2020

Correlates of Bird Collisions With Buildings Across Three North American Countries

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Original Publication Citation

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<PE-AT>Correlates of bird collisions with buildings across three North American countries

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ABSTRACT:

Collisions with buildings cause up to 1 billion bird fatalities annually in North America. Bird-building collisions have recently received increased conservation, research, and policy attention. However, efforts to reduce collisions would benefit from studies conducted at large spatial scales across multiple study sites, with standardized methods, and with consideration of species- and life history-related variation and correlates of collisions. We addressed these research needs with a coordinated data collection effort at 40 sites across North America. We estimated collision vulnerability for 40 bird species by accounting for their North American population abundance, distribution overlap with study sites, and sampling effort. Of 10 species we identified as most vulnerable to collisions, some have been identified in past studies (e.g., Black-throated Blue Warbler [*Setophaga caerulescens*]) while others emerged for the first time (e.g., White-breasted Nuthatch [*Sitta carolinensis*]), possibly because we used a more standardized sampling approach than past studies. Analyses of species-specific collision correlates revealed that building size and glass area were positively associated with numbers of collisions for 5 of 8 species with enough observations to analyze independently. Vegetation around buildings influenced collisions for only 1 of those 8 species (Swainson's Thrush [*Catharus fuscescens*]). We also found that life history predicted collisions; numbers of collisions were greatest for migratory, insectivorous, and woodland-inhabiting species. This coordinated, continent-wide study provides new insight into the species most vulnerable to building collisions, making them potentially in greatest need of conservation attention to reduce collisions. This study also lends insight into species- and life history-related variation and correlates of building collisions, information that can help refine collision management efforts. <PE-FRONTEND>

INTRODUCTION:

Globally, many bird populations are in decline. In addition to important indirect anthropogenic threats like climate change and habitat loss, many declines are likely caused in part by direct sources of human-caused mortality, including collisions with structures, chemical poisoning, and predation by domestic pets (Rosenberg et al. 2019). Collisions with buildings, communication towers, wind turbines, and other structures annually cause up to 1.5 billion bird fatalities in North America (Loss et al. 2015). Building collisions cause up to 1 billion of these avian deaths (Machtans et al. 2013; Loss et al. 2014).

Bird-building collisions that occur during the day are thought to result from birds mistaking reflections or open areas behind glass as safe flight passages (Klem 1989). At night, artificial light at night (ALAN; Longcore & Rich 2004) contributes to bird-building collisions. ALAN attracts and disorients nocturnally migrating birds, causing them to collide with buildings, become entrapped and later collide, become easy targets for predators, or succumb to exhaustion (Lao et al. 2020; Winger et al. 2019). As human population grows and shifts to urban areas, buildings and ALAN are increasing, which will likely result in increasing numbers of diurnal and nocturnal bird-building collisions if mitigation approaches are not identified and widely implemented.

Many factors influence spatial variation in bird-building collisions, including building size and location, nearby vegetation, and levels of regional urbanization (Hager et al. 2017). When considering total collisions across all bird species, large numbers of collisions occur at buildings with extensive glass area (Hager et al. 2008; Klem et al. 2009), ALAN (Winger et al. 2019), and nearby trees and shrubs (Hager et al. 2013; Cusa et al. 2015). Local-scale factors also interact with broad-scale factors to influence collisions. For example, a North American continent-wide study found that regional urbanization mediates the effect of

building characteristics, with large glassy buildings in relatively undeveloped landscapes causing more collisions than similar buildings in urbanized areas (Hager et al. 2017).

Numbers of building collision may also vary due to factors intrinsic to birds such as their life history (Cusa et al. 2015; Wittig et al. 2017). Migratory species are thought to collide in greater numbers than non-migratory species, and nocturnal migrants may collide more frequently than diurnal migrants (Machtans et al. 2013; Loss et al. 2014; Winger et al. 2019). Among-family variation in collisions also is thought to occur; for example, wood warblers (Parulidae) and hummingbirds (Trochilidae) are reported to collide in greater numbers than swallows (Hirundinidae). Some species may experience collisions in exceptionally large numbers (e.g., White-throated Sparrow [*Zonotrichia albicollis*]) or may be disproportionately vulnerable, colliding in numbers greater than expected based solely on abundance (e.g., Ruby-throated Hummingbird [*Archilochus colubris*], Ovenbird [*Seiurus aurocapilla*], Yellow-bellied Sapsucker [*Sphyrapicus varius*]) (Arnold & Zink 2011; Loss et al. 2014). These disproportionately vulnerable species are perhaps more likely to experience population declines associated with building collision mortality.

