








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 the United States and Canada. However, efforts to reduce collisions would benefit from studies conducted at large spatial scales across multiple study sites with standardized methods and consideration of species- and life-history-related variation and correlates of collisions. We addressed these research needs through coordinated collection of data on bird collisions with buildings at sites in the United States (35), Canada (3), and Mexico (2). We collected all carcasses and identified species. After removing records for unidentified carcasses, species lacking distribution-wide population estimates, and species with distributions overlapping fewer than 10 sites, we retained 269 carcasses of 64 species for analysis. We estimated collision vulnerability for 40 bird species with ≥ 2 fatalities based on their North American population abundance, distribution overlap in study sites, and sampling effort. Of 10 species we identified as most vulnerable to collisions, some have been identified previously (e.g., Black-throated Blue Warbler [*Setophaga caerulescens*]), whereas 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. Building size and glass area were positively associated with number 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 [*Catbarus ustulatus*]). Life history predicted collisions; numbers of collisions were greatest for migratory, insectivorous, and woodland-inhabiting species. Our results provide new insight into the species most vulnerable to building collisions, making them potentially in greatest need of conservation attention to reduce collisions and into species- and life-history-related variation and correlates of building collisions, information that can help refine collision management.

Keywords: amenazas antropogénicas, colisiones contra ventanas, colisiones de aves, historia de vida, mortalidad de fauna, urbanización, vulnerabilidad

Correlaciones de las Colisiones de Aves contra Edificios en Tres Países de América del Norte

Resumen: Las colisiones contra los edificios causan hasta mil millones de fatalidades de aves al año en los Estados Unidos y en Canadá. Sin embargo, los esfuerzos por reducir estas colisiones se beneficiarían con estudios realizados a grandes escalas espaciales en varios sitios de estudio con métodos estandarizados y considerando las variaciones relacionadas a la historia de vida y a la especie y las correlaciones de las colisiones. Abordamos estas necesidades de investigación por medio de una recolección coordinada de datos sobre las colisiones de aves contra edificios en los Estados Unidos (35), Canadá (3) y México (2). Recolectamos todos los cadáveres y los identificamos hasta especie. Después de retirar los registros de cadáveres no identificados, las especies sin estimaciones poblacionales a nivel distribución y las especies con distribuciones traslapadas en menos de diez sitios, nos quedamos con 269 cadáveres de 64 especies para el análisis. Estimamos la vulnerabilidad a colisiones para 40 especies con ≥ 2 fatalidades con base en la abundancia poblacional para América del Norte, el traslape de su distribución entre los sitios de estudio y el esfuerzo de muestreo. De las diez especies que identificamos como las más vulnerables a las colisiones, algunas han sido identificadas previamente (*Setophaga caerulescens*), y otras aparecieron por primera vez (*Sitta carolinensis*), posiblemente debido a que usamos una estrategia de muestreo más estandarizada que en los estudios previos. El tamaño del edificio y el área del vidrio estuvieron asociados positivamente con el número de colisiones para cinco de ocho especies con suficientes observaciones para ser analizadas independientemente. La vegetación alrededor de los edificios influyó sobre las colisiones solamente para una de esas ocho especies (*Catbarus ustulatus*). Las historias de vida pronosticaron las colisiones; el número de colisiones fue mayor para las especies migratorias, insectívoras y aquellas que habitan en las zonas boscosas. Nuestros resultados proporcionan una nueva perspectiva hacia las especies más vulnerables a las colisiones contra edificios, lo que las pone en una necesidad potencialmente mayor de atención conservacionista para reducir estas colisiones y de estudio de las variaciones relacionadas con la especie y la historia de vida y las correlaciones de las colisiones contra edificios, información que puede ayudar a refinar el manejo de colisiones.

