



Continent-wide analysis of how urbanization affects bird-window collision mortality in North America



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ABSTRACT

Characteristics of buildings and land cover surrounding buildings influence the number of bird-window collisions, yet little is known about whether bird-window collisions are associated with urbanization at large spatial scales. We initiated a continent-wide study in North America to assess how bird-window collision mortality is influenced by building characteristics, landscaping around buildings, and regional urbanization. In autumn 2014, researchers at 40 sites (N = 281 buildings) used standardized protocols to document collision mortality of birds, evaluate building characteristics, and measure local land cover and regional urbanization. Overall, 324 bird carcasses were observed (range = 0–34 per site) representing 71 species. Consistent with previous studies, we found that building size had a strong positive effect on bird-window collision mortality, but the strength of the effect on mortality depended on regional urbanization. The positive relationship between collision mortality and building size was greatest at large buildings in regions of low urbanization, locally extensive lawns, and low-density structures. Collision mortality was consistently low for small buildings, regardless of large-scale urbanization. The mechanisms shaping broad-scale variation in collision mortality during seasonal migration may be related to habitat selection at a hierarchy of scales and behavioral divergence between urban and rural bird populations. These results suggest that collision prevention measures should be prioritized at large buildings in regions of low urbanization throughout North America.

1. Introduction

Annual avian mortality resulting from collisions with buildings is estimated at nearly 1 billion birds in North America (Klem, 1990; Machtans et al., 2013; Loss et al., 2014). Numerous bird species are affected by bird-building collisions, including species of conservation concern (Machtans et al., 2013; Loss et al., 2014). Nocturnally migrating birds are known to strike the windows of buildings in large cities after becoming attracted to and disoriented by artificial lighting or when low cloud cover forces individuals to fly at altitudes below the top of many sky scrapers (Longcore and Rich, 2004). During the daytime hours, birds may strike windows after mistaking the reflected environment in sheet glass for habitat and open flight space (Klem, 1989; Martin, 2011).

Window collision risk is primarily related to structural features of buildings and land cover features immediately surrounding buildings. For example, mortality is highest at large buildings with many windows and lowest at small structures with proportionately fewer windows (O’Connell, 2001; Hager et al., 2008, 2013; Klem et al., 2009; Machtans et al., 2013; Loss et al., 2014; Kahle et al., 2016; Ocampo-Peñuela et al., 2016). Moreover, bird-window collisions are more frequent at buildings surrounded by low levels of impervious surfaces (e.g., paved roadways, sidewalks, and parking lots) and structures (e.g., buildings) (Hager et al., 2013; Cusa et al., 2015). Differences in building size and the patchy nature of development in cities and towns create strong spatial variation in the number of birds that collide with glass (Bayne et al., 2012; Hager et al., 2013; Machtans et al., 2013; Loss et al., 2014).

Although building characteristics and local land cover are important drivers of bird-window collisions, we do not understand how

urbanization at large spatial scales affects collision mortality. Regional urbanization may influence mortality by mediating bird community structure and abundance (e.g., Blair, 1996, Pennington et al., 2008), particularly if there is covariation between species distributions and susceptibility of species to collisions. Urbanization may also affect bird-window collisions by shaping intraspecific variation in behavioral traits associated with collision risk, such as flight behavior. For example, behavioral divergence is commonly found between urban and non-urban bird populations due to phenotypic plasticity or adaptation (Sol et al., 2013). The degree of broad-scale urbanization may work with local-scale factors to affect collision risk in an additive fashion. Alternatively, associations between urbanization and either community structure or behavioral traits may lead to variation in the effects of building features and landscaping on collision risk between urban and rural areas.

Our objective was to examine how local factors (i.e., building structural features and land cover) and large-scale urbanization together affect continent-wide variation in bird-window collision mortality. We monitored buildings that varied in size and land cover types for collision mortality at 40 locations across North America during the autumn migratory season, and then examined the relative effects of building size, local land cover, and regional urbanization on collisions. We included models with interaction terms to determine if the effects of building size and local land cover on collision mortality depended on broad-scale urbanization. Knowledge of local and regional-scale drivers of bird-window collisions would assist in prioritizing mitigation measures aimed at reducing collision mortality at the riskiest structures and landscapes in North America.

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2. Materials and methods

2.1. Study buildings

We surveyed 281 buildings for bird carcasses across 40 college and university campuses in North America with varying degrees of urbanization (Fig. 1). Stratified sampling was used to identify a target of six building strata composed of building size (small, medium, large) and nearby landscaping (high vs. low vegetation cover). The following guidelines informed our building selection: small buildings: 1–2 story single-family residences ($< 186 \text{ m}^2$); medium buildings: 2–4 story office buildings ($186\text{--}4181 \text{ m}^2$); and, large buildings ≥ 5 stories in height ($> 4181 \text{ m}^2$). We used Google Earth imagery to visually estimate the percent vegetation surrounding candidate study buildings within 50 m. Buildings at each site were separated by at least 100 m to reduce spatial dependence of land cover features. The median number of study buildings at each site was 6 (range: 4–21).