Most studies of factors influencing bird-building collisions are descriptive, occur in a single study area, or do not account for factors causing fatality counts to misrepresent collision vulnerability. Only two meta-analyses include evaluation of bird-building collisions across multiple sites and account for abundance and spatial sampling biases to generate vulnerability estimates (Arnold & Zink 2011; Loss et al. 2014). These quantitative syntheses included data from several independent studies with varying sampling protocols, which propagated uncertainty and bias into meta-analysis results. Further, few studies have considered how avian life histories influence collisions or how correlates of collisions vary among species. One such study suggests forest-inhabiting, foliage-gleaning species collide more frequently at buildings surrounded by extensive vegetation while open woodland-

inhabiting, ground-foraging species collide more at buildings surrounded by intense urban development (Cusa et al. 2015). Another study found that some collision correlates (e.g., glass area) are relatively consistent among bird species, but there is also among-species variation in correlates (Loss et al. 2019). As with much of the bird collision literature, these last two studies occurred at single study sites.

A broad-scale assessment using a coordinated data collection approach across multiple sites and considering species- and life history-related variation and correlates of collisions would help identify bird species and life history groups most likely to need conservation intervention. Such an analysis would also help identify suites of collision mitigation approaches that are effective across many bird species. We conducted such an assessment with a bird collision dataset collected under a coordinated sampling protocol at 281 buildings in 40 study sites across North America in fall 2014. Our objectives were to: (1) assess variation in species' vulnerability to building collisions, (2) identify building and landscape-related correlates of collision numbers for individual species, and (3) identify life history-related correlates of collisions.

METHODS:

Study area and design:

We collected collision data through the Bird-Window Collisions Project under the Ecological Research as Education Network (EREN) (Hager et al. 2017). Collaborators from 40 university or college campuses across North America (Fig. 1) collected data during fall migration (August-October) in 2014. At each campus, buildings (n=281 total; range=4–21 per site) were selected by stratifying candidate buildings by size (small, medium, large) and surrounding vegetation cover (high & low) within 50 m, resulting in 6 total building strata (details of strata classifications in Hager et al. 2017).

Collision surveys were conducted following a standardized protocol (Hager & Cosentino 2014) during fall migration, the season when the greatest number of collisions typically occur (Machtans et al. 2013; Loss et al. 2014). We designed our sampling protocol to minimize estimation biases associated with carcass removal (i.e., some carcasses removed by scavengers and humans between surveys) and detection (i.e., some carcasses that were present not detected by surveyors) (Hager & Cosentino 2014).

We minimized detection bias by making two passes around each building for each survey. Surveys consisted of one or two individuals searching within ~2 m of the entire building perimeter, including in, under, and around vegetation. When one individual conducted surveys, a single pass was made in each direction around the building; if two individuals conducted surveys, each made a single pass in opposite directions. Previous experiments showed that the probability of detecting a carcass during a single pass in this type of survey setting can vary from 0.70 to 0.95 depending on observer identity and conspicuousness of carcass coloration (Hager et al. 2013). Assuming detection probability is statistically independent between passes for the same carcass, this corresponds to cumulative detection probabilities of 0.91–0.99 (e.g., $1-(1-0.70)^2=0.91$).

Since carcass removal by scavengers and humans varies spatially, temporally, and among bird species, we minimized removal bias by conducting surveys daily (range: 5–60 consecutive days/site) between 1400–1600 h. Carcasses typically persist for multiple days (Hager et al. 2012; Riding & Loss 2018), so daily surveys maximize probability of encountering a carcass before removal. We usually conducted afternoon surveys because some studies suggest that most collisions occur during morning and that most carcass removal by scavengers occurs overnight (Bracey et al. 2016, Hager et al. 2012). However, surveys at Oklahoma State University were conducted from 0700–0900 h due to high numbers of collisions in predawn and early morning hours at this site and removal peaking in

the morning (Riding & Loss 2018). Although logistical constraints associated with coordinating research across 40 sites prevented experimental studies of carcass detection and removal at each site, the above protocol likely minimized detection and removal biases (Hager et al. 2012, 2013, 2017; Hager & Cosentino 2014).

