

1 **Factors influencing bird-building collisions in the downtown area of a major North**  
2 **American city**

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4 **Short title:** Bird-building collisions in a major city

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## 28 **Abstract**

29 Bird-building collisions are the largest source of avian collision mortality in North America.  
30 Despite a growing literature on bird-building collisions, little research has been conducted in  
31 downtown areas of major cities, and no studies have included stadiums, which can be extremely  
32 large, often have extensive glass surfaces and lighting, and therefore may cause many bird  
33 collisions. Further, few studies have assessed the role of nighttime lighting in increasing  
34 collisions, despite the often-cited importance of this factor, or considered collision correlates for  
35 different seasons and bird species. We conducted bird collision monitoring over four migration  
36 seasons at 21 buildings, including a large multi-use stadium, in downtown Minneapolis,  
37 Minnesota, USA. We used a rigorous survey methodology to quantify among-building variation  
38 in collisions and assess how building features (e.g., glass area, lighting, vegetation) influence  
39 total collision fatalities, fatalities for separate seasons and species, and numbers of species  
40 colliding. Four buildings, including the stadium, caused a high proportion of all collisions and  
41 drove positive effects of glass area and amount of surrounding vegetation on most collision  
42 variables. Excluding these buildings from analyses resulted in slightly different collision  
43 predictors, suggesting that factors leading some buildings to cause high numbers of collisions are  
44 not the exact same factors causing variation among more typical buildings. We also found  
45 variation in collision correlates between spring and fall migration and among bird species, that  
46 factors influencing collision fatalities also influence numbers of species colliding, and that the  
47 proportion, and potentially area, of glass lighted at night are associated with collisions. Thus,  
48 reducing bird collisions at large buildings, including stadiums, should be achievable by reducing  
49 glass area (or treating existing glass), reducing light emission at night, and prioritizing mitigation  
50 efforts for glass surfaces near vegetated areas and/or avoiding use of vegetation near glass.

## 51 **Introduction**

52 Up to 1.5 billion birds are killed annually in North America by colliding with vehicles and  
53 human-made structures, including buildings, communication towers, and energy infrastructure  
54 [1-3]. Bird-building collisions, particularly collisions with windows and other reflective surfaces,  
55 are by far the largest source of avian collision mortality, annually causing 365 to 988 million bird  
56 fatalities in the United States [4] and 16 to 42 million fatalities in Canada [5]. Bird-building  
57 collisions are most frequent in urban areas containing many residential and commercial  
58 structures; however, the species most frequently killed, as well as those appearing most  
59 vulnerable to population-level impacts of building collision fatalities, are migratory birds that  
60 collide during spring and fall while in transit between breeding and nonbreeding grounds (e.g.,  
61 hummingbirds, warblers, thrushes, and native sparrows) [4, 6].

62 Rates of bird-building collisions are influenced by many factors that interact across  
63 multiple spatial and temporal scales. At small scales, collisions are influenced by features of  
64 buildings (e.g., size, height, and window/glass area) [7-8] and their immediate surroundings (e.g.,  
65 nearby vegetation and greenspace) [9-13]. Such small-scale effects also appear to be mediated by  
66 regional patterns of urbanization and greenspace [14]. Collisions also vary through time in  
67 relation to bird migratory movements and changes in weather, bird behavior, and human-related  
68 factors that influence bird migration, behavior, and habitat use (e.g., use of ornamental  
69 vegetation, bird feeders, and artificial light at night, which confuses and attracts nocturnally  
70 migrating birds, elevating collision risk) [15-18]. Collisions are also influenced by the abundance  
71 of birds near buildings [19-21] and by traits of birds themselves, including visual perceptual  
72 ability [22-23] and life history (e.g., residency status, migratory strategy) [24-26].

