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RESEARCH ARTICLE

Bird–building collisions in the United States: Estimates of annual mortality and species vulnerability

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ABSTRACT

Building collisions, and particularly collisions with windows, are a major anthropogenic threat to birds, with rough estimates of between 100 million and 1 billion birds killed annually in the United States. However, no current U.S. estimates are based on systematic analysis of multiple data sources. We reviewed the published literature and acquired unpublished datasets to systematically quantify bird–building collision mortality and species-specific vulnerability. Based on 23 studies, we estimate that between 365 and 988 million birds (median = 599 million) are killed annually by building collisions in the U.S., with roughly 56% of mortality at low-rises, 44% at residences, and <1% at high-rises. Based on >92,000 fatality records, and after controlling for population abundance and range overlap with study sites, we identified several species that are disproportionately vulnerable to collisions at all building types. In addition, several species listed as national Birds of Conservation Concern due to their declining populations were identified to be highly vulnerable to building collisions, including Golden-winged Warbler (*Vermivora chrysoptera*), Painted Bunting (*Passerina ciris*), Canada Warbler (*Cardellina canadensis*), Wood Thrush (*Hylocichla mustelina)*, Kentucky Warbler (*Geothlypis formosa)*, and Worm-eating Warbler (*Helmitheros vermivorum)*. The identification of these five migratory species with geographic ranges limited to eastern and central North America reflects seasonal and regional biases in the currently available building-collision data. Most sampling has occurred during migration and in the eastern U.S. Further research across seasons and in underrepresented regions is needed to reduce this bias. Nonetheless, we provide quantitative evidence to support the conclusion that building collisions are second only to feral and free-ranging pet cats, which are estimated to kill roughly four times as many birds each year, as the largest source of direct human-caused mortality for U.S. birds.

Keywords: anthropogenic mortality, Birds of Conservation Concern, individual residence, low-rise, high-rise, systematic review, window collision

Colisiones entre aves y edificios en los Estados Unidos: Estimaciones de mortalidad anual y vulnerabilidad de especies

RESUMEN

Colisones con edificios, en particular contra ventanas, presentan una amenaza antropogénica importante para las aves, y se estima que causan la muerte de entre 100 millón a mil millones de aves anualmente. Sin embargo, no existen estimaciones para los Estados Unidos que estén basadas en un análisis sistemático de datos provenientes de multiples fuentes. Revisamos datos publicados y tambien adquirimos bases de datos inéditos para cuantificar de una manera sistemática la mortalidad causada por colisones entre aves y edificios, y la vulnerabilidad de diferentes especies. Basado en 23 estudios, estimamos que entre 365 y 988 millones de aves (promedio = 599 millones) mueren anualmente como consecuencia de colisiones con edificios en los Estados Unidos, con aproximadamente 56% de la mortalidad en edificios de baja altura, 44% en residencias, y <1% en edificios de muchos pisos. Basado en >92,000 fatalidades registradas, y luego do controlar por abundancia poblacional y solapamiento de rango con area de estudio, identificamos varias especies que son desproporcionalmente vulnerables a colisiones con todos los tipos de edificio. Además, varias especies listadas nacionalmente como Aves de Interés para la Conservación debido a sus poblaciones en declive fueron identificadas como altamente vulnerables a colisiones, incluyendo *Vermivora chrysoptera*, *Passerina ciris*, *Cardellina canadensis*, *Hylocichla mustelina*, *Geothlypis formosa*, y *Helmitheros vermivorum*. La identificación de estas cinco especies migratorias con rangos geográficos restringidos a Norteamérica oriental y central refleja sesgos estacionales y regionales en la disponibilidad de datos actuales disponibles de colisiones con edificios. La mayoría del muestreo ha ocurrido durante la época de migración y en el este de los Estados Unidos. Hacen falta investigaciones adicionales a través de estaciones y en regiones poco representadas par reducir este sesgo. Sin embargo, presentamos

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evidencia cuantitativa que apoya la conclusión que, como causa de mortalidad ligada derectamente a los humanos en los Estados Unidos, las colisiones con edificios son superados solamente por los gatos mascotas libres, los cuales matan aproximadamente cuatro veces la cantidad de aves anualmente.

Palabras clave: mortalidad antropogénica, Aves de Interés para la Conservación, residencia particular, edificio de baja altura, edificio de muchos pisos, revisión sistemática, colisión con ventana

INTRODUCTION

Collisions between birds and man-made structures, including communication towers, wind turbines, power lines, and buildings, collectively result in a tremendous amount of bird mortality. Buildings are a globally ubiquitous obstacle to avian flight, and collisions with buildings, especially their glass windows (Figure 1), are thought to be a major anthropogenic threat to North American birds (Klem 1990a, 2009, Machtans et al. 2013). Estimates of annual mortality from building collisions range from 100 million to 1 billion birds in the United States (Klem 1990a, Dunn 1993) and from 16 to 42 million birds in Canada (Machtans et al. 2013). This magnitude of mortality would place buildings behind only free-ranging domestic cats among sources of direct human-caused mortality of birds (Blancher 2013, Loss et al. 2013).

Research on bird–building collisions typically occurs at individual sites with little synthesis of data across studies. Conclusions about correlates of mortality and the total magnitude of mortality caused by collisions are therefore spatially limited. Within studies, mortality rates have been found to increase with the percentage and surface area of buildings covered by glass (Collins and Horn 2008, Hager et al. 2008, 2013, Klem et al. 2009, Borden et al. 2010), the presence and height of vegetation (Klem et al. 2009, Borden et al. 2010), and the amount of light emitted from windows (Evans Ogden 2002, Zink and Eckles 2010). In the most extensive building-collision study to date, per-building mortality rates at individual residences were higher in rural than urban areas and at residences with bird feeders than those without feeders (Bayne et al. 2012). However, compared with larger buildings in urban areas (e.g., skyscrapers and low-rise buildings on office and university campuses), detached residences appear to cause lower overall mortality rates and relatively high amounts of mortality during non-migratory periods (Klem 1989, Dunn 1993, O'Connell 2001, Klem et al. 2009, Borden et al. 2010, Machtans et al. 2013).

FIGURE 1. A Swainson's Thrush killed by colliding with the window of a low-rise office building on the Cleveland State University campus in downtown Cleveland, Ohio. Photo credit: Scott Loss

Despite the apparently large magnitude of bird–building collision mortality and the associated conservation threat posed to bird populations, there currently exist no U.S. estimates of building-collision mortality that are based on systematic analysis of multiple data sources. The most widely cited estimate (100 million to 1 billion fatalities per year) was first presented as a rough figure along with qualifications (Klem 1990a) but is now often cited as fact (Best 2008). Assessment of species-specific vulnerability to collisions is also critical for setting conservation priorities and understanding population impacts; however, existing estimates of species vulnerability are limited in spatial scope. In the most systematic U.S. assessment of building collisions to date, species vulnerability was calculated using data from only three sites in eastern North America, but vulnerability values from this limited sample were used to conclude that building collisions have no impact on bird populations continent-wide (Arnold and Zink 2011, but see Schaub et al. 2011, Klem et al. 2012).

We reviewed the published literature on bird–building collisions and also accessed numerous unpublished datasets from North American building-collision monitoring programs. We extracted >92,000 fatality records—by far the largest building collision dataset collected to date—and (1) systematically quantified total bird collision mortality along with uncertainty estimates by combining probability distributions of mortality rates with estimates of numbers of U.S. buildings and carcass-detection and scavenger-removal rates; (2) generated estimates of mortality for different classes of buildings (including residences 1–3 stories tall, low-rise non-residential buildings and residential buildings 4–11 stories tall, and high-rise buildings ≥12 stories tall); (3) conducted sensitivity analyses to identify which model parameters contributed the greatest uncertainty to our estimates; and (4) quantified species-specific vulnerability to collisions across all buildings and for each building type.