All carcasses were collected and identified to species. For all below-described analyses, we removed records for unidentified carcasses, species lacking distribution-wide population estimates, and species with distributions overlapping fewer than 10 sites. We conducted all analyses in R 3.4.4 (R Core Team 2018) unless otherwise mentioned.

Measuring potential collision correlates:

Building characteristics, local vegetation, and regional urbanization were computed as described in Hager et al. (2017). Briefly, building metrics included window area (m^2; calculated with tape measure or ImageJ [Abramoff et al. 2004]), number of stories above ground-level, and floor space area (m^2; building footprint area). A single author used high-resolution aerial imagery in ArcMap 10.3 (ESRI 2011) to digitize and calculate local vegetation variables, including percent cover of grass, impervious surface, water, structure, and woody vegetation within 50 m of buildings. We characterized regional urbanization by using a minimum convex polygon to estimate the proportion of urban cover within 5 km of the edge of the sampled cluster of buildings at each site. Because this study included the exact same buildings as in Hager et al. (2017), we used exact results of their principal components analysis (PCA), which identified principal components capturing characteristics of buildings and their surroundings. To achieve multivariate normality, which improves PCA interpretation (McGarigal et al. 2000), all building metrics were log-transformed and all local vegetation variables were logit-transformed. The PCA was computed on the correlation matrix and three principal components (PCs) with eigenvalues ≥1 were retained as collision

correlates with axis scores accounting for 70% of variance. The 3 PCs represented building size (e.g., number of stories, window area), local vegetation (within 50 m), and regional urbanization (within 5 km) (Hager et al. 2017).

Estimating species' vulnerability to collisions:

We defined species' vulnerability to collisions as the number of collisions relative to population size and geographic distribution overlap with study sites. This definition follows previous studies (Arnold and Zink 2011; Loss et al. 2014) in assuming that species with greater abundance and broader distribution overlap collide more frequently than less abundant or narrowly-distributed species. To estimate continent-wide population size, we used the Partners in Flight Population Estimates Database version 3.0 (Partners in Flight 2019). To estimate distribution overlap, we used Python 2.7 with ArcGIS 10.3 to count the intersection of our 40 campuses with species distribution maps (BirdLife International 2016; ESRI 2011). Species distribution maps were visually examined in ArcGIS to ensure all parts of each species' distribution were included, and if portions were missing (usually the migration range), we used information from field guides to fill in missing portions (Sibley 2000; Rodewald 2015). For the subsequent vulnerability analysis, we only included species with ≥2 fatalities across study sites.

We estimated species' vulnerability using the approach of Arnold & Zink (2011) and Loss et al. (2014), with one modification. Briefly, their approach estimates vulnerability by using residuals from a fitted regression between species fatality counts and both population size and distribution overlap with study sites. However, we regressed a novel response variable (hereafter "birds per effort", BPE) on only a single predictor variable (population size) because BPE accounts for species' distribution overlap with sites, as well as varying numbers of surveys at different sites and buildings. We indexed BPE by each species i, and

calculated BPE$_i$ by dividing total numbers of fatalities by the total number of days surveyed at all buildings within that species' distribution. We treated species as replicates and fit the relationship between BPE$_i$ and population size (while fixing regression coefficients to 1) as:

$\text{Log}_{10}(\text{BPE}_i) = \beta_0 + \beta_1 * \log_{10}(\text{population size}_i).$

We calculated residuals from this equation and used them to calculate vulnerability indices as follows:

$\text{Vulnerability}_i = 10^{\wedge |\text{residual for } i|}.$

This approach assumes that a 10–fold increase in population size results in a 10–fold increase in collisions. The vulnerability index designates the factor by which a species has greater (positive residual) or lesser (negative residual) probability of experiencing a collision compared to an average species. To assess potential effects of observer detection probability on vulnerability, we conducted Pearson's correlations between vulnerability estimates and species-specific indices from Arnold and Zink (2011) that reflect carcass size and conspicuousness (index ranges=0-2; with small, cryptic species scored 0 and large, conspicuously-plumaged species scored 2).