73           Despite a growing literature on bird-building collisions, many important information gaps  
74 remain. First, few replicated, standardized studies have been conducted in downtown areas of  
75 major cities, where per building collision rates peak [4] likely as a result of the large size of  
76 buildings and intense nighttime lighting [27-28]. Second, few studies have investigated collisions  
77 | at large buildings other than skyscrapers ~~{~~(but see [10, 20]), and none have focused on a stadium.  
78 | Research at stadiums would be beneficial because, in addition to their large size, many of the  
79 hundreds of existing and planned stadiums in North America have extensive glassy surfaces and  
80 are brightly illuminated by external and internal lighting during spring and/or fall migration  
81 periods. Many stadiums thus appear capable of causing high bird collision rates. Third, while  
82 nighttime lighting is frequently cited as a factor contributing to building collisions, few formal  
83 | assessments have been conducted ~~{~~(but see [18, 29]). Fourth, most collision studies, including  
84 | the most rigorous studies in downtown areas [7, 21, 30], have not accounted for scavenger and  
85 human removal of bird carcasses between collision surveys or for imperfect detection of  
86 carcasses that are present. Failing to account for these factors causes underestimation of  
87 collisions and can mislead comparisons among buildings [31-33]. Further, rates of human  
88 removal of bird carcasses (e.g., by cleaning crews) are often much greater in downtown areas  
89 than on university campuses or in residential neighborhoods where past removal studies were  
90 conducted. Fifth, few studies of bird-building collisions have gone beyond assessing factors  
91 influencing total collisions to also investigate collision correlates for different seasons and bird  
92 species. Such information would provide valuable insight into developing effective collision  
93 reduction approaches that target certain seasons (e.g., fall migration, when collisions peak in  
94 most regions) and species (e.g., endangered/declining species with collision correlates that may  
95 differ from common species). Finally, although species composition of birds killed at windows

96 appears influenced by features of the surrounding landscape [25], no studies have formally  
97 investigated how building and landscape-related factors influence the number of species that  
98 collide at a building.

99 To address these research gaps, we conducted a bird collision monitoring study that  
100 covered four migration seasons and included 21 buildings, including a large multi-use stadium,  
101 in downtown Minneapolis, Minnesota, USA. We used a rigorous methodology that included  
102 daily standardized collision surveys at all buildings and experimental trials to estimate and  
103 account for removal and imperfect surveyor detection of bird carcasses. Our research questions  
104 were: (1) How do numbers of bird collisions vary among the monitored buildings? (2) What  
105 building features (e.g., height, glass area, nighttime lighting, and surrounding vegetation and  
106 greenspace) influence collision fatalities, including total fatalities, fatalities in spring and fall,  
107 and fatalities for the most frequently colliding species? and (3) What building features influence  
108 numbers of species that collide, including overall and in spring and fall?

109

## 110 **Materials and methods**

### 111 **Study area and design**

112 We conducted bird collision monitoring at 21 buildings in downtown Minneapolis,  
113 Minnesota (44.9772 ° N, 93.2637° W), which is immediately west of the Mississippi River—the  
114 largest river system in North America and an important bird migration corridor—and is part of  
115 the Minneapolis-St. Paul (Twin Cities) metropolitan region (population = ~3.1 million people).  
116 The Twin Cities are located near the intersection of the North Central Hardwoods and Western  
117 Corn Belt Plains Level III Ecoregions of the United States [34]; non-urban land cover types

118 surrounding and within the Twin Cities include forests and woodlands dominated by deciduous  
119 species, numerous lakes and wetlands, extensive croplands, and limited grassland cover.

120 Due to interests of the funding organizations, U.S. Bank Stadium formed the initial basis  
121 for the research and was therefore non-randomly selected to be studied. This indoor stadium was  
122 completed in summer 2016. Concerns about the risk of bird collisions at the stadium were raised  
123 in 2012 [35] and repeated in 2013 when the stadium design was revealed to have several  
124 elements making it likely to cause bird collisions [36]. These elements include approximately  
125 18,000 m<sup>2</sup> (i.e., 1.8 ha, or ~37% of the stadium's vertical surfaces) of highly reflective glass  
126 surfaces throughout the building's exterior—including approximately 6,000 m<sup>2</sup> of uninterrupted  
127 glass on one portion of the stadium's northwest façade, which faces an open park space with  
128 trees and manicured lawns—and the use of LED lighting at night inside, outside, and directed  
129 onto the stadium, and in ground-based lighting features on the stadium grounds.