METHODS

Literature Search

We searched Google Scholar and the Web of Science database (using the Web of Knowledge search engine) to locate peer-reviewed publications about bird–building collisions. We used the search terms "bird window collision" and "bird building collision" and both terms with "bird" replaced by "avian." We checked reference lists and an annotated bibliography (Seewagen and Sheppard 2012) to identify additional studies. Data from collision-monitoring programs were located using a Google search with the term "window collision monitoring program" and by contacting program coordinators listed on project websites. We cross-checked the datasets we found with a comprehensive list of "Lights Out" programs provided by C. Sheppard. Additional unpublished datasets were located based on our knowledge of ongoing studies presented at professional conferences or in published abstracts. Finally, we learned of unpublished datasets when contacting first authors of published studies; these additional datasets were either more extensive versions of authors' published datasets, completely new datasets, or in one case, a dataset from an independent citizen scientist.

Inclusion Criteria and Definition of Fatality

Different studies employed different sampling designs and data collection protocols. To reduce this variability, to ensure a baseline for the rigor of studies we used, and to minimize bias in our analyses, we implemented inclusion criteria to filter data at both the study and record levels. Inclusion criteria were different for the analyses of total mortality and species vulnerability. As a first step, we only included studies for in-depth review if they were conducted in the U.S. or Canada and provided original data on bird–building collisions. We implemented study-level inclusion criteria for the estimate of total mortality as follows. We excluded studies that were based on sampling at a single structure; these studies often focus only on unique building types with non-representative mortality rates (e.g., museums, convention centers, or exceptionally tall high-rises). We included datasets that were based on systematic carcass surveys or systematic surveys of homeowners, but we excluded those that were based on sampling in response to predicted building kills, incidental observations, opportunistically sampled collections, or undocumented methods. Because estimating per-building mortality rates was a major component of the mortality estimate, we also excluded studies if they did not record numbers of buildings monitored or provide street addresses of buildings that would have allowed us to estimate numbers of buildings.

Because the species vulnerability analysis was based on count proportions rather than on per-building mortality rates, we implemented a different set of inclusion criteria than that used for the total mortality estimate. This resulted in the use of some studies that were excluded from the total mortality estimate. Studies were only included in the species analysis if they identified carcasses to species. We excluded studies documenting fewer than 100 collision records because proportions based on small samples are more likely to be abnormally high or low. As with the total mortality estimate, we excluded data that were based on incidental or opportunistic sampling or undocumented methods. However, we did include studies even if data were based on sampling of a single structure or if we could not determine the number of buildings sampled. Thus, we assume that species composition within a site is independent of the number of buildings sampled. The study-level inclusion criteria resulted in 23 and 26 datasets used for the total mortality and species vulnerability estimates, respectively (Table 1). Seven studies were excluded from all analyses (Table S1 in Supplemental Material Appendix A).

Many datasets include some collision records that were collected during standardized surveys and others found incidentally. In addition, definitions of fatalities differ among studies. We therefore applied inclusion criteria to filter individual records and set our own definition of what constitutes a fatality. The record-level inclusion criteria were the same for all of our analyses. We excluded records clearly denoted as incidental finds (i.e. not collected during surveys), records with a disposition of "alive" or "survived," and records of released birds. We also excluded records of blood and/or feather spots on windows with no carcass found. From the remaining records, we defined fatalities to include any record with a disposition including "dead," "collected," or any disposition indicating severe injury (e.g., "disabled," "squashed," "fracture," or "injured"). All other records were considered to have unknown disposition (e.g., "stunned," "exhausted," "weak," "dis-oriented," or any disposition indicating a bird was sent to rehabilitation) and were excluded from all analyses. The record-level criteria resulted in 92,869 records that we used to generate total mortality and species vulnerability estimates. It was not possible to confirm whether fatalities were caused by collisions with windows or with other non-reflective portions of buildings; therefore, for the purposes of this study, we treated all records as building–collision fatalities. Nonetheless, the majority of bird mortality at buildings likely occurs due to collision with windows or other reflective surfaces (Klem 2009).

TABLE 1. Sampling coverage, number of buildings sampled, and mortality rates documented in studies meeting inclusion criteria for estimation of total annual U.S. mortality from bird–building collisions and/or calculation of species-specific collision vulnerability.

Building class	Location	Year-round sampling?	Used for mortality estimate?	Used for vulnerability analysis?	Buildings sampled	Mortality per building		Study
						Average	Range	
Residences (1–3 stories)	Alberta	Yes	Yes	No[c]	1,747	0.7	0–43	Bayne et al. 2012
	U.S. & Canada	No	Yes	Yes	1,165	0.85	0–21	Dunn 1993
	Duluth, MN	No	Yes	Yes	42	2.3[f]	?	Bracey 2011
	Illinois	Yes	Yes	No[c]	242	1.5	?	Weiss & Horn 2008
	Carbondale, IL	Yes	No[a]	Yes[h]	1	33.0	NA	Klem 1979
	Purchase, NY	Yes	No[a]	Yes[h]	1	26.0	NA	Klem 1979
Low-rises	Richmond, VA	Yes	Yes	Yes	4	29.0	21–38	O'Connell 2001
	Cleveland, OH	Yes	Yes	Yes	18	15.1	?	Borden et al. 2010
	Elsah, IL	Yes	Yes	Yes	4	24.0	?	Hager et al. 2008
	Decatur, IL	Yes	Yes	Yes	11	7.5[f]	?	Collins & Horn 2008
	Washington, DC	No	Yes	Yes	21–38[e]	4.0	1–30	Lights Out DC 2010–2012
	Rock Island, IL	No	Yes	No[d]	20	2.6	0.3–52.1	Hager et al. 2013
	Decatur, IL	No	Yes	No[d]	11	4.8	?	Horn personal communication
	Murray, KY	No	Yes	No[d]	13	1.6	0–7	Somerlot 2003
	Stillwater, OK	Yes	No[a]	Yes	1	32.0	NA	O'Connell personal communication
	Rock Island, IL	Yes	No[a]	Yes	1	54.8	NA	Hager et al. 2008
	Chicago, IL	No	No[a]	Yes	1	1,028.0[g]	NA	McCormick Place 1978–2012
	Rochester, MN	No	No[b]	Yes	?	?	?	Project Birdsafe Minnesota 2010–2011
	San Francisco, CA	Yes	No[a]	Yes	1	47.2[g]	NA	California Academy of Sciences 2008–2012
High-rises	Indianapolis, IN	No	Yes	Yes	48	3.3	1–14	Lights Out Indy 2009–2010
	Atlanta, GA	No	Yes	Yes	53	8.4	0–40	Sexton 2006
	Calgary, AB	No	Yes	Yes	15–36	5.5[g]	1–89	Collister et al. 1996, 1997, Booth & Collister 1998
	Baltimore, MD	No	Yes	Yes	16–48[e]	7.1[g]	1–81	Lights Out Baltimore 2008–2012
	Twin Cities, MN	No	Yes	Yes	118	3.0[g]	?	Project Birdsafe Minnesota 2007–2012
	New York, NY	No	Yes	Yes	17–31[e]	5.5[g]	1–52	Project Safe Flight New York 2009–2011
	Philadelphia, PA	No	Yes	Yes	10	13.2[g]	?	Pennsylvania Audubon 2008–2011
	Columbus, OH	No	Yes	No[d]	20[e]	1.4	0–5	Lights Out Columbus 2012
	Portland, OR	No	Yes	No[d]	21–44	1.0[g]	?	Bird Safe Portland 2009–2011
	Toronto, ON	No	Yes	Yes	74–194[e]	17.4[g]	1–535	Fatal Light Awareness Program 2000–2010
	Winston-Salem, NC	No	Yes	Yes	16	3.6[g]	0–10	Lights Out Winston-Salem 2011–2012
	Toronto, ON	No	No[a]	Yes	1	157.0	NA	Ranford & Mason 1969
	Chicago, IL	No	No[b]	Yes	?	?	?	Chicago Bird Collision Monitors 2002–2012
	Milwaukee, WI	No	No[b]	Yes	?	?	?	Wisconsin Night Guardians 2007–2011
	Toronto, ON	No	No[b]	Yes	?	?	?	Fatal Light Awareness Prog. 2007, 2011
	New York, NY	No	No[b]	Yes	?	?	?	Klem 2009