Identifying collision correlates for individual species:

To identify correlates of collision numbers for individual species, we used generalized linear mixed models (GLMMs) in the glmmTMB package (Brooks et al. 2017) to examine relationships between the three PCA-derived latent variables (predictors) and species' fatality counts (response variable), with individual buildings as replicates (n=281). These models

were similar to those used by Hager et al. (2017); however, instead of assessing total

collisions as the response variable, we conducted separate analyses for 8 species with ≥10

collisions observed. For each species, we considered models with 14 different combinations

of predictor variables: a null model, models for each additive combination of predictors, and

models with a single interaction effect and up to one additional predictor (Supplementary

Information). For each variable combination, we specified one model with a negative

binomial (NB) error distribution (to account for over-dispersion) and one model with a zero-

inflated negative binomial (ZINB distribution) due to the large number of buildings with no

collisions observed. For all 28 resultant candidate models, we specified an offset for log-

transformed numbers of surveys (to account for varying effort). We used AIC in the bbmle

package to rank models (Bolker 2017), eliminated uninformative parameters, and considered

models supported when their ΔAIC=0–2 and at least 2 above the null model (Arnold 2010). If

multiple models were strongly supported, we used conditional model averaging in the

MuMIn package (Barton 2018) to generate coefficient estimates. Regardless of whether

coefficient estimates were from a single model or averaged models, we considered predictor

variables meaningful if 95% confidence intervals (CIs) of coefficient estimates did not

overlap zero.

Assessing influence of life history on collisions:

We classified species according to their migratory status and primary habitat

(Langham et al. 2015), and their main food resource (González-Salazar et al. 2012, Rodewald

2015). To analyze life history influence on collision numbers, we merged classifications for

these three characteristics into binary categories describing migration status (migratory/non-

migratory), primary food (insectivorous/non-insectivorous), and primary habitat

(woodland/non-woodland). We used GLMMs with a NB error distribution because a

preliminary analysis comparing NB and ZINB versions of the below-described full models determined there was greater support for the NB distribution. We specified an offset for log-transformed numbers of surveys, and a random effect for building nested within site to account for non-independence of multiple replicates for each building and buildings within sites. We included the three PCA-derived latent variables from the species-level correlate analysis as predictors to account for known sources of variance, but because these were not of primary interest for this analysis we did not interpret the significance of these predictors.

As opposed to the species-specific correlate analysis, which we based on 14 defined candidate models, we used a more exploratory approach for this analysis. The response variable for this analysis was fatality counts at each building for each combination of binary-coded predictor category (n=281 buildings*6 life history combinations=1686; e.g., one replicate for the count of migrant woodland insectivores at a building, one for non-migrant woodland insectivores, etc.). We defined a full model including all two-way interactions among life history and PCA-derived predictors. Dredging and model ranking were conducted in the MuMIn package (Barton 2018), with maximum number of predictor variables set to 7 to limit the many possible combinations of predictors in each model (resulting in comparison of 1,733 models; Supporting Information). For this model set, we used the same approach to model comparison and coefficient assessment as described for species-specific correlates analyses.

RESULTS:

Surveyors found 324 bird carcasses at 281 buildings on 40 academic campuses. After applying our filtering protocol for species with limited information or distributions, we retained for analysis 269 carcasses of 64 species. The most frequently found species were

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Ruby-throated Hummingbird and Common Yellowthroat (*Geothlypis trichas*) with 22 and 21 collisions respectively.

Species' vulnerability to collisions:

After removing species with ≤ 2 fatalities, we retained 240 carcasses from 40 species for our estimation of collision vulnerability. Estimated collision vulnerability varied, with one species 32 times more likely than average to collide, to another species 10 times less likely to collide than average (all estimated vulnerabilities in Supporting Information). The 10 most vulnerable species were Black-throated Blue Warbler (*Setopahga caerulescens*), Ovenbird, Ruby-throated Hummingbird, Yellow-bellied Sapsucker, Wood Thrush (*Hylocichla mustelina*), Brown Thrasher (*Toxostoma rufum*), White-breasted Nuthatch (*Sitta carolinensis*), American Goldfinch (*Spinus tristis*), Gray Catbird (*Dumetella carolinensis*), and Common Yellowthroat (Table 1). We found no correlation between vulnerability and either body size (r=-0.04, p =0.79) or plumage conspicuousness (r=0.15, p-value=0.35), suggesting minimal influence of observer detection probability on vulnerability estimates.