2.2. Carcass surveys

Carcass surveys were completed in the autumn migratory season (late August through late October) in 2014. We chose the autumn

season because the incidence of collision mortality across North America is consistently highest in the autumn compared to other seasons (e.g., Klem, 1989). Surveys were conducted daily between 1400 and 1600 h as mortality predominantly occurs between sunrise and early afternoon (Hager and Craig, 2014; Kahle et al., 2016) and scavengers are most likely to remove carcasses between sunset and sunrise (Klem, 1989; Hager et al., 2012; Hager and Craig, 2014; Kahle et al., 2016). Conducting surveys between the time of peak mortality and peak scavenging should minimize detection bias associated with scavengers (following Hager and Cosentino, 2014). Surveys were occasionally completed in the morning if inclement weather was expected in the afternoon, and all surveys at one site (Oklahoma State University) were conducted in the morning due to evidence of significant collision mortality during the pre-dawn hours and some scavenging during the morning and afternoon (T. O'Connell, S. Loss, and C. Riding unpublished data).

We conducted a 'clean up' survey one day prior to the start of official carcass surveys. During clean up surveys, all bird carcasses that may have accumulated in the time before the study period were removed. Failing to remove carcasses in this manner would likely have led to positive bias in estimates of bird mortality (Hager et al., 2013).

Buildings were surveyed for a median of 21 consecutive days (range:

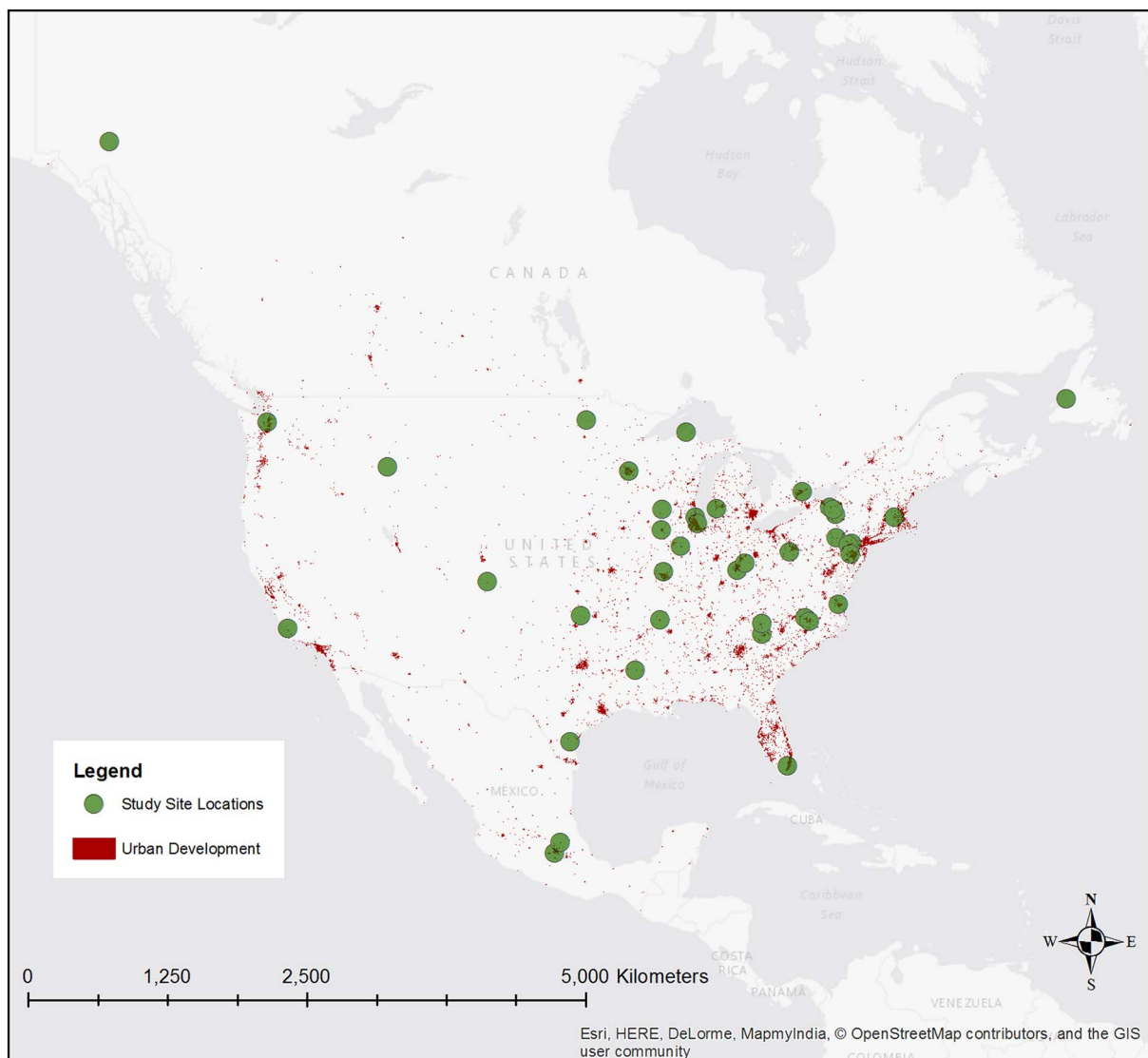


Fig. 1. Map depicting urban development and locations of study sites ($N = 40$) that conducted bird-window collision monitoring to assess the building structural, local land cover, and regional urbanization affecting bird-window collision mortality in North America in autumn 2014.