[a] Study excluded from total mortality estimate because sampling conducted at a single building.
[b] Study excluded from total mortality estimate because number of buildings sampled not recorded and no information provided to calculate this number.
[c] Study excluded from species estimates because species data not provided.
[d] Study excluded from species estimates because sample size <100.
[e] Number of buildings is an estimate based on the average of potential minimum and maximum (see text); range indicates year-to-year variation in number of buildings sampled.
[f] Mortality rate is corrected for scavenger removal and searcher detection rates.
[g] Mortality rate is an average per-building rate across all years of the study/monitoring program.
[h] Study used for species risk assessment for building class but not assessment across all building classes (sample size <100).

Data Extraction

We classified studies into three building classes thought to cause different mortality rates (Machtans et al. 2013) and for which data on the number of U.S. buildings is available. These classes include residences 1–3 stories tall (detached houses and multi-unit residences; hereafter, "residences"), low-rise non-residential buildings and residential buildings 4–11 stories tall (hereafter, "low-rises"), and high-rise buildings $\geq$12 stories tall (hereafter, "high-rises"). For unpublished data from downtown areas of major cities, we assumed that all data came from high-rises because it was not possible to determine building height without visiting each site. For all other data sources, we were able to confirm the building type from which data were collected. Published studies that met our inclusion criteria either reported an annual mortality rate per building (averaged across buildings) or presented both the number of dead birds found and the number of buildings sampled, thus allowing us to calculate this rate. For published studies, we extracted a single annual mortality rate for each study unless the study included data from more than one non-adjacent site, in which case we extracted a separate rate for each site (e.g., Klem 1979). For unpublished datasets that included the number of buildings sampled, we always extracted a single mortality rate. This value was generated by first calculating a single-year per-building mortality rate (averaged across buildings) for each year of the study and then averaging these rates across years. In some cases, we determined that two or more sources presented duplicate data when we observed that the data were collected at the same study sites and during the same range of dates. In these instances, we extracted the data from the source that provided more detailed methods or more extensive fatality data, and we excluded the duplicated data when extracting from the other source.

Data from collision-monitoring programs often include the street address or intersection where a carcass was found but not the number of buildings sampled. Single buildings can have more than one address, and a single address can include more than one building. In addition, some monitoring programs have no systematic protocol for recording addresses, resulting in multiple similar entries for an address (e.g., 1 Main, 1 Main St., and 1 Main—Smith Tower). To account for these issues, we entered addresses into Google Maps and used satellite view to determine if addresses referred to one or more buildings. If it was still unclear from mapping whether an address referred to one or more buildings, we assumed it referred to one. Likewise if we could not confirm that two or more similar addresses referred to one building, we assumed they were separate buildings. If addresses with different cardinal directions were possible (e.g., 1 Main E and 1 Main W), we assumed they referred to separate buildings, but if they were not possible (i.e. only 1 Main exists), we assumed data entry error and combined addresses.

Recognizing that these methods could not account for all duplicate addresses and data entry errors, we estimated a minimum and maximum number of buildings sampled in each year. We estimated a maximum number based on the number of unique addresses remaining after following the above steps and the assumption that intersections referred to a number of buildings equal to the number of carcasses found up to four (i.e. four or more carcasses may result from collision with four separate buildings, one at each intersection corner). We estimated a minimum number by combining similar addresses that may have been from one building, even if we could not confirm this with mapping, and assuming that all intersections referred to one building. We used the average of the minimum and maximum number to estimate per-building mortality rates.

Quantification of Annual Mortality from Building Collisions

The studies we used cover varying portions of the year, but most focus all or most of sampling effort on migration periods. Using raw per-building mortality rates would therefore result in a national estimate that is only relevant to spring and fall migration periods. We sought to account for partial-year sampling and to generate estimates that reflected the entire year, because several studies have indicated that building collision mortality can be substantial during summer and winter (Dunn 1993, Klem 2009, Bayne et al. 2012, Hager et al. 2013). Given enough year-round studies, partial-year mortality rates can be standardized to year-round estimates using year-round studies as a baseline (Longcore et al. 2012, Loss et al. 2013). However, there were few year-round studies that met inclusion criteria (Table 1), so we could not adjust individual studies to year-round estimates. Instead, we accounted for this limitation in our estimation model (details below) by only using a year-round study for residences, repeating estimation using a subset of studies that sampled year-round for low-rises, or incorporating a correction factor to account for mortality during periods other than migration for high-rises, a building type for which little data exists for summer and winter (see definition of and rationale for this correction factor in Supplemental Material Appendix B). Despite the limitation of applying a post hoc correction factor to the high-rise estimate, we argue that this approach is preferable to assuming that no mortality occurs during the summer and winter.

We estimated mortality in each building class by multiplying data-derived probability distributions of per-building mortality rates by distributions of numbers of buildings. For residences, we followed Machtans et al.

(2013), which based mortality rates on the only year-round building collision survey to date that sampled across a large number of residences, a study of 1,458 Alberta residents in single and multi-unit residences (Bayne et al. 2012). This study documented higher mortality rates at rural residences compared with urban residences and at residences with bird feeders compared with those without feeders. The study also documented increasing mortality with increasing age of urban residences. We incorporated these elements into our residence sub-model:

$$\text{Mortality}_{\text{rural with feeder}}(M_{\text{RF}}) = N_{\text{residence}} \times R \times F \times K_{\text{rural with feeder}} \times D_{\text{residence}} \tag{1}$$

$$\text{Mortality}_{\text{rural no feeder}}(M_{\text{RNF}}) = N_{\text{residence}} \times R \times (1-F) \times K_{\text{rural no feeder}} \times D_{\text{residence}} \tag{2}$$

$$\text{Mortality}_{\text{urban with feeder}}(M_{\text{UF}}) = N_{\text{residence(age)}} \times (1-R) \times F \times K_{\text{urban with feeder(age)}} \times D_{\text{residence}} \tag{3}$$

$$\text{Mortality}_{\text{urban no feeder}}(M_{\text{UNF}}) = N_{\text{residence(age)}} \times (1-R) \times (1-F) \times K_{\text{urban no feeder(age)}} \times D_{\text{residence}} \tag{4}$$

$$\text{Mortality}_{\text{residences}}(M_{\text{R}}) = M_{\text{RF}} + M_{\text{RNF}} + M_{\text{UF}} + M_{\text{UNF}} \tag{5}$$

where N is the number of residences in the U.S., R is the percentage of residences in rural areas, F is the percentage of residences with bird feeders, K is the annual per-building mortality rate, and D is a correction factor to account for two biases that lead to underestimation of mortality (Hager et al. 2013): removal of carcasses by scavengers prior to fatality surveys and imperfect detection of the carcasses remaining at the time of surveys. For Equations (3) and (4), we calculated mortality by building age classes (0–8, 9–18, and 19–28 years, and all ages $\geq$29 years), and summed estimates across age classes. These age classes correspond closely to those in Machtans et al. (2013), but we shifted classes slightly (e.g., 9–18 years instead of 10–20 years) to match housing age data from the U.S. Census Bureau.