Collision correlates for individual species:

Collision correlates were evaluated for 8 species with ≥10 fatalities (vulnerability range for these species: +6.2 to –2.5) (Table 2). For all species, top models included NB distributions as opposed to ZINB distributions, despite the fact that most counts were zero. The first PC described building size and included positive loadings of building height, window area, and floor space area. That PC was a positive predictor of collision numbers for 5 of the 8 species (all except Swainson's Thrush [*Catharus ustulatus*], White-throated Sparrow, and Dark-eyed Junco [*Junco hyemalis*]). The second PC represented vegetation cover within 50 m of buildings and included a positive loading of impervious surface and

negative loading of woody vegetation. That PC was a negative predictor of collisions only for Swainson's Thrush. Some top models included variables not meaningfully associated with fatalities such as the third PC (which included a positive loading for regional urbanization) and an interaction between the building size PC and local vegetation PC for one species; other interactions were not included in top models for any species (Table 2; Supplementary Information).

Influence of life history on collisions:

The top and only competitive model for the life history analysis included the building size PC and all 2–way interactions among the 3 life history variables (Figure 2; model rankings in Supporting Information). The interaction terms in our models indicate that migratory species collide more than non-migratory species, and that this difference is more pronounced for woodland-inhabiting and insectivorous species. Likewise, traits associated with being insectivorous increase collision numbers for woodland-inhabiting species but decrease collisions for species inhabiting other vegetation types (stated alternatively, traits associated with being a woodland-inhabitant are associated with increased collisions for insectivores and decreased collisions for non-insectivores). However, differences in collision numbers between primary food and primary habitat were small (Figure 2c).

DISCUSSION:

Species' vulnerability to collisions:

Of the 10 bird species most vulnerable to building collisions, 7 (Black-throated Blue Warbler, Ovenbird, Ruby-throated Hummingbird, Yellow-bellied Sapsucker, Wood Thrush, Gray Catbird, Common Yellowthroat) have been documented as highly vulnerable in past multi-site studies (Arnold & Zink 2011; Loss et al. 2014). The other 3 (Brown Thrasher,

White-breasted Nuthatch, American Goldfinch) have not previously been identified as highly vulnerable. These novel findings may have arisen from our coordinated sampling, varying geographic or seasonal coverage of our study, the more-recent bird population estimates we used, or the more-limited number of species analyzed (i.e., some species may have ranked as highly vulnerable only because of the smaller number of "competing" species that we ranked).

Estimating collision vulnerability, as opposed to raw fatality counts, may provide insight into the likelihood of population-level effects of building collisions. Of our 10 most-vulnerable species, American Goldfinch, Brown Thrasher, Wood Thrush, and Common Yellowthroat have experienced population declines since 1970 (Rosenberg et al. 2019), and Wood Thrush is a US Bird of Conservation Concern (NABCI 2016). Other human-related factors like habitat loss are undoubtedly driving declines for these and many other migratory bird species. Nonetheless, our results and past studies (Arnold and Zink 2011; Loss et al. 2014) indicate that building collisions are also potentially contributing to declines, especially for the most vulnerable species colliding in greatest numbers relative to their abundance. Further, studies have identified that mortality during migration can affect bird populations, including for species we found to be highly vulnerable to collisions (e.g., Black-throated Blue Warbler, Wood Thrush; Sillett & Holmes 2002; Rushing et al. 2017). Although these studies did not identify specific sources of mortality, we suggest that building collisions during migration could be a major factor, and further research is needed to analyze the link between collisions and demography for migratory bird species.

Our continent-wide, coordinated sampling approach expands on previous vulnerability analyses (Arnold & Zink 2011; Loss et al. 2014) in part by accounting for biases associated with among-site variation in data collection protocols. That said, our analysis would be improved if we had observed more species with distributions that overlapped ≥10

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sites. As a result of only including only 40 such species, some of those we analyzed that had low population sizes or distribution overlap with sites could have artificially high vulnerability estimates if observed in relatively large numbers at a small number of sites. Similarly, incorporating local abundance estimates, rather than continent-wide estimates, would further improve vulnerability estimates (see also "Future Directions"). Finally, like all other vulnerability studies, the indices we calculated are not comparable to those from other studies. This limitation is especially important to consider for rare species that may collide in low numbers. These taxa are difficult to detect in short-term collision surveys (Beston et al. 2015), but their populations may be affected by only a few collisions.

