfortunately, one field worker could not start all building surveys at sunrise, and buildings needed to be surveyed in an ordered fashion. We found two of four carcasses during the 'sunrise' survey 30 and 60 minutes after official sunrise at the second and third buildings surveyed, respectively.

Mortality between sunrise and early afternoon may correlate with bird activities throughout the day (e.g., foraging), and a lack of collisions in the late afternoon hours may reflect periods of inactivity when birds are behaviorally thermoregulating due to high ambient temperatures (Robbins, 1981).

Population and conservation implications

Generally, the carcass species we found conformed to the species and species groups considered to be highly vulnerable to BWCs, such as Ruby-throated Hummingbird and Nuthatches, tits, and chickadees (e.g., Black-capped Chickadee). Moreover, we observed limited mortality in birds whose species groups are considered to be at low risk of collisions, e.g., Orioles (Baltimore Oriole), Vireos (Red-eyed Vireo), and Flycatchers (Eastern Wood-Pewee). However, we found no carcasses of some high-risk species, such as Cedar Waxwings.

Discerning a pattern of species susceptibility remains difficult because of the paucity of data collected during the breeding season (Loss et al., 2014). Moreover, the factors affecting bird community structure at the local scale would be expected to result in variation in the species affected by windows. For example, a low-rise building in High Intensity Development (greater than 80 percent impervious surfaces) should affect urban exploiters (e.g., European Starlings) and another identical low-rise building in Open Space Development (less than 20 percent impervious surfaces) should affect urban adapted and urban sensitive species, some of which are species of conservation concern (Chace and Walsh, 2006; Loss et al., 2014).

At broad scales, the nature of bird communities among urban areas should reflect landscape structure and functional connectivity (Chace and Walsh, 2006; Ramalho and Hobbs, 2012), which would result in variation in the species and magnitude of BWCs. For example, American Robins (an urban adapted species) respond positively to urbanization throughout much of its range including desert scrub, closed canopy forest, and grasslands (Blair, 2004; Chace and Walsh, 2006), and high levels of juvenile mortality documented in this study may be occurring in urban landscapes throughout the range of this species. However, differences in avian communities among the major habitat types (i.e., desert scrub, closed canopy forest, and grasslands) should result in unique suites of urban sensitive species that may be vulnerable to window collisions. Future work should assess variation in species affected by BWCs for breeding bird communities across multiple spatial scales, which could then inform studies on demography and population health of those species.

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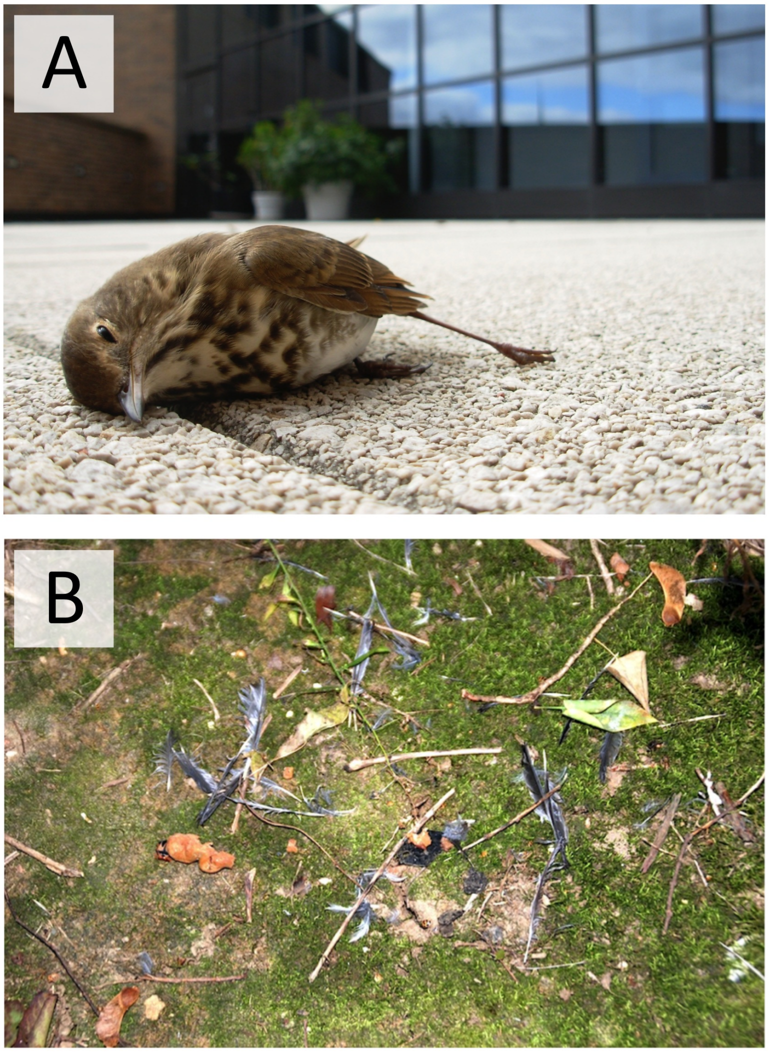