Palabras Clave: anthropogenic threats, bird strikes, urbanization, wildlife mortality, window collisions, life history, vulnerability

摘要: 在美国和加拿大, 每年有多达10亿只鸟类死于撞击建筑物。在大空间尺度上跨多个研究地点、采用标准化方法, 并考虑鸟类物种及生活史变异和其它撞击相关因素的研究, 将有助于减少鸟类与建筑物的碰撞。本研究通过整理收集美国、加拿大和墨西哥多个位点(数量分别为 35 个、3 个和 2 个) 鸟类撞击建筑物的数据来满足以上的研究需求。我们首先收集了所有鸟类尸体并进行物种鉴定。在排除掉不能辨认的尸体、缺少分布范围内种群估计数据的物种、分布区与少于 10 个位点有重叠的物种后, 我们保留了 64 个物种的 269 个死亡事件进行分析。我们根据鸟类的北美种群数量、分布区与研究位点的重叠情况和抽样工作量, 估计了死亡个体 ≥ 2 只的 40 种鸟类的撞击脆弱性。本研究确定了最易发生撞击的 10 个物种, 其中包括已经被以往研究提及的物种(如黑喉蓝林莺 [*Setophaga caerulescens*]), 也有首次报道的物种(如白胸鹀 [*Sitta carolinensis*]), 这可能是因为使用了比以往研究更注重标准化的抽样方法。在有足够观察数据以支持独立分析的 8 个物种中, 有 5 个物种的撞击次数与建筑大小和玻璃面积呈正相关; 只有 1 个物种(斯氏夜鸫 [*Catbarus ustulatus*]) 的撞击受到建筑物周围植被的影响。生活史也可以预测撞击情况: 迁徙鸟类、食虫鸟类和林栖鸟类的撞击次数最多。我们的研究结果为最易发生建筑物撞击伤害的鸟类物种提供了新的见解, 这些物种可能最需要保护以减少撞击, 本研究还深入探究了鸟类物种及生活史变异和其它撞击相关因素, 这些信息有助于改进鸟类撞击管理。【翻译: 胡怡思; 审校: 聂永刚】

关键词: 异速增长, 人为威胁, 鸟类撞击, 城市化, 野生动物死亡, 窗户碰撞, 生活史, 脆弱性

Introduction

Globally, many bird populations are in decline. In addition to important indirect threats such as climate change and habitat loss, many declines are likely caused in part by direct sources of anthropogenic mortality, including collisions with structures, chemical poisoning, and predation by 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 the United States and Canada (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 (ALAN) (Longcore & Rich 2004) contributes to bird-building collisions. The 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 areas of glass (Hager et al. 2008; Klem et al. 2009), with ALAN (Winger et al. 2019), and with 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 study in the United States, Canada, and Mexico showed 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 collisions may also vary due to factors intrinsic to bird species such as their life history (Cusa et al. 2015; Wittig et al. 2017). Migratory species are thought to collide in greater numbers than nonmigratory 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 collide with buildings 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 be subject to 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 their meta-analysis results. Further, there are few studies on 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, whereas open woodland-inhabiting, ground-

foraging species collide more at buildings surrounded by intense urban development (Cusa et al. 2015). Results of another study show 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 2 studies were conducted at single study sites.

A broad-scale assessment based on 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. 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 data set collected under a coordinated sampling protocol at 281 buildings across 40 study sites in the United States, Canada, and Mexico in fall 2014. Our objectives were to assess variation in species' vulnerability to building collisions; identify building and landscape-related correlates of collision numbers for individual species; and 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 in the United States ($n = 35$), Canada ($n = 3$), and Mexico ($n = 2$) (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 in Hager et al. 2017).

We conducted collision surveys 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 present not detected by surveyors) (Hager & Cosentino 2014).

We minimized detection bias by making 2 passes around each building for each survey. Surveys consisted of 1–2 individuals searching within ~ 2 m of the entire building perimeter, including in, under, and around