5–60), not including the ‘clean up’ survey. Daily surveys consisted of observers making two complete passes, one clockwise and one counterclockwise, around the perimeter of each building (Hager and Cosentino, 2014). One or two observers conducted each survey. When surveyed by a single observer, the observer walked the perimeter in one direction, and the second pass was made in the opposite direction. All bird carcasses noted in single-observer surveys were documented and collected immediately upon finding a carcass. When surveyed by two observers, each observer walked the building perimeter once in opposite directions. Carcasses located by each observer during surveys were not immediately collected. Instead, observers quickly noted the general location of a carcass on the data sheet. After observers finish surveys, they compared notes on carcasses observed, and then returned to those sites for carcass documentation and collection. Multiple passes should result in greater cumulative detection probability compared to a single pass. Overall, the survey protocol minimized bias associated with imperfect detection of bird carcasses resulting from window collisions by (a) surveying between known times of peak bird mortality and removal of carcasses by scavengers, and (b) maintaining high cumulative detection probability of carcasses by field observers (Hager et al., 2012, 2013; Hager and Cosentino, 2014; Kahle et al., 2016).

Observers searched for bird carcasses in areas clear of vegetation, on the top, inside, and ground around all shrubs, in thick ground cover (e.g., ivy, *Hedera* sp.), and around and under objects such as trashcans. Carcasses were counted if they were located under a building window within 2 m of the edge of the building (Hager and Craig, 2014). Observers recorded the location of carcasses seen during each pass. When two observers surveyed buildings, observers were instructed to not share information about their survey with each other until after surveys were completed.

We identified bird carcasses to species either during carcass surveys or in the laboratory following collection (following Hager and Cosentino, 2014). Bird carcasses that lacked species-specific anatomic features were classified as ‘unidentified’. All carcasses were deposited in museums and teaching collections or were disposed of according to animal welfare guidelines (see Document S1 for details).

2.3. Building structural and land cover covariates

Three metrics of building size were quantified for each building: window area, number of stories above ground, and floor space area (i.e., summed area of each floor of a building). A tape measure was used to quantify window area by measuring all accessible exposed sheet glass (including clear, tinted, and reflective windows) on all sides of each building. Window area for out-of-reach exposed sheet glass was measured from digital photographs in ImageJ (Abramoff et al., 2004). We excluded window measurements for windows behind screening material (which we assumed reduces the collision effect by covering sheet glass) and for windows above portions of a building's perimeter that could not be surveyed for bird carcasses (e.g., ledges and roof tops). The median window area for study buildings was 156 m² (range = 0.05–2879) (Fig. S1). We counted the number of stories or floors above ground level (median = 2 stories, range = 1–14), and floor space area estimates were either measured with a tape or obtained through building maintenance personnel (median = 2183 m², range = 18–33,031) (Fig. S1).

The proportion of local land cover was estimated within 50 m of the perimeter of each building using ArcMap 10.3 (Fig. S1). We used high-resolution Bing Maps aerial imagery (Microsoft® Bing™ Maps Platform APIs, 2016) to digitize five land cover categories: a) grass (landscaped and natural grass that may have included bare ground), b) impervious surface (areas of pavement, including sidewalks, roadways, and parking lots), c) water (natural and artificial waterways, including ponds and lakes), d) structures (buildings, such as office buildings, residential apartments and houses, and sheds), and e) woody vegetation (woody shrubs and trees; Fig. S2). A single observer (SBH) digitized land cover

for all buildings.

Regional urbanization for each site was characterized as the proportion of ‘urban and built up space’ within 5 km of a minimum convex polygon enclosing all study buildings at a site (Fig. S2; Latifovic et al., 2010). Urbanization data came from the 2010 North American Land Change Monitoring System (NALCMS) database (250 m resolution; Latifovic et al., 2010). ‘Urban and built up space’ was used as it negatively covaries with a variety of possible land cover categories among study sites that may be important to birds, including forest, grassland, and scrubland. We used ArcMap 10.3 to derive a minimum convex polygon that enclosed all study buildings for each site and create the 5 km buffer. A 5 km buffer was used because previous research found that bird density during migration was affected by land cover (e.g., forest) at 5 km (Bonter et al., 2009). We also performed a sensitivity analysis for buffer distance. This analysis suggested that the degree of urbanization was correlated between 3 and 50 km around minimum convex polygons (Pearson's $r > 0.48$), and inferences were the same regardless of the spatial extent used to quantify urbanization (Cosentino and Hager, unpublished data).

2.4. Statistical analysis

We used principal components analysis (PCA) to identify latent variables that summarized covariation among building size, local land cover around buildings, and regional urbanization. The specific metrics assessed included window area; floor space area; number of stories; proportions of woody vegetation, grass, impervious surface, and structures within 50 m; and urbanization within 5 km. Proportion of water within 50 m was zero for almost all sites, so we excluded it from the analysis. In order to help meet the assumption of multivariate normality for PCA (McGarigal et al., 2000), we applied log transformations to window area, floor space, and number of stories, and logit transformations were applied to all land cover variables (Warton and Hui, 2011). The PCA was computed on the correlation matrix, and all principal components with eigenvalues ≥ 1 were retained.