Figure 1. (A) Hermit Thrush (*Catharus guttatus*) fatally wounded after crashing into a window. (B) Feather pile of a Gray Catbird (*Dumetella carolinensis*) carcass, which resulted from a window collision. Feather piles are produced when decomposers and vertebrate scavengers, such as raccoons (*Procyon lotor*), remove most soft and bony tissue, but leave behind various feathers (e.g., remiges, nonflight feathers, and rectrices), body parts (e.g., wing, tail, and legs), and soft tissue (e.g., intestines) (Hager et al., 2012). Moreover, they may remain detectable by field workers for short periods of time, and thus, provide evidence of collisions (Stevens et al., 2011).

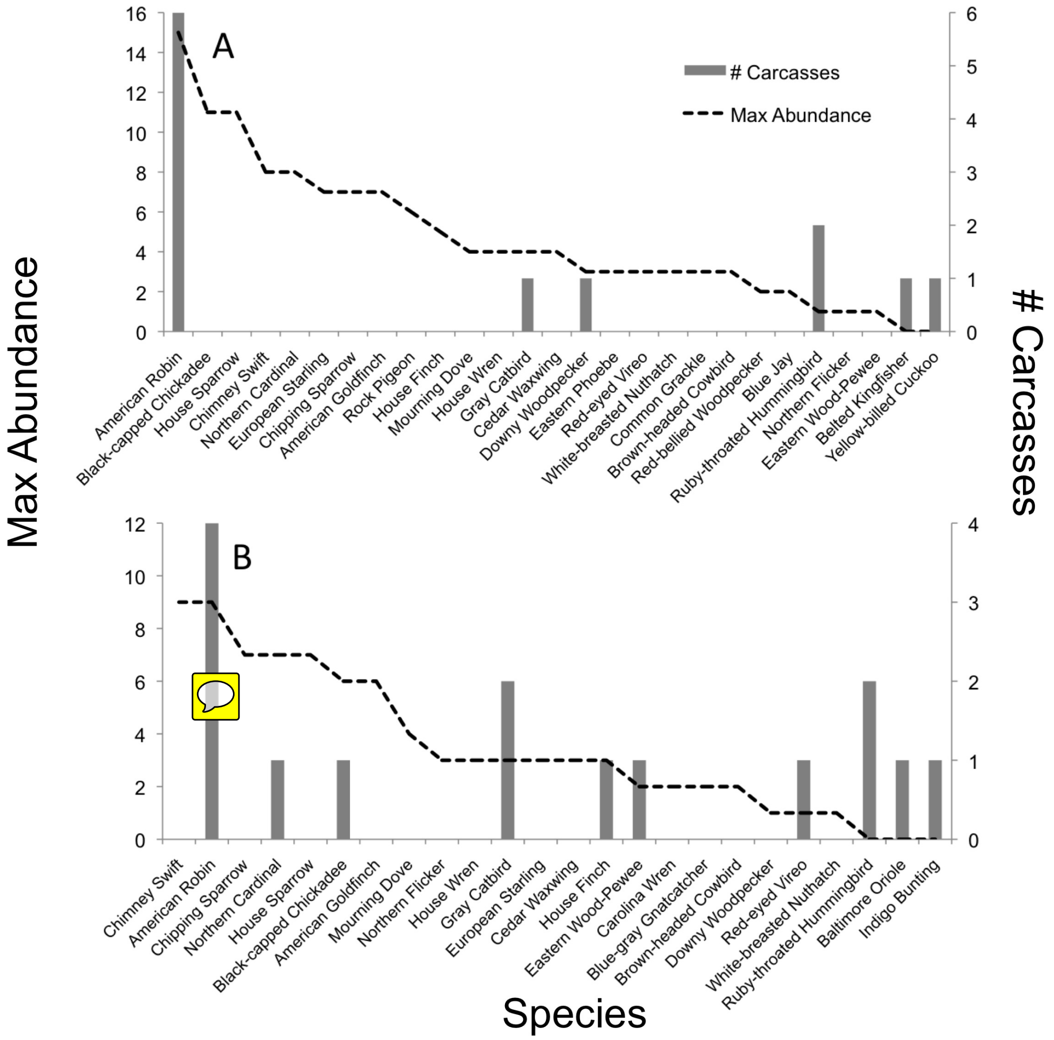

Figure 2. Maximum abundance of live birds observed during point counts and total abundance of carcasses resulting from window collisions in northwestern Illinois, USA, in two summer breeding seasons: (A) 2009 and (B) 2010.