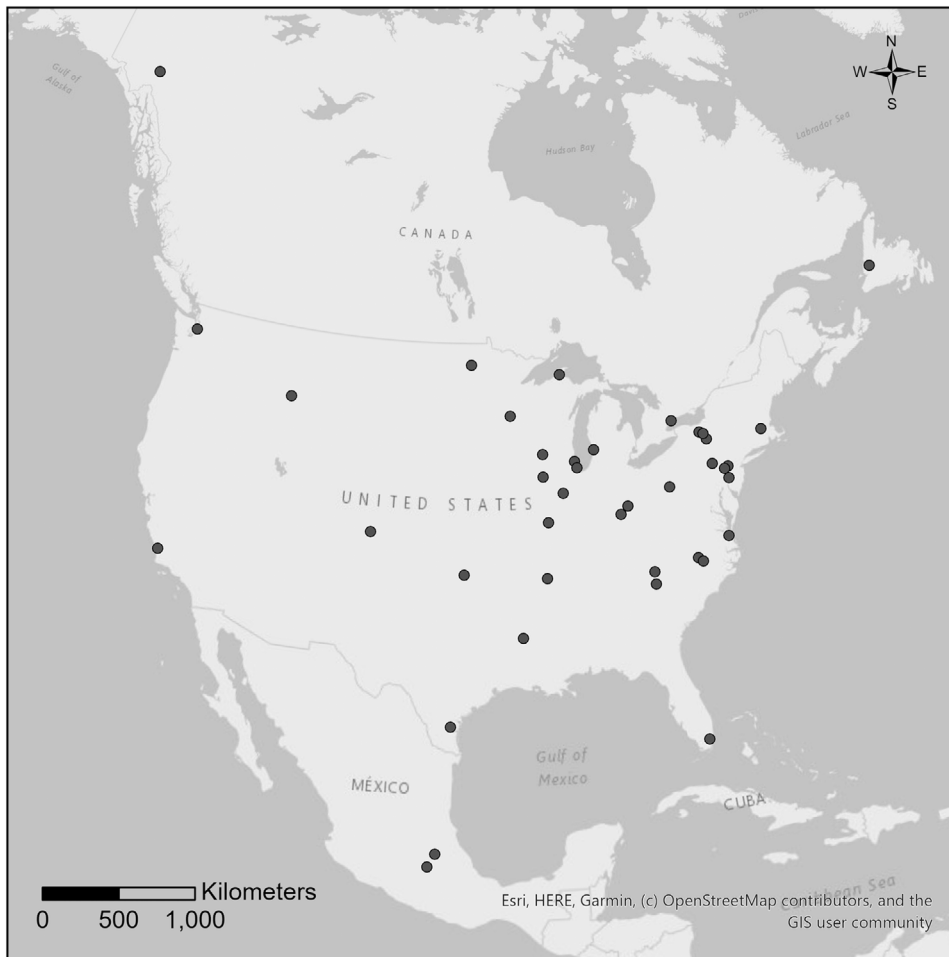


Figure 1. Locations in Canada, the United States, and Mexico where bird-building collision monitoring was conducted during Fall of 2014.

vegetation. When 1 individual conducted surveys, a single pass was made in each direction around the building. When 2 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 corresponded to cumulative detection probabilities of 0.91–0.99 (e.g., $1 - [1 - 0.70]^2 = 0.91$).

Because 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 and 1600. Carcasses typically persist for multiple days (Hager et al. 2012; Riding & Loss 2018), so daily surveys maximized 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 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 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 noted. Survey protocols were approved by animal care and use committees at each authors' institution, and carcasses were collected under state permits and a U.S. Fish and Wildlife Service Salvage Permit (number MB08907A-0).

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 (square meters calculated with tape measure or ImageJ [Abramoff et al. 2004]), number of stories above ground-level, and floor space area (square meters [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 same buildings as in Hager et al. (2017), we used the 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 3 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 that it is based on the assumption 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 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 included only species with ≥ 2 fatalities across study sites.

We estimated species' vulnerability with the approach of Arnold and Zink (2011) and Loss et al. (2014), with 1 modification. Briefly, they estimated 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, 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 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

$$\log_{10}(BPE_i) = \beta_0 + \beta_1 * \log_{10}(\text{population size}_i). \quad (1)$$

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

$$\text{vulnerability}_i = 10^{|\text{residual for } i|}. \quad (2)$$

This approach is based on the assumption 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 with 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 reflected carcass size and conspicuousness (index ranges 0–2; 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 3 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 1 additional predictor (Supporting Information). For each variable combination, we specified 1 model with a negative binomial (NB) error distribution (to account for overdispersion) and 1 model with a 0-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 $\Delta\text{AIC} = 0\text{--}2$ 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 0.