For low-rises, we generated two separate estimates of collision mortality, one using mortality rates based on all eight studies meeting our inclusion criteria and one based only on four year-round studies. We used the following sub-model for both estimates:

$$\text{Mortality}_{\text{low-rise}}(M_{\text{L}}) = N_{\text{low-rise}} \times K_{\text{low-rise}} \times D_{\text{low-rise}} \tag{6}$$

For high-rises, there are no datasets based on year-round systematic sampling. We incorporated a correction factor (Y) into the mortality estimation sub-model to account for additional fatalities occurring outside of migration periods:

$$\text{Mortality}_{\text{high-rise}}(M_{\text{H}}) = N_{\text{high-rise}} \times K_{\text{high-rise}} \times Y \times D_{\text{high-rise}} \tag{7}$$

We estimated total annual building collision mortality by summing estimates for individual building classes; we conducted estimation twice, once using each of the low-rise estimates:

$$\text{Mortality}_{\text{total}} = M_{\text{R}} + M_{L} + M_{\text{H}} \tag{8}$$

All of the above parameters were treated as probability distributions. From the probability distribution of each parameter (see Table 2 for specific distributions, Supplemental Material Appendix B for rationale for all distributions, and Table S2 in Supplemental Material Appendix C for numbers of buildings), we randomly drew one value and used the above formulas. We used "runif" and "rnbinom" commands (for uniform and negative binomial distributions, respectively) in Program R and conducted 10,000 iterations to generate a range of estimate uncertainty.

Sensitivity Analysis

We used multiple linear regression analyses assuming a normal error distribution (function "lm" in Program R) to investigate the percentage of uncertainty in mortality estimate ranges explained by each model parameter (Blancher 2013, Loss et al. 2013). We treated the 10,000 mortality-estimate replicates as the values of the dependent variable and randomly drawn values of each parameter as values of predictor variables. We used partial R^2 values to interpret the percentage of variance in the estimate range explained by each parameter. We repeated this regression analysis four times: once for the total mortality estimate (including all parameters) and once for each of the three building class estimates (with each regression model only including the parameters relevant to that building class).

Quantification of Species Vulnerability

In addition to estimating total annual mortality, we calculated vulnerability for species and taxonomic groups. We followed Arnold and Zink (2011), who identified "super-collider" and "super-avoider" species using collision records from three unpublished datasets. We greatly expanded upon the earlier study by using 26 datasets from across North America (Table 1). All analyses described below were conducted across all datasets to estimate overall building collision vulnerability, as well as separately

TABLE 2. Probability distributions used to estimate total annual U.S. mortality from bird–building collisions. We defined uniform distributions for most parameters because not enough data exist to ascribe higher probability to particular values in the defined range. We defined negative binomial distributions for the low-rise and high-rise mortality rate distributions because they allowed the majority of probability density to match the confidence intervals indicated by the data while also allowing for a small probability of higher collision mortality rates, reflecting the exceptionally high mortality rates that have been documented at some low-rises and high-rises (see mortality rates in Table 1).

Parameter	Distribution type	Distribution parameters	Source
Residences (1–3 stories)			
Number of residences	Uniform	Varies by age (Supplemental Material Appendix C)	U.S. Census Bureau 2011
Percentage in urban areas	Uniform	Min = 72.6%; Max = 88.8%	U.S. Census Bureau 2012
Percentage with bird feeders	Uniform	Min = 15%; Max = 25%	Dunn 1993
Mortality rate			
Rural with feeders (all ages)	Uniform	Min = 2.17; Min = 4.03	Bayne et al. 2012, Machtans et al. 2013
Rural without feeders (all ages)	Uniform	Min = 0.98; Max = 1.82	Bayne et al. 2012, Machtans et al. 2013
Urban with feeders			
Age 0–8	Uniform	Min = 0.28; Max = 0.52	Bayne et al. 2012, Machtans et al. 2013
Age 9–18	Uniform	Min = 0.42; Max = 0.78	Bayne et al. 2012, Machtans et al. 2013
Age 19–28	Uniform	Min = 0.56; Max = 1.04	Bayne et al. 2012, Machtans et al. 2013
Age 29+	Uniform	Min = 0.63; Max = 1.17	Bayne et al. 2012, Machtans et al. 2013
Rural without feeders			
Age 0–8	Uniform	Min = 0.11; Max = 0.20	Bayne et al. 2012, Machtans et al. 2013
Age 9–18	Uniform	Min = 0.18; Max = 0.33	Bayne et al. 2012, Machtans et al. 2013
Age 19–28	Uniform	Min = 0.25; Max = 0.46	Bayne et al. 2012, Machtans et al. 2013
Age 29+	Uniform	Min = 0.28; Max = 0.52	Bayne et al. 2012, Machtans et al. 2013
Scavenging/detectability correction	Uniform	Min = 2; Max = 4	Dunn 1993
Low-rises			
Number of low-rises	Uniform	Min = 14.0 million; Max = 16.2 million	Multiple sources (see Supplemental Material Appendix C)
Mortality rate (all studies)	Neg. bin.	$n = 4.6$; $p = 0.35$	95% of distribution prob. density = 4–18[a]
Mortality rate (year-round studies)	Neg. bin.	$n = 5.1$; $p = 0.26$	95% of distribution prob. density = 5–28[b]
Scavenging/detectability correction	Uniform	Min = 1.28; Max = 2.56	Hager et al. 2012, 2013
High-rises			
Number of high-rises	Uniform	Min = 19,854; Max = 21,944	Sky Scraper Source Media 2013
Mortality rate	Neg. bin.	$n = 4.0$; $p = 0.37$	70% of distribution prob. density = 4–11[b]
Partial-year sampling correction	Uniform	Min = 1.05; Max = 1.20	Additional 5–20% mortality outside of migration
Scavenging/detectability correction	Uniform	Min = 1.37; Max = 5.19	Ward et al. 2006, Hager 2012, 2013

[a] Range represents 95% confidence interval of mortality rates calculated across all eight studies of low-rises meeting inclusion criteria.
[b] Range represents 95% confidence interval of mortality rates calculated from four year-round studies of low-rises meeting inclusion criteria.
[c] Range represents 95% confidence interval of mortality rates calculated from 11 studies of tall buildings meeting inclusion criteria.

for each building class to estimate class-specific vulnerability. As described previously, we only included datasets with more than 100 records for the overall vulnerability analysis. However, because there were only two datasets for residences that had more than 100 records, we also included two smaller datasets to calculate collision vulnerability for this building class.