130 In addition to the stadium, 20 buildings were selected for monitoring (Fig 1). Sixteen of  
131 these were selected from a set of 64 downtown Minneapolis buildings that were monitored for  
132 collisions from 2007 to 2016 for Project BirdSafe, a research, outreach, and education program  
133 with the goals of increasing awareness of the bird collision issue and working with building  
134 managers and policy makers to develop and implement collision reduction guidelines [37]. These  
135 64 buildings were grouped into quintiles (groupings of 0-20%, 20-40%, etc.,) using total  
136 collisions observed from 2007 to 2015; we did not use 2016 Project BirdSafe data because  
137 fieldwork was ongoing when we began designing the current study in fall 2016. From each  
138 quintile, we randomly selected three buildings (15 total) with the constraints that: (1) building  
139 perimeters at ground level were 50-100% accessible (this range of percentages balanced the need  
140 for building access with the need to include a large enough sample of buildings for each

141 quintile); and (2) buildings captured a broad spatial representation of the downtown area,  
142 especially with regard to distance to the Mississippi River, a factor we expected to influence  
143 collisions due to the importance of this corridor for migratory birds [38]. Shortly after study  
144 initiation, we selected one additional building from the 80-100<sup>th</sup> percentile because part of one  
145 originally-selected building from this quintile was inaccessible in spring 2017. Because the  
146 stadium was spatially separate from these other buildings, we also selected four previously  
147 unmonitored buildings within 0.7 km of the stadium and under the same access constraint as  
148 above. The resultant 20 buildings represented a variety of structures typical to downtown areas;  
149 they ranged from 2 to 57 stories and included hotels, apartments, and office buildings (building  
150 characteristics in Table 1).

151

152 **Fig 1. Study area.** (a) General location of study area in the United States and (b) location of  
153 study area containing 21 buildings, including U.S. Bank Stadium (large, gray, irregularly shaped  
154 building in lower right of image), monitored for bird collisions in downtown Minneapolis,  
155 Minnesota, USA, 2017-2018; (image sources: USGS National Map Viewer base map [\(a\)](#) and  
156 NAIP Plus aerial imagery [\(b\)](#)).

157 **Table 1. Characteristics of monitored buildings.**

Building ID <sup>a</sup>	Quintile <sup>b</sup>	Height (m) <sup>c</sup>	Glass area (m <sup>2</sup> ) <sup>d</sup>	Area light <sup>e</sup>	Prop. light <sup>f</sup>	Footprint (m <sup>2</sup> ) <sup>g</sup>	Distance to river (m) <sup>h</sup>	Prop. vegetation <sup>i</sup>	
								50 m buffer	100 m buffer
1 (Stadium)	NA	83	11,319	7,722	0.68	51,863	612	0.16	0.10
2	1	26	980	494	0.50	5,956	955	0.01	0.02
3	5	139	4,255	996	0.23	3,233	998	0.22	0.10
4	5	241	16,913	2,454	0.15	2,415	1,096	0.00	0.01
5	3	19	1,825	232	0.13	2,576	494	0.02	0.02
6	4	127	1,434	624	0.44	4,727	660	0.00	0.01
7	2	95	682	128	0.19	1,029	831	0.00	0.00
8	2	46	782	375	0.48	1,583	999	0.00	0.01
9	5	64	3,476	1,112	0.32	3,835	857	0.03	0.03
10	4	73	452	234	0.52	1,522	761	0.01	0.01
11	4	34	2,165	367	0.17	1,504	553	0.06	0.03
12	3	30	1,947	895	0.46	2,725	538	0.02	0.03
13	1	61	1,651	1,317	0.80	5,762	1,368	0.00	0.00
14	1	26	452	172	0.38	4,294	1,290	0.01	0.01
15	3	171	8,245	1,772	0.21	3,724	741	0.00	0.00
16	2	12	296	23	0.08	1,505	1,407	0.04	0.03
17	5	123	6,537	4,277	0.65	4,615	811	0.19	0.12
18	NA	29	773	233	0.30	1,636	338	0.00	0.01
19	NA	92	3,698	261	0.07	5,461	451	0.03	0.12
20	NA	15	4,476	1,048	0.23	5,779	385	0.04	0.05
21	NA	19	933	377	0.40	2,799	398	0.00	0.00