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. 2014; Rodewald 2015). To analyze life-history influence on collision numbers, we merged classifications for these 3 characteristics into binary categories describing migration status (migratory or nonmigratory), primary food (insectivorous or noninsectivorous), and primary habitat (woodland or nonwoodland). 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 nonindependence of multiple replicates for each building and buildings within sites. We included the 3 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 (281 buildings*6 life-history combinations = 1686; e.g., 1 replicate for the count of migrant woodland insectivores at a building, 1 for non-migrant woodland insectivores, etc.). We defined a full model including all 2-way interactions among life-history and PCA-derived predictors. Dredging and model ranking were conducted in the MuMIn package (Barton 2018); maximum number of predictor variables was 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.

Table 1. Building collision vulnerability estimates for 10 most vulnerable bird 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

Results

Surveyors found 324 bird carcasses. 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 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 from 1 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 (*Setopabga 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). Vulnerability was not correlated with body size ($r = -0.04$, $p = 0.79$) or plumage conspicuousness ($r = 0.15$, $p = 0.35$), 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 +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 0. 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

Table 2. Direction of the relationship^a of correlates^b of bird-building collision fatalities for individual species.

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

^a Key: +, positive; -, negative; 0, variables not in top models. Two-way interactions, except building size * local vegetation, are excluded because they did not appear in top models.

^b From top supported generalized linear mixed models compared with Akaike's Information Criterion.

^c Represent principal components derived by Hager et al. (2017).

^d Variables with 95% CIs of coefficients overlapping 0.

^e Species with >1 competitive model; results shown are from model-averaged coefficient estimates.

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 1 species. Other interactions were not included in top models for any species (Table 2 & Supporting 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 (Fig. 2; model rankings in Supporting Information). The interaction terms in our models indicated that migratory species collided more than nonmigratory species, and that this difference was more pronounced for woodland-inhabiting and insectivorous species. Likewise, traits associated with being insectivorous increased collision numbers for woodland-inhabiting species but decreased collisions for species inhabiting other vegetation types (i.e., traits associated with being a woodland-inhabitant were associated with increased collisions for insectivores and decreased collisions for noninsectivores). However, differences in collision numbers between primary food and primary habitat were small (Fig. 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 multisite studies (Arnold & Zink 2011; Loss et al. 2014). The other 3 (Brown Thrasher, White-breasted Nuthatch, American Goldfinch) have not been identified previously as highly vulnerable. These novel findings may have arisen due to our coordinated sampling and differences in geographic extent and survey season between our study and previous studies, 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 populations have declined since 1970 (Rosenberg et al. 2019), and Wood Thrush is a "bird of conservation concern" in the United States (NABCI 2016). Other human-related factors, such as habitat loss, are undoubtedly driving declines for these and many other migratory bird species. Nonetheless, our results and those of 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, mortality during migration can affect bird