We used generalized linear mixed models to examine the relationship of PCA-derived variables of building size, local land cover, and regional urbanization with the number of bird carcasses. The response variable was the number of carcasses found at each building across all surveys. We specified the log-transformed number of surveys at each building as an offset variable to account for varying effort. We used a Poisson distribution and log link as the error distribution for number of carcasses. Site was included as a random effect to account for non-independence in mortality among buildings at the same site.

We analyzed 14 models with different combinations of the explanatory variables. Models included a null model (intercept only), additive combinations of the explanatory variables, and models with a single interaction effect and up to one additional explanatory variable. Interaction effects were examined between each possible pair of the three explanatory variables. We compared the relative support of models with Akaike's Information Criterion (AIC), and models were considered to have competitive support when the difference between AIC of each model and the most-supported model was ≤ 2 (Burnham and Anderson, 2002).

3. Results

We documented 324 bird carcasses at 40 sites across North America in autumn 2014 (mean = 8.1 carcasses per site, range = 0–34) (Table S1). Of these, 275 carcasses (84.9%) were identified to species. Mortality in several species was relatively widespread across sites, such as Common Yellowthroat, *Geothlypis trichas* (13 sites), Ovenbird, *Seiurus aurocapilla* (11 sites), and Ruby-throated Hummingbird, *Archilochus colubris* (8 sites). Moreover, mortality was highest in migrants (91%) compared to residents (9%), and nearly all carcasses observed (99%) were passerine and near-passerine species (e.g., doves, hummingbirds,

cuckoos, and woodpeckers) (Table S1).

We retained three principal components with eigenvalues ≥ 1 that described covariation in building size, landscaping around buildings, and regional urbanization. The three components collectively accounted for 70% of the variance (Table 1). The first axis (PC1) explained 29% of the variance and had high positive loadings for window area, floor space area, and number of stories; therefore, we interpreted PC1 as an index of building size. The second axis (PC2) explained 21% of the variance and had a strong negative loading for woody vegetation and a strong positive loading for impervious surfaces within 50 m of buildings. We therefore interpreted PC2 as an index of landscaping around buildings that was independent of regional urbanization. The third axis (PC3) explained 20% of the variance and had a negative loading for grass within 50 m and positive loadings for structures within 50 m of buildings and urbanization within 5 km of study sites. We therefore interpreted PC3 as an index of regional urbanization, which influences variation in coverage by grass and structures in the immediate vicinity around study buildings.

Bird-window collision mortality was strongly associated with an interaction effect between building size (PC1) and regional urbanization (PC3), which was included in the only two models with competitive support (Table 2). Collision mortality was positively related to building size, but the positive effect of building size on mortality was strongest in areas with low levels of regional urbanization and weak to nonexistent in regions with high levels of urbanization (Fig. 2, Fig. S3). Collision mortality was consistently low for small buildings, regardless of large-scale urbanization (Fig. 2). Landscaping around buildings was included in the second-best supported model, but was not an important driver of collision mortality compared to building size and regional urbanization (Table 2).

4. Discussion

We found that building size had a strong positive effect on bird-

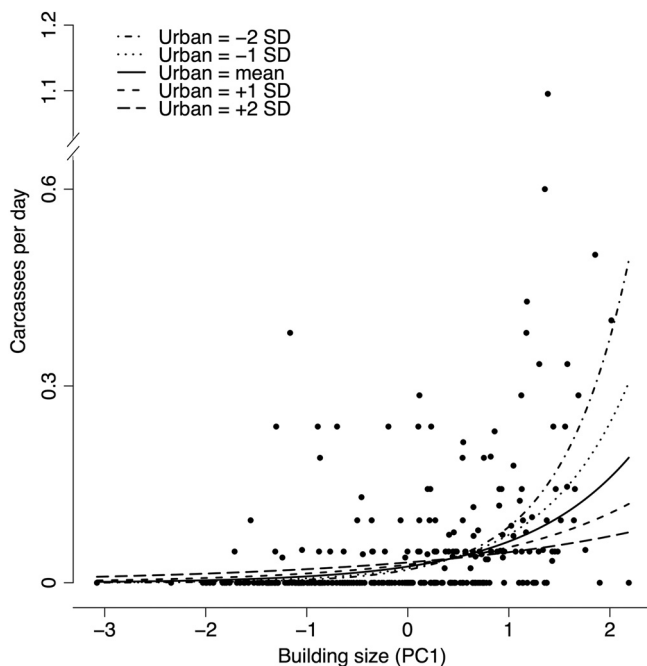


Fig. 2. Interaction effect between building size and regional urbanization on number of bird carcasses. Number of bird carcasses is expressed as the number of carcasses collected per day. Best-fit lines represent model-averaged predictions across all models in Table 1 when urbanization is held at low (-2 SD, -1 SD), average, and high ($+1$ SD, $+2$ SD) values. Landscaping and number of surveys were held constant at their means. Building size, local landscaping, and regional urbanization are latent variables from a principal component analysis (Table 1). Note the break point on the y-axis.