Collision correlates for individual species:

The PC for building size, and specifically the building height, window area, and floor space area variables, were positively related to numbers of collision for 5 of 8 species assessed. Previous studies evaluating correlates of bird collisions have shown a similar increase in collisions with increasing building size and window area for both individual species (Loss et al. 2019) and total number of carcasses found (Klem et al. 2009; Hager et al. 2013, 2017; Machtans et al. 2013; Cusa et al. 2015; Ocampo-Peñuela et al. 2016; Schneider et al. 2018). Our results suggest large, glassy, multi-storied buildings cause large numbers of collisions for many bird species. This finding appears to apply the same for the medium-sized buildings (1–14 stories tall) on academic campuses in our study as it does for the larger buildings in other studies (Klem et al. 2009; Cusa et al. 2015; Loss et al. 2019). Conservation efforts focused on these types of buildings may result in the greatest per-building collision reductions.

Although past studies suggest more collisions occur at buildings surrounded by extensive vegetation and limited impervious surface (Hager et al. 2013; Cusa et al. 2015;

Ocampo-Peñuela et al. 2016; Schneider et al. 2018), we only found evidence for such effects for one species, Swainson's Thrush. Since Swainson's Thrush is commonly associated with forested habitat with dense undergrowth (Mack & Yong 2020), this species may be more likely to frequent areas near buildings with extensive woody vegetation, increasing numbers of collisions.

Small numbers of collisions for most species likely limited our ability to identify other correlates of species-level collision numbers. Assessing correlates of species-specific collisions should be considered in future studies, especially when the goal is to reduce collisions for particular species of conservation concern (e.g., rare or declining species); management based on correlates of total bird collisions may not always result in collision reductions for species of concern. In particular, amount of lighting emitted from buildings at night strongly influences total bird collisions (Lao et al. 2020), and vulnerability to lighting may vary among species in association with life history (e.g., nocturnal vs. diurnal migrants) and vision (e.g., lighting effects variable with species-specific differences in visual sensitivity and acuity).

Influence of life history on collisions:

Life history was associated with numbers of collisions, a finding with important implications for predicting and managing collisions across species with similar traits, and for understanding how traits mediate collision risk. Migratory species collided more than non-migrants (see also Arnold & Zink 2011; Loss et al. 2014; Wittig et al. 2017; and discussion of our sampling-related limitations below). Migrants may collide more because nocturnally migrating species, which comprise the majority of migrants, are more prone to attraction and disorientation from ALAN (Lao et al. 2020; Winger et al. 2019). More generally, migrants

could be at greater collision risk as a result of encountering more buildings over their annual cycle due to traversing a greater area and longer distances.

The larger number of collisions for woodland-inhabitants relative to non-woodland inhabitants that we documented could reflect physical, behavioral, or physiological adaptations associated with living in woodlands (e.g., habitat selection strategy, flight style/maneuverability, visual acuity) that influence perception and avoidance of buildings or ALAN. We hypothesize that the greater number of insectivore collisions could reflect increased attraction due to abundant insects in urban environments (Frankie & Ehler 1978), including near buildings due to ALAN (Longcore & Rich 2004). This pattern could also reflect alteration of birds' primary diets during migration due to resource availability influencing habitat selection. For example, insectivores may supplement their diet with fruits or seeds due to lack of insects (Parrish 1997), which may bring birds closer to buildings. Our results could also reflect life history traits (e.g., feeding behavior or location) not captured in the categories we defined. For example, insectivores are often foliage gleaners that fly through small openings in the forest canopy, a foraging strategy that may increase collision susceptibility due to reflections of vegetation and sunlight in windows (Wittig et al. 2017).

It is possible that our classification of life history using binary predictor variables (e.g., migratory/non-migratory) resulted in the loss of some potentially valuable information. Future studies with larger numbers of collisions and more species observed may allow assessment of more refined categories (e.g., long, medium, and short distance migrants) to provide greater understanding of how life history influences numbers of collisions. Further, our focus of sampling during fall migration led to an inherent bias towards migratory species, as migrants typically collide more than residents do during migration seasons (Riding 2019); future studies could assess life history-related effects across different seasons.