Numbers of fatalities can vary among species due to population abundance and the degree of range overlap with study locations (Arnold and Zink 2011). To account for population abundance, we extracted national population size estimates from the Partners in Flight Population Estimates Database (Rich et al. 2004), which includes North American population estimates generated using U.S. Breeding Bird Survey data (Sauer et al. 2012). We used North American abundance rather than regional abundance because it is difficult to link study sites where mortality occurs to the affected regional subsets of bird populations, especially for species that are killed primarily during migration (Loss et al. 2012). To account for range overlap with study sites, we counted the number of sites overlapping with each species' breeding, wintering, and/or migration range (Sibley 2000). We followed Arnold and Zink's (2011) approach for calculating species vulnerability. To give each site equal weighting, we first standardized each dataset to 36,000, the largest single-site total

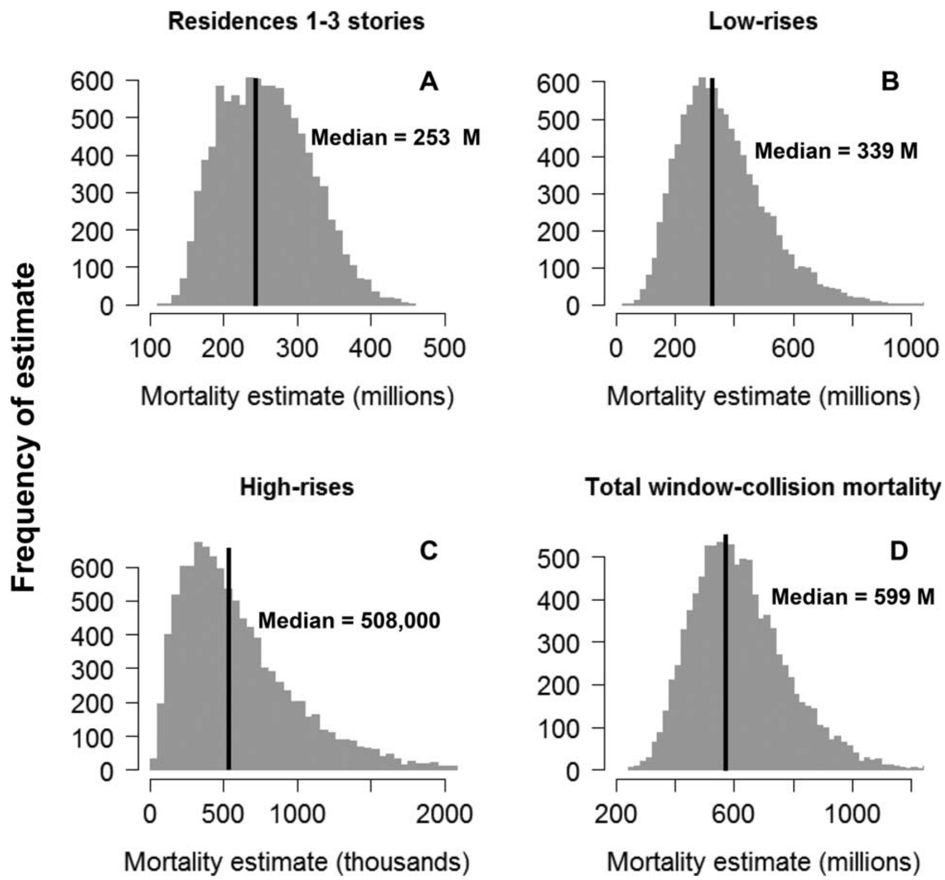

FIGURE 2. Frequency histograms for estimates of annual U.S. bird mortality caused by collisions with (**A**) residences 1–3 stories tall, (**B**) low-rises (residences 4–11 stories tall and all non-residential buildings $\leq$11 stories tall), (**C**) high-rises (all buildings $\geq$12 stories tall), and (**D**) all buildings. Estimates for low-rises and for all buildings are based on the average of two estimates: one calculated with all eight low-rise studies meeting inclusion criteria and one calculated with a subset of four low-rise studies that conducted year-round sampling.

number of fatalities, and then summed standardized counts across studies for each species. We regressed $\log_{10}(X+1)$ species counts ($X + 1$ transformation to account for zero counts for some species at some sites) on $\log_{10}$ population size and $\log_{10}$ range overlap. Vulnerability was estimated by fixing coefficients for population size and range overlap to 1.0 (this assumes that, for example, a 10-fold increase in abundance is associated with a 10-fold increase in collision mortality, all else being equal; Arnold and Zink 2011), calculating residuals, and raising 10 to the power of the absolute value of residuals. This approach of fixing model coefficients was taken because there was an unknown level of error in both the dependent and independent variables and, therefore, standard regression models could not produce unbiased slope estimates (Warton et al. 2006, Arnold and Zink 2011). Calculated vulnerability values indicate the factor by which a species has a greater chance (positive residuals) or smaller chance (negative residuals) of experiencing building collision mortality compared with a species with average vulnerability. We estimated vulnerability for taxonomic groups by averaging residuals across species occurring in at least two studies.

RESULTS

Estimates of Bird–Building Collision Mortality

The 95% confidence interval of annual bird mortality at residences was estimated to be between 159 and 378 million (median = 253 million) (Figure 2A and Table 3) after correcting for scavenger removal and imperfect detection. This equates to a median annual mortality rate of 2.1 birds per building (95% CI = 1.3–3.1). Reflecting the large number of residences in urban areas and residences without bird feeders, we estimate that urban residences without feeders cumulatively account for 33% of mortality at residences, followed by rural residences without feeders (31%), urban residences with feeders (19%), and rural residences with feeders (17%).

TABLE 3. Estimates of annual bird mortality caused by building collisions at U.S buildings. For low-rises (and therefore, for the total mortality estimate), we generated two separate estimates of collision mortality, one using mortality rates based on all eight low-rise studies meeting our inclusion criteria and one based on a subset of four low-rise studies that sampled mortality year-round.

		Point estimate		95% CI	
Building class	Mean no. of buildings in U.S.	Total	Per building	Total	Per building
Residences (1–3 stories)	122.9 million	253.2 million	2.1	159.1–378.1 million	1.3–3.1
Low-rises	15.1 million	245.5 million[a]	16.3[a]	62.2–664.4 million[a]	4.1–44.0[a]
		409.4 million[b]	27.1[b]	114.7–1,028.6 million[b]	7.6–68.1[b]
High-rises	20,900	508,000	24.3	104,000–1.6 million	5.0–76.6
Total	138.0 million	507.6 million[a]	3.7[a]	280.6–933.6 million[a]	2.0–6.8[a]
		667.1 million[b]	4.8[b]	349.9–1,296 million[b]	2.5–9.4[b]

[a] Estimate based on low-rise estimate using all eight studies meeting inclusion criteria.
[b] Estimate based on low-rise estimate using subset of four year-round studies meeting inclusion criteria.

The 95% confidence interval of annual low-rise mortality based on all studies meeting inclusion criteria was estimated to be between 62 and 664 million birds (median = 246 million). The 95% confidence interval based on the four year-round low-rise studies was estimated to be between 115 million and 1.0 billion birds (median = 409 million). The average of the two median figures is 339 million (95% CI = 136–715 million) (Figure 2B), equating to a median annual rate of 21.7 birds per building (95% CI = 5.9–55).

The 95% confidence interval of high-rise mortality was estimated to be between 104,000 and 1.6 million birds (median = 508,000) (Table 3 and Figure 2C) after correcting for scavenger removal, imperfect carcass detection, and mortality during periods other than migration. Despite causing the lowest total mortality, high-rises had the highest median annual mortality rate: 24.3 birds per building (95% CI = 5–76). Combining estimates from all building classes (using the average of the two low-rise estimates) results in an estimate of 599 million birds killed annually across all U.S. buildings (95% C.I. = 365–988 million) (Figure 2D).