Table 1

Principal component analysis (PCA) of building size (PC1), landscaping within 50 m of buildings (PC2), and urbanization within 5 km of sites (PC3).

| Variable | Factor loadings | | |
|----------------------------------|-----------------|-------|-------|
| | PC1 | PC2 | PC3 |
| Window area | 0.92 | 0.12 | 0.03 |
| Floor space | 0.94 | 0.10 | -0.05 |
| Stories | 0.78 | -0.01 | 0.27 |
| Wooded (50 m) | -0.07 | -0.92 | 0.24 |
| Grass (50 m) | -0.09 | 0.12 | -0.78 |
| Impervious (50 m) | 0.11 | 0.87 | 0.26 |
| Structures (50 m) | 0.02 | 0.10 | 0.55 |
| Developed (5 km) | 0.07 | 0.00 | 0.70 |
| Eigenvalue | 2.60 | 1.66 | 1.35 |
| Proportion of variance explained | 0.29 | 0.21 | 0.20 |

window collision mortality during autumn migration, but the strength of this effect depended on the degree of urbanization at the regional scale. The positive relationship between collision mortality and building size was greatest in regions of low urbanization containing locally extensive landscaped grass and few structures (i.e., ‘rural’ landscapes with low values of PC3). Collision mortality was low to nonexistent in regions that were highly urbanized. The mechanisms shaping broad-scale variation in bird-building collision mortality during autumn migration may be related to habitat selection and habitat use at a hierarchy of scales and behavioral divergence among urban and rural populations.

Habitat selection and habitat use in migratory birds occurs at a hierarchy of spatial scales that would ultimately place birds in close proximity to buildings and at risk of fatal collisions with windows (Johnson, 1980; Hutto, 1985; Jones, 2001). At large scales, migrating birds select among numerous widely spaced habitat types using geophysical (rivers, mountains, celestial, and magnetic), meteorological (weather), and social (intraspecific vocalizations) cues and experience (Berthold, 2001). For example, forest-adapted birds often select rural habitats (e.g., open and low-intensity developed spaces containing high levels of lawn grasses, some structures, and low levels of impervious surfaces) over other available habitats, such as areas of high urbanization (Zuckerberg et al., 2016). In addition to the cues birds use in selecting rural areas during migration, data from RADAR studies suggest migrating birds are negatively influenced during nighttime by broad scale city glow wherein birds become entrapped by artificial light (Buler and Dawson, 2014). Regional lighting patterns should be associated with urbanization, and light radiating from low-rise and large buildings in small cities within rural areas may be more of an attractant compared to similar sized buildings in a highly urbanized landscape. If so, a large-scale beacon effect would cause birds and collisions to be more diluted among large buildings in urban areas (resulting in less of an effect of building size) than in rural areas (resulting in more of an effect of building size).

Once settled in rural areas, collision risk would be influenced at the local scale by the manner in which birds use habitats. In contrast to the generalized cues associated with broad scale habitat selection, birds engage in relatively short-distance exploratory forays in search of food and shelter (Hutto, 1985; Cohen et al., 2014; Slager et al., 2015). ‘Morning flight’ is one such foray during migration that occurs within 2 h after sunrise wherein migrants move throughout the landscape above tree height in search of preferred or higher quality habitats (Wiedner et al., 1992; Van Doren et al., 2015). As morning gives way to afternoon, birds settle in habitats with movements becoming localized and restricted to short-distance foraging bouts (e.g., Hutto, 1985; Paxton and O’Brien, 2008). Thus, window collision risk would be relatively high for birds flying above tree height during morning flight since they would be exposed to windows at this height in low-rise and

Table 2

Model selection statistics and beta coefficients (b) for associations between number of bird carcasses and building size (B; PC1), landscaping around buildings (L; PC2), and urbanization (U; PC3) (note that building size, landscaping, and urbanization are latent variables from a principal component analysis (Table 1)). Δ AIC is the difference between AIC of each model and the most-supported model, ω_i is the Akaike weight of model i , L is the log-likelihood, and K is the number of parameters.

| Model | Δ AIC | ω_i | L | K | b_B (SE) | b_L (SE) | b_U (SE) | b_{INT} (SE) |
|-------------------|--------------|------------|----------|-----|-------------|-------------|---------------|----------------|
| B + U + B * U | 0.00 | 0.61 | - 420.10 | 5 | 0.94 (0.08) | - | 0.12 (0.10) | - 0.28 (0.08) |
| B + U + B * U + L | 1.12 | 0.35 | - 419.66 | 6 | 0.94 (0.08) | 0.07 (0.07) | 0.11 (0.10) | - 0.27 (0.08) |
| B | 7.67 | 0.01 | - 425.94 | 3 | 0.84 (0.07) | - | - | - |
| B + L | 8.12 | 0.01 | - 425.16 | 4 | 0.84 (0.07) | 0.09 (0.07) | - | - |
| B + L + B * L | 8.45 | 0.01 | - 424.33 | 5 | 0.86 (0.08) | 0.13 (0.08) | - | - 0.11 (0.08) |
| B + U | 9.67 | 0.00 | - 425.93 | 4 | 0.84 (0.07) | - | 0.00 (0.09) | - |
| B + L + U | 10.11 | 0.00 | - 425.16 | 5 | 0.84 (0.07) | 0.09 (0.07) | 0.00 (0.09) | - |
| B + L + B * L + U | 10.45 | 0.00 | - 424.33 | 6 | 0.86 (0.08) | 0.13 (0.08) | 0.00 (0.09) | - 0.11 (0.08) |
| B + L + U + L * U | 12.05 | 0.00 | - 425.13 | 6 | 0.84 (0.07) | 0.09 (0.07) | - 0.01 (0.09) | 0.02 (0.07) |
| Intercept | 161.65 | 0.00 | - 503.92 | 2 | - | - | - | - |
| L | 162.30 | 0.00 | - 503.25 | 3 | - | 0.07 (0.06) | - | - |
| U | 163.64 | 0.00 | - 503.92 | 3 | - | - | 0.01 (0.08) | - |
| L + U | 164.27 | 0.00 | - 503.24 | 4 | - | 0.08 (0.06) | - 0.02 (0.08) | - |
| L + U + L * U | 165.50 | 0.00 | - 502.85 | 5 | - | 0.08 (0.06) | 0.01 (0.09) | - 0.06 (0.06) |