Future Directions:

The large spatial extent of our study required us to sample in one fall migration only; future research would benefit by including multiple seasons and years. Related, future studies should attempt to sample more collisions while maintaining a coordinated sampling approach. In addition to a longer sampling period, numbers could be increased by coordinating citizen science efforts to study bird collisions across multiple cities, and using molecular techniques to identify bird carcasses that would otherwise be unidentifiable. Future studies could also quantify and account for bird abundance, which influences collision numbers and varies regionally relative to factors such as latitude, longitude, and proximity to major migration flyways, including those associated with geographical features (e.g., coastlines and mountain ranges). Local species abundance could be estimated with data from public databases (e.g., eBird; Sullivan et al. 2009) or surveys conducted near buildings, and total abundance of migrants could be quantified with weather radar (Van Doren and Horton 2018). Studies should also evaluate sampling bias associated with birds colliding and exiting the survey area before dying, and assess risk correlates related to bird vision and morphology, which may influence collision avoidance or the proportion of collisions that are fatal. Finally, future research should attempt to verify species and life history-related correlates of collisions because our 16 assessments of 95% CIs of model coefficients to infer variable importance increased probability of Type I error (i.e., apparently significant effects arising by chance). Using the Bonferroni correction to account for multiple assessments (i.e., increasing the CI width used to infer meaningful effects) results in all supported variables having coefficient CIs that overlap zero. However, many of our documented effects may be biologically important as the Bonferroni correction has been criticized for being overly conservative (i.e., resulting in Type II error, or false negatives; Moran 2003).

Conclusions:

Building collisions kill large numbers of birds and will likely increase with increasing human population, number of buildings, and ALAN. The vulnerability rankings we produced can assist conservation by highlighting species that experience the greatest numbers of collisions relative to population abundance, which are pertinent species on which mitigation steps to reduce building collisions should be focused. Our analyses of species-specific collision correlates at buildings on academic campuses provide further evidence for focusing mitigation on relatively large buildings in these settings, and to even larger buildings in urban centers (e.g., skyscrapers in major cities). Our results also support the importance of constructing buildings with smaller expanses of reflective or transparent glass, and treating glass on existing buildings. Policies and guidelines to reduce collision risk at new and existing buildings are becoming much more common (San Francisco Planning Department 2019), and there are a growing number of commercially available options to make existing and new glass more bird-friendly (e.g., using fritted glass or installing films, decals, netting, or shades; Klem 2015). Our results also highlight that no single mitigation approach may be effective for all birds and that species-specific correlates should be considered when managing collisions. Finally, our life history analysis may aid in developing mitigation approaches that address life history-related risk factors (e.g., reduction of ALAN during migration to reduce mortality of migrants; Winger et al. 2019).

SUPPORTING INFORMATION:

Candidate models, coefficients, and CIs from top models for analysis of species-specific collision correlates (Appendix S1), list of participants collecting data (Appendix S2), full candidate model and output for all life history models (Appendix S3), and estimated collision vulnerability for all species (Appendix S4) are available online. The authors are solely responsible for content and functionality of these materials. Queries (other than absence of material) should be directed to the corresponding author.

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Table 1. Collision vulnerability estimates for 10 most vulnerable species from fall 2014 collision monitoring at 40 sites across North America.

Common Name	Fatality Count	Vulnerability
Black-throated Blue Warbler	5	32.24
Ovenbird	17	6.21
Ruby-throated Hummingbird	22	6.09
Yellow-bellied Sapsucker	8	5.15
Wood Thrush	4	3.58
Brown Thrasher	2	3.31
White-breasted Nuthatch	3	2.83
American Goldfinch	12	2.48
Gray Catbird	7	2.29
Common Yellowthroat	21	2.26

Table 2. Correlates of building collision fatalities for individual bird species; correlates are from top models in AIC comparisons. Direction of relationship for variables in top models indicated by + (positive) and − (negative); (0 indicates variables not in top models). Building size, local vegetation, and regional urbanization correlates represent principal components derived in Hager et al. (2017). All two-way interactions except building size * local vegetation were excluded from this table as they did not appear in top models.

Common Name	Number of collisions	Vulnerability	Building size	Local vegetation	Regional urbanization	Building size*local vegetation
Ovenbird	17	6.21	+	−[a]	0	0
Ruby-throated Hummingbird	22	6.09	+	0	0	0
American Goldfinch	12	2.48	+	0	0	0
Common Yellowthroat	21	2.26	+	+[a]	0	0
Tennessee Warbler	14	1.18	+	0	0	0
Swainson's Thrush*	10	−1.51	0	−	−[a]	0
White-throated Sparrow*	10	−1.65	+[a]	−[a]	+[a]	−[a]
Dark-eyed Junco	10	−2.48	0	0	0	0

*Species with >1 competitive model; results shown are from model-averaged coefficient estimates.
[a]Variables with 95% CIs of coefficients overlapping zero.