Factors Explaining Estimate Uncertainty

Due to the large number of low-rises and uncertainty about low-rise mortality rates, sensitivity analyses indicated that the low-rise mortality rate explained a large amount of uncertainty for the estimates of both low-rise mortality (85%) and total mortality (75%). Other parameters explaining substantial uncertainty for the total estimate included the correction factors for scavenger removal and carcass detection at low-rises (10%) and residences (9%). For residences, 70% of uncertainty was explained by the correction factor for scavenging and detection and 15% was explained by the proportion of residences in urban areas. For the high-rise estimate, the greatest uncertainty was explained by the mortality rate (67%), followed by the correction factor for scavenging and detection (25%).

Species Vulnerability to Building Collisions

Of 92,869 records used for analysis, the species most commonly reported as building kills (collectively representing 35% of all records) were White-throated Sparrow (*Zonotrichia albicollis*), Dark-eyed Junco (*Junco hyemalis*), Ovenbird (*Seiurus aurocapilla*), and Song Sparrow (*Melospiza melodia*). However, as expected, there was a highly significant correlation between fatality counts and population size ($r = 0.53$, $P < 0.001$, df =213) and between counts and range overlap with study sites ($r = 0.25$, $P < 0.001$, df = 223). After accounting for these factors, estimated vulnerability across all buildings was highly variable, ranging from 1,066 times more likely to collide than average to 273 times less likely to collide than average (high vulnerability species in Table 4; all values in Tables S3–S6 in Supplemental Material Appendix D).

Several species exhibit disproportionately high vulnerability to collisions regardless of building type, including Ruby-throated Hummingbird (*Archilochus colubris*), Brown Creeper (*Certhia americana*), Ovenbird, Yellow-bellied Sapsucker (*Sphyrapicus varius*), Gray Catbird (*Dumetella carolinensis*), and Black-and-white Warbler (*Mniotilta varia*). Seven species that are disproportionately vulnerable to building collisions are national Birds of Conservation Concern and 10 are listed regionally (Table 4; U.S. Fish and Wildlife Service 2008). Species in the former group include Golden-winged Warbler (*Vermivora chrysoptera)* and Canada Warbler (*Cardellina canadensis*) at low-rises, high-rises, and overall, Painted Bunting (*Passerina ciris*) at low-rises and overall, Kentucky Warbler (*Geothlypis formosa*) at low-rises and high-rises, Worm-eating Warbler (*Helmitheros vermivorum*) at high-rises, and Wood Thrush (*Hylocichla mustelina*) at residences. For species with vulnerability indices calculated from a

TABLE 4. Estimates of species vulnerability to building collisions. Risk values indicate the factor by which species are at a greater risk of collision compared with a species with average risk. Species in boldface italics are Birds of Conservation Concern at the national level and species in boldface are Birds of Conservation Concern in at least one U.S. region (U.S. Fish and Wildlife Service 2008). Scientific names are in Supplemental Material Appendix D.

All buildings		Residences (1–3 stories)		Low-rises		High-rises	
Species	Risk	Species	Risk	Species	Risk	Species	Risk
Anna's Hummingbird[a]	1,066.4	**Purple Finch**	257.2	***Golden-winged Warbler***	141.7	Townsend's Solitaire	167.4
Black-throated Blue Warbler	45.5	Ruby-throated Hummingbird	174.7	***Painted Bunting***	129.3	Black-throated Blue Warbler	78.5
Ruby-throated Hummingbird	37.0	Ovenbird	112.1	Ruby-throated Hummingbird	103.7	Connecticut Warbler	52.0
Townsend's Solitaire	36.3	Brown Creeper	81.1	Black-throated Blue Warbler	86.4	Brown Creeper	44.3
Golden-winged Warbler	35.3	House Finch	80.1	Swamp Sparrow	50.6	Ovenbird	43.7
Painted Bunting	32.1	Black-and-white Warbler	68.7	***Canada Warbler***	46.7	Ruby-throated Hummingbird	43.4
Brown Creeper	26.2	Cedar Waxwing	50.5	**Louisiana Waterthrush**	46.4	***Worm-eating Warbler***	26.5
Connecticut Warbler	22.9	**Field Sparrow**	48.3	Brown Creeper	44.8	***Canada Warbler***	25.8
Ovenbird	21.8	***Wood Thrush***	41.0	**Yellow-bellied Sapsucker**	38.3	Gray Catbird	23.9
Canada Warbler	17.9	Swainson's Thrush	34.7	Connecticut Warbler	35.7	**Yellow-bellied Sapsucker**	23.7
Swamp Sparrow	16.7	Northern Cardinal	27.5	Ovenbird	30.4	***Golden-winged Warbler***	23.1
Yellow-bellied Sapsucker	16.2	Blue Jay	26.5	Sharp-shinned Hawk	27.8	American Woodcock	22.1
Louisiana Waterthrush	14.3	White-breasted Nuthatch	25.0	Rose-breasted Grosbeak	24.1	Common Yellowthroat	20.4
Gray Catbird	12.8	**Yellow-bellied Sapsucker**	22.6	Gray Catbird	23.2	Scarlet Tanager	18.5
Pine Grosbeak[a]	12.4	Northern Waterthrush	22.5	Black-and-white Warbler	22.7	Black-and-white Warbler	18.3
American Woodcock	11.7	Nashville Warbler	22.2	American Woodcock	21.1	Swamp Sparrow	18.1
Pygmy Nuthatch[a]	11.4	Gray Catbird	20.7	***Kentucky Warbler***	20.2	Rose-breasted Grosbeak	16.2
Black-and-white Warbler	11.1	**Northern Flicker**	20.2	Mourning Warbler	19.3	***Kentucky Warbler***	14.0
Pied-billed Grebe[a]	11.0	Downy Woodpecker	18.7	Common Yellowthroat	18.4	**Northern Goshawk**	13.6
Common Yellowthroat	10.9	Black-capped Chickadee	14.9	Cape May Warbler	16.7	**Eastern Whip-poor-will**	13.4

[a] Species is ranked for all buildings but not individual classes because it occurs in $\geq$2 total studies, but $<$2 studies within building class.

relatively small sample of studies (e.g., those noted with a superscript in Table 4), vulnerability indices may be biased. For example, the exceptionally high vulnerability value for Anna's Hummingbird (*Calypte anna*) likely results from this species occurring in only two studies and experiencing exceptionally high mortality in one of these studies.

Vulnerability estimates for taxonomic groups are in Table 5. Several high-risk bird groups are represented in our dataset by only one or two species (e.g., grebes, shorebirds, kingfishers, and gulls and terns); average risk values for these groups may not represent the entire taxonomic family. Other taxa, particularly the hummingbirds and swifts and the warblers, appear especially vulnerable to building collisions, with more than one species ranking in the overall high-vulnerability list. In particular, warblers experience disproportionately high collision risk, with 10 species ranking among the 25 most vulnerable species overall and 12 and 14 species ranking among the 25 most vulnerable species for low-rises and high-rises, respectively. Taxonomic groups with particularly low collision risk include ducks and geese, swallows, herons, upland game birds, and blackbirds, meadowlarks, and orioles.

TABLE 5. Average vulnerability of bird groups to building collisions across all building types. Risk values indicate the factor by which a species has a greater chance (for positive residuals) or a smaller chance (for negative residuals) of mortality compared with a species with average risk.