tall buildings, and collision risk should be magnified in rural areas containing proportionately more migrants than in urban areas. Fewer birds flying below tree height during morning flight would result in lower collision risk at windows close to ground level, such as those in houses (1–3 stories in height), regardless of the degree of urbanization.

An alternative (though not necessarily mutually exclusive) explanation for the influence of regional urbanization on collision mortality is behavioral divergence between urban and rural populations of birds. Behavioral divergence along urbanization gradients may occur due to phenotypic or behavioral plasticity, e.g., learning from non-fatal strikes based on previous experience and gaining new anti-collision behaviors as novel solutions to the problems posed by sheet glass in buildings (Dukas, 1998, 2004; Sol et al., 2013). For example, the number of structures is associated with degree of urbanization (e.g., PC3), and thus birds in urban areas would experience more opportunities for bird-building collisions and subsequent learning from those strikes than rural populations. There is evidence that the relatively large brain size in birds makes them primed for behavioral plasticity, and especially learning (Lefebvre and Sol, 2008; Møller and Erritzoe, 2017). Learning to avoid windows may be further influenced by variation between urban and rural populations in boldness or rates of activity, motivational states, and strategies related to life history traits, such as migration, that would affect the value of learning (Dukas, 1998). Moreover, individuals in urban populations may simply move less or shorter distances across the environment due to highly localized and abundant food sources (i.e., fruiting trees, feeders). If urban individuals move less, the probability of striking windows may be reduced. Juveniles (hatch-year birds) are reported to suffer higher rates of collision mortality than adults (Hager et al., 2013; Kahle et al., 2016). For those urban-dwelling juveniles that do not die, learning may occur early in development, which could alter nervous system functioning that controls motor responses to avoid windows later in life (Sol et al., 2013).

Aside from phenotypically plastic behaviors, evolutionary processes may underpin differential behavioral adjustments for urban and rural bird populations that lead to variation in collision mortality (Brown and Brown, 2013; Sol et al., 2013). For example, variation in the ability of migratory birds to see and avoid windows may exist between populations. This variation would be expected to result in proportionately lower collision mortality in urban birds en-route to areas of winter residency (during autumn migration) and summer breeding (during spring migration). Over time, this same variation could be adjusted by natural selection to bring urban populations to a new adaptive landscape (Dingemans and Wolf, 2013). Such a scenario would assume the relative strength of selection to perceive windows as barriers to flight in urban areas is high and population size is large (Sol et al., 2013).

Overall, birds have adapted to urban environments in the evolutionary history of their migratory behavior (Sol and Lefebvre, 2006; Marzluff, 2014), and behavioral divergence may be important in generating differences in collision mortality between rural and urban populations.

4.1. Conservation implications

The results of this research allow for a better appreciation of the spatial context for why up to 1 billion birds die annually throughout much of North America after hitting windows in buildings (Klem, 1990; Machrans et al., 2013; Loss et al., 2014). At broad-scales, the beacon effect we hypothesize in rural landscapes suggests the potential benefit of implementing lights out programs (e.g., visit <http://www.audubon.org/conservation/project/lights-out>) in cities and towns of all sizes, not just in large cities characterized by dense urbanization. At local scales, collision mortality can be reduced or eliminated with effective prevention measures that account for variation in (a) window size, tinting, and surface treatments and (b) visual systems in birds vulnerable to striking windows (Martin, 2011). For example, collision risk may be reduced by constructing buildings with a small amount of sheet glass, and retrofitting windows in existing buildings with frit patterns on glass surfaces (Barton et al., 2017). Indeed, effective prevention measures would be further informed by understanding how bird-window collisions are influenced by the degree of urbanization (a) at sites other than college campuses, and (b) in building types that were not well-sampled in our study, e.g., convention centers, stadiums, extremely tall and abnormally-shaped buildings with exterior walls composed almost entirely of sheet glass.

The spatial complexities of this issue become amplified as one also considers the temporal scale of bird-window collisions. The driving factors of collision mortality reported here for autumn migration may be the same factors influencing collision mortality during spring migration. However, the intrinsic (e.g., hormonal) and extrinsic (e.g., geographic cues) biologic features that influence bird migratory behavior differ between spring and autumn migration, leading to variation in habitat selection, habitat use, and behavioral divergence between the seasons. Relatively little is known about bird-window collisions outside of migration periods, and therefore about the structural-environmental and behavioral-ecological drivers of mortality during the winter and summer (Hager and Craig, 2014; Kummer et al., 2016).