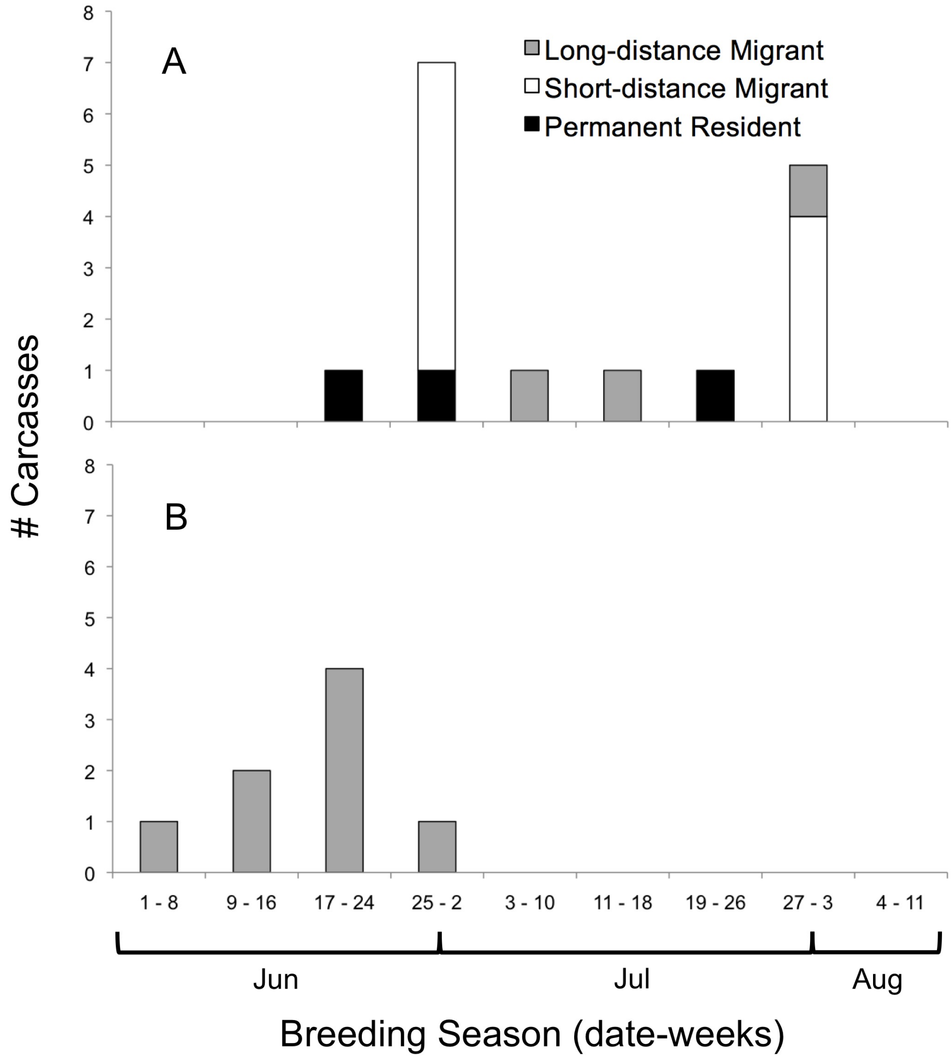

Figure 3. Migration guilds and number of (A) juvenile and (B) adult birds collected as carcasses from window collisions in northwestern Illinois, USA, for each of nine weeks of the