Group	Residual	Risk
Hummingbirds and swifts	1.52	33.2
Grebes	1.04	11.0
Shorebirds	0.68	4.7
Kingfishers[a]	0.56	3.6
Waxwings	0.55	3.6
Warblers	0.54	3.4
Gulls and terns[a]	0.52	3.3
Nuthatches, tits, and creeper	0.50	3.1
Cuckoos	0.46	2.9
Mimic thrushes	0.41	2.6
Diurnal raptors	0.40	2.5
Cardinaline finches	0.36	2.3
Kinglets	0.36	2.3
Thrushes	0.25	1.8
Cardueline finches	0.23	1.7
Nightjars	0.16	1.4
Woodpeckers	0.15	1.4
Owls	0.10	1.3
Doves and pigeons	0.08	1.2
Sparrows	0.08	1.2
House Sparrow[a]	−0.15	1.4
Wrens	−0.20	1.6
Coots and rails	−0.24	1.7
Flycatchers	−0.41	2.6
Vireos	−0.55	3.6
Starling[a]	−0.56	3.6
Corvids	−0.61	4.1
Blackbirds, meadowlarks, and orioles	−0.64	4.4
Upland game birds	−0.77	5.9
Herons	−1.05	11.3
Swallows	−1.07	11.6
Ducks and geese	−1.25	17.9
Gnatcatchers[a]	−1.68	48.1

[a] Values based on data from a single species.

DISCUSSION

Comparison of Mortality Estimate to Previous Estimates

Our estimate of 365–988 million birds killed annually by building collisions is within the often-cited range of 100 million to 1 billion (Klem 1990a). Other estimates are either outdated (3.5 million, Banks 1979) or are simply a mid-point of the above range (550 million, Erickson et al. 2005). Our larger estimate of low-rise mortality based only on year-round studies suggests that total annual building collision mortality could exceed one billion birds, as suggested by Klem (2009). Using the year-round low-rise estimate results in an annual mortality estimate of up to 1.3 billion birds. Regardless of which figure is interpreted, our results support the conclusion that building collision mortality is one of the top sources of direct anthropogenic mortality of birds in the U.S. Among other national estimates that are data-driven and systematically derived, only predation by free-ranging domestic cats is estimated to cause a greater amount of mortality (Loss et al. 2013). A similar ranking has been made for anthropogenic threats in Canada (Blancher et al. 2013, Machtans et al. 2013). Major sources of direct anthropogenic bird mortality currently lacking systematically derived estimates include collisions with automobiles and other vehicles, collisions and electrocution at power lines, and poisoning caused by agricultural chemicals, lead, and other toxins. Additional systematic quantification of mortality is needed to allow rigorous comparisons among all mortality sources.

A general pattern across and within building classes is that a large proportion of all mortality occurs at structures that kill small numbers of birds on a per-building basis but collectively constitute a high percentage of all buildings (e.g., residences compared to low-rises and high-rises; urban compared to rural residences; residences without feeders compared to those with feeders). This finding suggests that achieving a large overall reduction in mortality will require mitigation measures to be applied across a large number of structures (e.g., urban residences). Our conclusion about the relative importance of residences for causing U.S. mortality is similar to that made for Canada by Machtans et al. (2013). This similarity arises because residences are estimated to comprise a similar proportion of all buildings in both countries (87.5% in the U.S and 95.3% in Canada). Even assuming the low-end mortality estimate for residences (159 million), total mortality at high-rises would have to be 100 times greater than our high-end estimate for that building class (1.6 million) for the two building classes to cause equivalent mortality. On a per-building basis, if each residence killed one bird per year, each high-rise would have to kill >5,800 birds per year to cause equivalent mortality. No evidence exists that high-rises kill this large number of birds.

The species composition of window collision mortality also differs by building class. While the high risk group for individual residences includes several non-migratory resident species—including Downy Woodpecker (*Picoides pubescens*), Black-capped Chickadee (*Poecile atricapillus*), and Northern Cardinal (*Cardinalis cardinalis*)—nearly all high-risk species for low-rise and high-rise buildings are migratory. Compared with resident species, migratory species traverse longer distances, use a greater diversity of habitat types, and encounter more building types and total buildings during the annual cycle. Additionally, migratory species are attracted to large lighted buildings during their nocturnal migration; this attraction causes a large amount of mortality at low-rises and high-rises as birds either immediately collide with lighted buildings or become entrapped before later dying of collision or exhaustion (Evans Ogden 1996). The greater representation of resident species in the high-risk group for residences may be due to the propensity for many of these species to congregate at bird feeders, a behavior that may place them at a greater risk of colliding with windows (Dunn 1993, Klem et al. 2004, Bayne et al. 2012).

Despite the critical importance of reducing mortality at residences, mitigation measures targeted at a relatively small number of buildings with high per-building mortality rates (e.g., some high-rises and low-rises) will likely result in large per-building reductions in mortality and therefore may represent a cost-efficient starting point for reducing mortality. The mortality proportions that we attribute to different residence types are similar to those estimated by Machtans et al. (2013). This result arises from both the previous study and ours basing analysis on Bayne et al. (2012), a Canadian study that provides a reasonable approximation of U.S. mortality rates as evidenced by rates documented in U.S. studies (Dunn 1993, Weiss and Horn 2008, Bracey 2011).

Species Vulnerability to Building Collisions

Our vulnerability analysis indicates that several species experience a disproportionately high risk of building collision mortality. Of particular concern within the list of high-risk species (Table 4) are those identified as national Birds of Conservation Concern (species likely to become candidates for listing under the U.S. Endangered Species Act without further action based on population trends, threats to populations, distribution, abundance, and relative density; U.S. Fish and Wildlife Service 2008). For species that are vulnerable to collisions at more than one building class or overall, including Golden-winged Warbler, Painted Bunting, Kentucky Warbler, and Canada Warbler, building collision mortality appears substantial and may contribute to or exacerbate population declines. For species identified as highly vulnerable to collision for one building class but not across building types (Wood Thrush at residences, Worm-eating Warbler at high-rises), building collisions may still represent a threat. However, risk rankings for these species are more likely to be inflated by high mortality rates at a few sites, and further research is required to clarify the degree to which populations of these species are threatened by collision mortality.

Inferences about population impacts of a mortality source should ideally be based on incorporating mortality estimates into demographic models (Loss et al. 2012) or comparing estimates to population abundance (Longcore et al. 2013). Data limitations preclude intensive population modeling of building collision impacts. Sampling bias toward densely populated areas east of the Mississippi River, and therefore toward certain bird species, prevented us from estimating species-specific annual mortality. We initially attempted to apply average species proportions to the overall mortality estimate following Longcore et al. (2013), but this method returned unrealistically high estimates for species that comprised a high percentage of counts in many studies (e.g., 140% of the total population of Ovenbirds estimated to be killed each year by building collisions). Our vulnerability estimates controlled for abundance and range overlap with study sites and therefore provide a less biased approximation of species-specific collision risk.

Our vulnerability analysis expanded upon the analysis of Arnold and Zink (2011), which was based on three sites in the northeastern U.S. and adjacent Canada. Nonetheless, we documented some of the same vulnerable species, including Brown Creeper, Black-throated Blue Warbler (*Setophaga caerulescens*), and Swamp Sparrow (*Melospiza georgiana*), and similar high- and low-risk taxonomic groups (e.g., warblers and swallows, respectively). As in the previous study, the vast majority of highly vulnerable species were long-distance migrants. Unlike the previous study, we did not assess whether population trends were correlated with building collision vulnerability. This approach has received criticism (Schaub et al. 2011, Klem et al. 2012) and shifts focus away from identifying which individual species of conservation concern face a high risk of colliding with buildings.