Many of the studies on habitat selection of birds during migration cite the importance of rural landscapes for conservation and management. Annual estimates of avian survival suggest that mortality is highest during migration (Sillett and Holmes, 2002), and conserving rural landscapes may positively affect survival. The tradeoff with this conservation approach is the inherent threats to survival that rural

landscapes pose to birds, such as predation by domestic and feral cats and collisions with communication towers, automobiles, and buildings (Drewitt and Langston, 2006; Longcore et al., 2013; Loss et al., 2013, 2014). Hierarchical and full life-cycle population models that include anthropogenic sources of mortality, such as bird-window collisions, should be used to assess the population dynamics of vulnerable species (Hostetler et al., 2015).

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References

- Abràmoff, M.D., Magalhães, P.J., Ram, S.J., 2004. Image processing with ImageJ. *Biophoton. Int.* 11 (7), 36–42.
- Barton, C.M., Riding, C.S., Loss, S.R., 2017. Magnitude and correlates of bird collisions at glass bus shelters in an urban landscape. *PLoS One* 12 (6), e0178667.
- Bayne, E.M., Scobie, C.A., Rawson-Clark, M., 2012. Factors influencing the annual risk of bird–window collisions at residential structures in Alberta, Canada. *Wildl. Res.* 39 (7), 583–592.
- Berthold, P., 2001. *Bird Migration: A General Survey*. Oxford University Press on Demand.
- Blair, R.B., 1996. Land use and avian species diversity along an urban gradient. *Ecol. Appl.* 6 (2), 506–519.
- Bonter, D.N., Gauthreaux Jr., S.A., Donovan, T.M., 2009. Characteristics of important stopover locations for migrating birds: remote sensing with radar in the Great Lakes basin. *Conserv. Biol.* 23 (2), 440–448.
- Brown, C.R., Brown, M.B., 2013. Where has all the road kill gone? *Curr. Biol.* 23 (6), R233–R234.
- Buler, J.J., Dawson, D.K., 2014. Radar analysis of fall bird migration stopover sites in the northeastern US. *Condor* 116 (3), 357–370.
- Burnham, K.P., Anderson, D.R., 2002. Information and likelihood theory: a basis for model selection and inference. In: *Model Selection and Multimodel Inference: A Practical Information-theoretic Approach*. 2. pp. 49–97.
- Cohen, E.B., Moore, F.R., Fischer, R.A., 2014. Fuel stores, time of spring, and movement behavior influence stopover duration of Red-eyed Vireo *Vireo olivaceus*. *J. Ornithol.* 155 (3), 785–792.
- Cusa, M., Jackson, D.A., Mesure, M., 2015. Window collisions by migratory bird species: urban geographical patterns and habitat associations. *Urban Ecosyst.* 18 (4), 1427–1446.
- Dingemanse, N.J., Wolf, M., 2013. Between-individual differences in behavioural plasticity within populations: causes and consequences. *Anim. Behav.* 85 (5), 1031–1039.
- Drewitt, A.L., Langston, R.H., 2006. Assessing the impacts of wind farms on birds. *Ibis* 148 (s1), 29–42.
- Dukas, R., 1998. *Cognitive Ecology: The Evolutionary Ecology of Information Processing and Decision Making*. University of Chicago Press.
- Dukas, R., 2004. Evolutionary biology of animal cognition. *Annu. Rev. Ecol. Evol. Syst.* 35, 347–374.
- Hager, S.B., Cosentino, B.J., 2014. Surveying for Bird Carcasses Resulting From Window Collisions: A Standardized Protocol (No. e406v1). *PeerJ PrePrints*.
- Hager, S.B., Craig, M.E., 2014. Bird-window collisions in the summer breeding season. *PeerJ* 2, e460.
- Hager, S.B., Trudell, H., McKay, K.J., Crandall, S.M., Mayer, L., 2008. Bird density and mortality at windows. *Wilson J. Ornithol.* 120 (3), 550–564.
- Hager, S.B., Cosentino, B.J., McKay, K.J., 2012. Scavenging affects persistence of avian carcasses resulting from window collisions in an urban landscape. *J. Field Ornithol.* 83 (2), 203–211.
- Hager, S.B., Cosentino, B.J., McKay, K.J., Monson, C., Zuurdeeg, W., Blevins, B., 2013. Window area and development drive spatial variation in bird-window collisions in an urban landscape. *PLoS One* 8 (1), e53371.
- Hostetler, J.A., Sillett, T.S., Marra, P.P., 2015. Full-annual-cycle population models for migratory birds. *Auk* 132 (2), 433–449.
- Hutto, R.L., 1985. Habitat selection by nonbreeding, migratory land. In: *Habitat Selection in Birds*, pp. 455.
- Johnson, D.H., 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61 (1), 65–71.
- Jones, J., 2001. Habitat selection studies in avian ecology: a critical review. *Auk* 118 (2), 557–562.
- Kahle, L.Q., Flannery, M.E., Dumbacher, J.P., 2016. Bird-window collisions at a west-coast urban park museum: analyses of bird biology and window attributes from Golden Gate Park, San Francisco. *PLoS One* 11 (1), e0144600.
- Klem Jr., D., 1989. Bird-window collisions. *Wilson Bull.* 606–620.