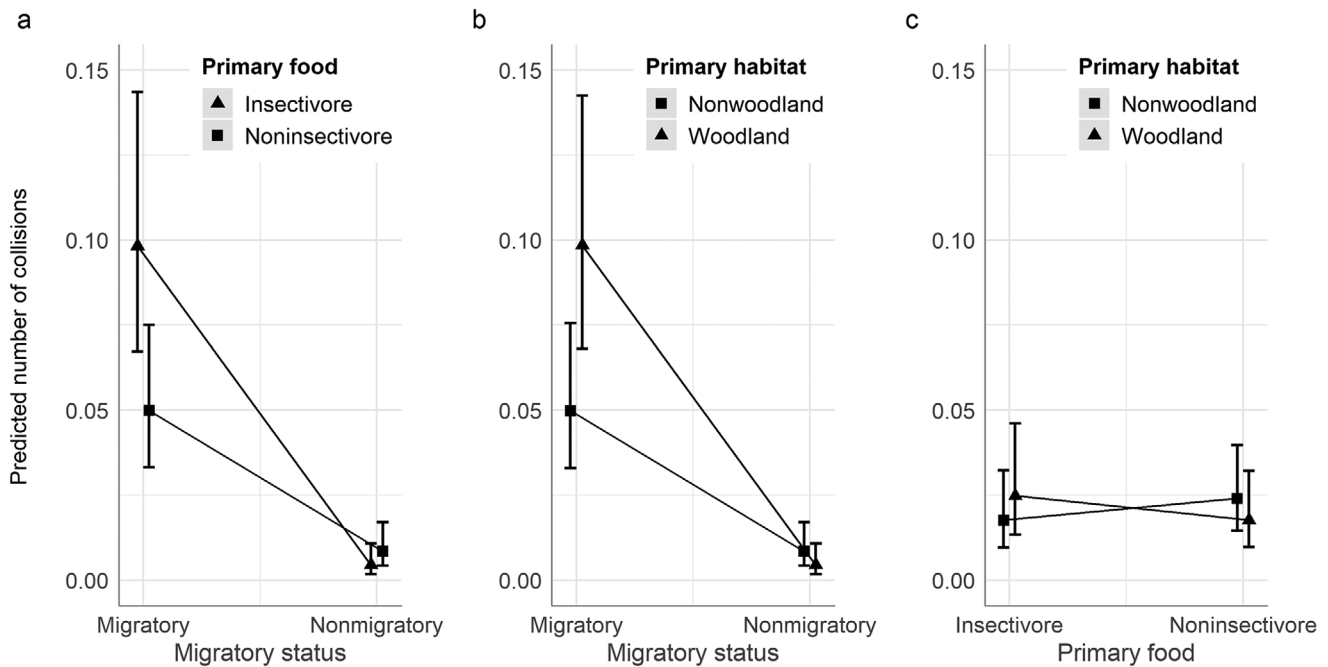


Figure 2. Associations of life-history characteristics with numbers of bird-building collisions per replicate (predicted effects based on the fitted generalized linear mixed model): (a) interaction between migratory status and primary food, (b) interaction between migratory status and primary habitat, and (c) interaction between primary food and primary habitat (bars, 95% CIs).

populations, including for species we found to be highly vulnerable to collisions (e.g., Black-throated Blue Warbler, Wood Thrush) (Sillert & Holmes 2002; Rushing et al. 2017). Although specific sources of mortality have not been identified, we suggest 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 broadscale, 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 results would have been more robust if we had observed more species with distributions that overlapped ≥ 10 sites. As a result of 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 “Future Directions”). Finally, like all other vulnerability studies, the exact value of indices for species are not comparable with 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, were positively related to numbers of collision for 5 of 8 species assessed. Previous studies evaluating correlates of bird collisions show similarly that collisions increase as building size and window area increase 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, multistoried 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 1 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 number 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 nonmigrants (Arnold & Zink 2011; Loss et al. 2014; Wittig et al. 2017). 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 (Moore & Aborn 2000).

The larger number of collisions for woodland inhabitants relative to nonwoodland inhabitants 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 our classification of life history based on binary predictor variables (e.g., migratory or nonmigratory) 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 toward migratory species because migrants typically collide more than residents do during migration (Riding 2019). Future studies could assess life-history-related effects across different seasons.

Future Directions

The large spatial extent of our study required sampling during 1 fall migration only; including multiple seasons and years would be an improvement. Related, future studies should attempt to sample more collisions while maintaining a coordinated sampling approach. In addition to a longer sampling period, number of collisions and species 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 & 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). We chose to not use the Bonferroni correction to account for multiple assessments (i.e., increasing the CI width used to infer meaningful effects) because it would have resulted in all supported variable having coefficient CIs that overlapped 0. Many of our documented effects may be biologically important, and Bonferroni correction has been criticized for being overly conservative (i.e., resulting in type II error) (Moran 2003).

Implications

The rankings of vulnerability to building collisions we produced highlighted species with 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 on 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., fritted glass, 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).

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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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