Research Needs and Protocol Improvements

Sensitivity analyses indicated that more research of mortality rates at low-rises will contribute greatly to improving mortality estimates. Future research should sample a variety of low-rise types, including residential, commercial, and industrial buildings. Research at low-rises has occurred mostly at buildings that are known to cause large numbers of fatalities (e.g., office or university campus buildings with many windows and/or near favorable bird habitat). Random selection of buildings for monitoring (for all building classes) allows for less-biased conclusions about local mortality rates and more reliable extension of results within study areas and across regions. Mortality data specific to different low-rise building types will allow improvement upon the current approach of assuming that all low-rise buildings have similar mortality rates. Because we based our low-rise estimate on the number of U.S. "establishments," and because the relationship between numbers of establishments and numbers of buildings is unknown, we suggest that improved data be collected and made available for the number of U.S. low-rise buildings. Non-residential low-rises are not currently included in assessments by the U.S. Census Bureau.

Sensitivity analyses also indicate that mortality estimates will benefit from quantification of searcher efficiency and scavenger removal rates. Recent research has resulted in major advancements in understanding these biases, including studies that estimate carcass detection and/or scavenger removal rates (Collins and Horn 2008, Hager et al. 2012, 2013) or apply methods to simultaneously account for both biases (Bracey 2011, Etterson 2013). In the future, studies should account for these biases when possible and investigate how these rates are affected by size and species of carcasses, abundance and community composition of scavengers, and characteristics of vegetation and habitat near buildings.

A large portion of the unpublished data we used were collected by volunteer-led collision-monitoring programs in major cities. These citizen-science programs have contributed greatly to the understanding of bird–building collisions; however, standardization of data collection and recording procedures is necessary to make these data more comparable across programs and across years within programs. As a first step, all monitoring programs should record sampling effort, including (1) a record of all surveys conducted, even those with zero fatalities found; (2) the number of person-hours of sampling in every survey; (3) the number of buildings and building facades sampled; (4) street addresses of buildings (with attention to avoiding multiple addresses referring to one building and clarifying when one address includes >1 building); and (5) separate records of fatalities found during surveys on official routes and those found incidentally outside of survey periods and/or off of routes. This information will allow increased comparability of data among regions, improved understanding of seasonal and regional mortality patterns, and reduced bias in estimates of per-building mortality rates and overall mortality. Combining effort-corrected mortality data with information about buildings (e.g., height in stories and meters; orientation and area of building facades; glass area, type, extent, and reflectivity; vegetation presence, type, density, and height; and amount of light emitted), will allow identification of mortality rate correlates, prediction of mortality rates from building characteristics, and implementation of techniques to reduce mortality. Monitoring programs could also expand to incorporate sampling at multiple building types, including individual residences and additional types of low-rises and high-rises. A national reporting system and database for bird mortality data would facilitate standardization of data collection for building collisions and other mortality sources (Loss et al. 2012). Until this type of comprehensive system is developed and launched, window collision monitoring programs can use simple user-defined data entry portals that will increase standardization of data recording, formatting, and compilation (see example at https://docs.google.com/spreadsheet/viewform?usp=drive_web&formkey=dDA1dDVTSVUzS1NfX0NxWmZxTEctbHc6MQ#gid=0), and therefore benefit research that synthesizes multiple datasets.

Model Limitations

Because data collection methods varied greatly among studies, we could not account for all differences among the datasets we synthesized. How this limitation influenced our estimates is unclear. Nonetheless, our inclusion criteria removed studies that lacked a systematic component to sampling, and we accounted for partial-year sampling by either estimating mortality using only year-round studies or applying correction factors to mortality estimates. We also accounted for sample size differences when estimating species vulnerability. However, the data we analyzed overrepresented the eastern U.S. and underrepresented the Great Plains, Interior West, and West Coast. Because of this data limitation, the mortality rate distributions that we applied to all U.S. buildings were primarily based on data from the eastern U.S. This could have biased our estimates if mortality rates in the West differ consistently from those documented in the East; however, the lack of western data prevents conclusions about such regional variation. In addition, our species vulnerability estimates do not cover species with a large proportion of their range in the West. Further research of bird–building collisions in areas west of the Mississippi River is needed to document whether per-building mortality rates differ consistently from those in well-studied regions of the east and to assess building collision vulnerabilities for western bird species. Our mortality estimates are limited by the assumption that all non-residential establishments listed by the U.S. Census Bureau are ≤11 stories tall and that all buildings sampled by monitoring programs in major downtown areas are >12 stories tall. These assumptions were unavoidable because U.S. low-rise building data are not available and building height information was not recorded in most studies.

Our mortality estimates may be conservative because data from buildings that cause exceptionally high annual rates of collision were removed from our analysis before extending average rates to the scale of the entire U.S. Hundreds to greater than one thousand birds per year have been found at intensively monitored buildings in or near areas with a high concentration of birds during migration (e.g., Taylor and Kershner 1986, M. Mesure and D. Willard personal communication). Other factors that may have contributed to underestimation include crippling bias (e.g., an uncertain percentage of birds fly away from sampling areas before dying) and sub-lethal effects that may influence social interactions and migration behavior even if not causing eventual death (Klem 1990b). Further research to quantify crippling bias and sub-lethal effects is crucial for continued improvement in the accuracy of mortality and species vulnerability estimates.

Finally, we were unable to quantify seasonal patterns of mortality due to a limited sample of studies that surveyed throughout the year. Additionally, several studies employed varying sampling effort across seasons and did not record effort data that could be used to account for this variation. Among records meeting our inclusion criteria, 60.0% were found during fall migration (August–November) and 37.0% were found during spring migration (March–May). These figures are likely inflated relative to non-migratory periods because most studies sampled only during spring and fall. Despite varying sampling effort among seasons, mortality during fall migration appears to be consistently greater than during spring migration; this pattern was seen in most of the datasets and could be related to larger populations of birds in the fall due to presence of young-of-the-year birds. Notably, several studies have indicated substantial building collision mortality during periods outside of migration, including in winter at individual residences (Dunn 1993, Klem 2009) and in summer at low-rise buildings (Bayne et al. 2012, Hager et al. 2013). Our methods accounted for partial-year sampling by either using only year-round studies (for residences and low-rises) or applying a correction factor that assumed additional mortality during summer and winter (for high-rises, a building type for which little data exists for non-migration periods). Species vulnerability estimates were also likely to be influenced by seasonal sampling biases, with in-transit migratory species likely overrepresented compared with summer and winter residents. Additional year-round studies are needed at all building types to clarify how mortality rates and species composition of fatalities vary by season.

Conclusions

As human populations and numbers of buildings increase in the U.S. and globally, actions to reduce bird mortality from building collisions will be necessary at all types of buildings. For residences, mitigation techniques could include reducing vegetation near windows, angling windows to reduce reflection, and installing netting, closely spaced decals, or UV light-reflecting glass (Klem et al. 2004, Klem 2006, 2009). For low-rises and high-rises, mortality can be reduced by minimizing light emission at night (Evans Ogden 1996, 2002) and incorporating bird friendly design elements into new and existing buildings (e.g., Brown and Caputo 2007, Sheppard 2011). A long-term approach to reducing mortality is the continued adaptation of Green Building certification standards to include bird collision risks (Klem 2009).

We provide quantitative evidence of the large amount of bird mortality caused by building collisions in the U.S. Our estimates represent roughly 2–9% of all North American birds based on a rough estimate of 10–20 billion total birds in North America (U.S. Fish and Wildlife Service 2002). However, because our results illustrate that not all species are equally vulnerable to building collisions, and because considerable uncertainty remains regarding species-specific mortality and population abundance, the actual impacts of collisions on population abundance are uncertain. Despite this uncertainty, our analysis indicates that building collisions are among the top anthropogenic threats to birds and, furthermore, that the several bird species that are disproportionately vulnerable to building collisions may be experiencing significant population impacts from this anthropogenic threat.

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