breeding seasons of 2009 and 2010.

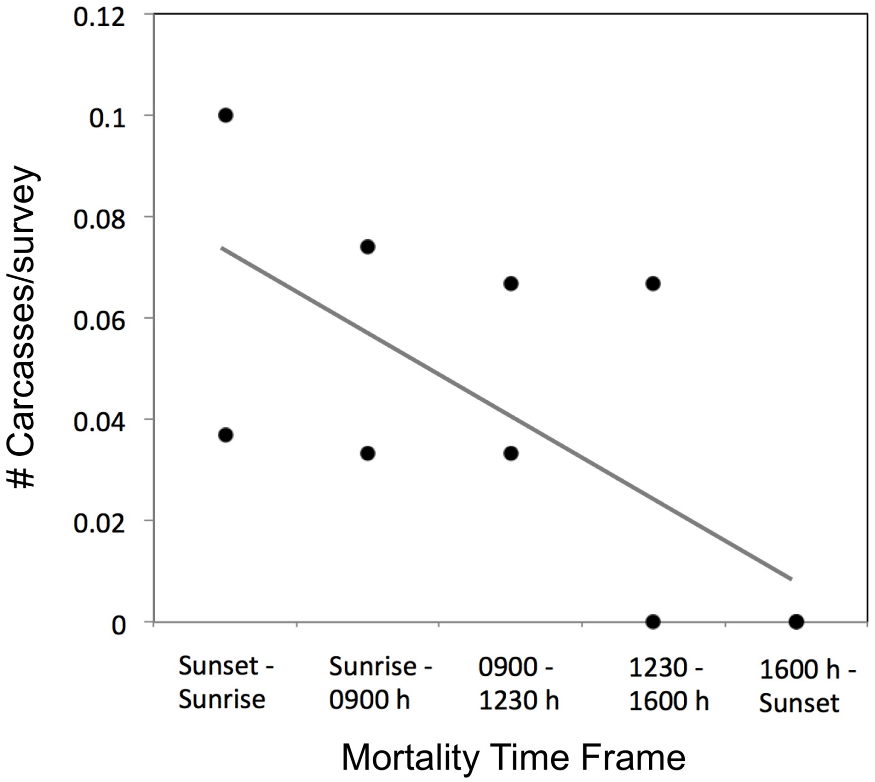

Figure 4. Number of carcasses per survey throughout a 24-h period during the 2011 and 2012 summer breeding seasons in northwestern Illinois, USA.