- Klem Jr., D., 1990. Collisions between birds and windows: mortality and prevention (Colisiones de pájaros con ventanas: mortalidad y prevención). *J. Field Ornithol.* 120–128.
- Klem Jr., D., Farmer, C.J., Delacretaz, N., Gelb, Y., Saenger, P.G., 2009. Architectural and landscape risk factors associated with bird–glass collisions in an urban environment. *Wilson J. Ornithol.* 121 (1), 126–134.
- Kummer, J.A., Bayne, E.M., Machtans, C.S., 2016. Use of citizen science to identify factors affecting bird–window collision risk at houses. *Condor* 118 (3), 624–639.
- Latifovic, R., Homer, C., Ressler, R., Pouliot, D., Hossain, S.N., Colditz Colditz, R.R., Olthoff, I., Giri, C., Victoria, A., 2010. North American Land Change Monitoring System (NALCMS). Remote Sensing of Land Use and Land Cover: Principles and Applications. CRC Press, Boca Raton.
- Lefebvre, L., Sol, D., 2008. Brains, lifestyles and cognition: are there general trends? *Brain Behav. Evol.* 72 (2), 135–144.
- Longcore, T., Rich, C., 2004. Ecological light pollution. *Front. Ecol. Environ.* 2 (4), 191–198.
- Longcore, T., Rich, C., Mineau, P., MacDonald, B., Bert, D.G., Sullivan, L.M., Mutrie, E., Gauthreaux, S.A., Avery, M.L., Crawford, R.L., Manville, A.M., 2013. Avian mortality at communication towers in the United States and Canada: which species, how many, and where? *Biol. Conserv.* 158, 410–419.
- Loss, S.R., Will, T., Marra, P.P., 2013. The impact of free-ranging domestic cats on wildlife of the United States. *Nat. Commun.* 4, 1396.
- Loss, S.R., Will, T., Loss, S.S., Marra, P.P., 2014. Bird–building collisions in the United States: estimates of annual mortality and species vulnerability. *Condor* 116 (1), 8–23.
- Machtans, C., Wedeles, C., Bayne, E., 2013. A first estimate for Canada of the number of birds killed by colliding with building windows. *Avian Conserv. Ecol.* 8 (2).
- Martin, G.R., 2011. Understanding bird collisions with man-made objects: a sensory ecology approach. *Ibis* 153 (2), 239–254.
- Marzluff, J.M., 2014. *Welcome to Suburbia: Sharing Our Neighborhoods With Wrens, Robins, Woodpeckers, and Other Wildlife*. Yale University Press.
- McGarigal, K., Cushman, S., Stafford, S.G., Stafford, S.G., 2000. *Multivariate Statistics for Wildlife and Ecology Research*. vol. 279 Springer, New York.
- Microsoft® Bing™ Maps Platform APIs, 2016. Retrieved from: <https://www.microsoft.com/maps/product/print-rights.html>.
- Møller, A.P., Erritzøe, J., 2017. Brain size in birds is related to traffic accidents. *Royal Soc. Open Sci.* 4 (3), 161040.
- Ocampo-Peñuela, N., Winton, R.S., Wu, C.J., Zambello, E., Wittig, T.W., Cagle, N.L., 2016. Patterns of bird-window collisions inform mitigation on a university campus. *PeerJ* 4, e1652.
- O'Connell, T.J., 2001. Avian window strike mortality at a suburban office park. *Raven* 72 (2), 141–149.
- Paxton, K.L., O'Brien, C., 2008. Movement patterns and stopover ecology of Wilson's Warblers during spring migration on the lower Colorado River in southwestern Arizona. *Condor* 110 (4), 672–681.
- Pennington, D.N., Hansel, J., Blair, R.B., 2008. The conservation value of urban riparian areas for landbirds during spring migration: land cover, scale, and vegetation effects. *Biol. Conserv.* 141 (5), 1235–1248.
- Sillett, T.S., Holmes, R.T., 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. *J. Anim. Ecol.* 71 (2), 296–308.
- Slager, D.L., Rodewald, P.G., Heglund, P.J., 2015. Experimental effects of habitat type on the movement ecology and stopover duration of spring migrant Northern Waterthrushes (*Parkesia noveboracensis*). *Behav. Ecol. Sociobiol.* 69 (11), 1809–1819.
- Sol, D., Lefebvre, L., 2006. Behavioral flexibility and response in birds to changes in the environment. In: *Journal of Ornithology* (vol. 147, no. 5, pp. 34–34). Springer, 233 Spring Street, New York, NY 10013 USA (August).
- Sol, D., Lapidra, O., González-Lagos, C., 2013. Behavioural adjustments for a life in the city. *Anim. Behav.* 85 (5), 1101–1112.
- Van Doren, B.M., Sheldon, D., Geevarghese, J., Hochachka, W.M., Farnsworth, A., 2015. Autumn morning flights of migrant songbirds in the northeastern United States are linked to nocturnal migration and winds aloft. *Auk* 132 (1), 105–118.
- Warton, D.I., Hui, F.K., 2011. The arcsine is asinine: the analysis of proportions in ecology. *Ecology* 92 (1), 3–10.
- Wiedner, D.S., Kerlinger, P., Sibley, D.A., Holt, P., Hough, J., Crossley, R., 1992. Visible morning flight of Neotropical landbird migrants at Cape May, New Jersey. *Auk* 500–510.
- Zuckerberg, B., Fink, D., La Sorte, F.A., Hochachka, W.M., Kelling, S., 2016. Novel seasonal land cover associations for eastern North American forest birds identified through dynamic species distribution modelling. *Divers. Distrib.* 22 (6), 717–730.