Figure 1. Locations of 40 study sites across North America with bird-building collision monitoring conducted during fall 2014.
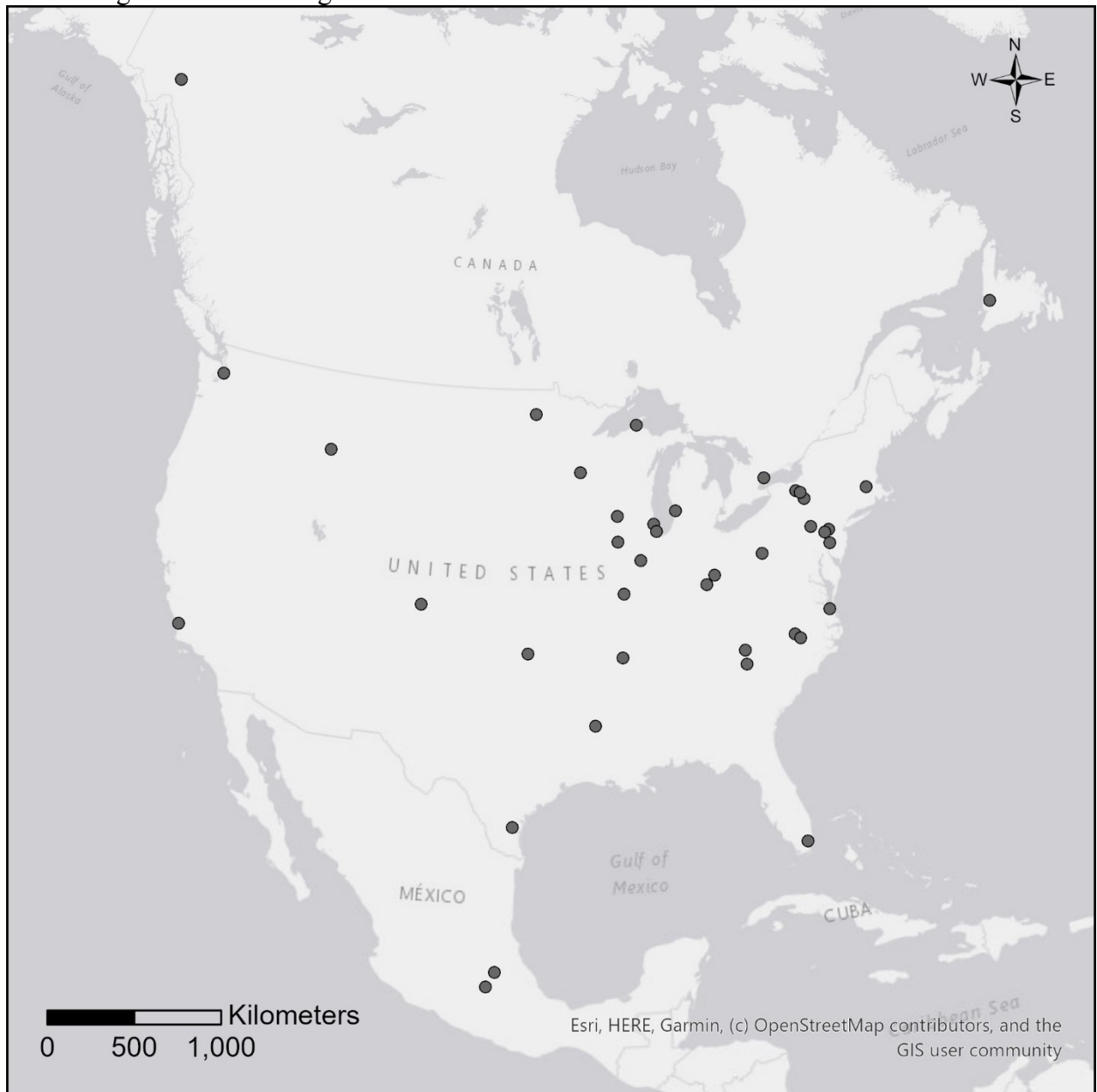
Figure 2. Associations among life history and numbers of bird-building collisions per replicate (predicted based on the fitted generalized linear mixed model), including (a) interaction between migratory status and primary food, (b) interaction between migratory status and primary habitat, and (c) interaction between primary food and primary habitat.