158 Characteristics of 21 buildings, including U.S. Bank Stadium, monitored for bird collisions in  
 159 downtown Minneapolis, Minnesota, USA, 2017-2018.

160 <sup>a</sup>Unique numeric code for each building used for purposes of current study

161 <sup>b</sup>For buildings previously monitored in Project BirdSafe, the quintile into which they were placed for  
 162 stratified random selection approach in the current study (see text for details); quintiles are based on total  
 163 collisions observed across 64 buildings originally monitored in that earlier study (1 = 0-20 percentile of  
 164 observed collisions; 2 = 20-40%; 3 = 40-60%; 4 = 60-80%; 5 = 80-100%; NA indicates buildings with no  
 165 past history of collision monitoring)

166 <sup>c</sup>Estimated height of the main roof of the building

167 <sup>d</sup>Total estimated area of glass (including windows and other glass surfaces) across all building facades,  
 168 excluding glass recessed from the main façade for which collision casualties were likely to land on  
 169 elevated surfaces not covered by surveys

170 <sup>e</sup>Area of all windows emitting artificial light during nighttime periods

171 <sup>f</sup>Proportion of all glass surfaces emitting artificial light during nighttime periods (calculated by dividing  
 172 Area light by Glass area)

173 <sup>g</sup>Horizontal ground area covered by the building (based on building's outer edge)

174 <sup>h</sup>Distance from building centroid to nearest edge of the Mississippi River corridor

175 <sup>i</sup>Proportion of land covered by vegetation within 50 and 100m of building (includes grass/shrub and  
 176 deciduous/coniferous trees; excludes bare soil, roads and other paved surfaces, and other buildings)



## 177 **Collision surveys**

178           We conducted daily collision monitoring at all 21 buildings during spring migration (15  
179 Mar-31 May), early summer (1-30 Jun), and fall migration (15 Aug-31 Oct) of 2017 and 2018.  
180 We did not conduct monitoring in July or from November to early-March because relatively few  
181 collisions occur during these periods, both in downtown Minneapolis and elsewhere in central  
182 North America [3, 37]. There were some days within the above date ranges for which we were  
183 unable to survey all or a portion of some buildings due to safety considerations (e.g.,  
184 construction or maintenance activities) or security measures associated with major events.  
185 However, the statistical estimator we used to adjust raw fatality counts for carcass removal and  
186 detection rates (see following sub-sections) accounted for this issue by allowing specification of  
187 varying time intervals between carcass searches.

188           We used a standardized survey protocol adapted from [39]. One day prior to each spring  
189 and fall season, “clean sweep” surveys were conducted in which we removed all bird carcasses  
190 and remains to avoid counting birds from non-surveyed periods. In spring 2017, buildings were  
191 split into two fixed routes, and the order in which they were surveyed was shifted by one  
192 building each day to account for time-of-day effects such as different patterns of human removal  
193 of bird carcasses at different buildings. In June 2017, the two routes were merged for the  
194 remainder of the study, and we used a random number generator to select the start building each  
195 day—with the exception of several days in fall 2017 when maintenance activities at the stadium  
196 required us to start there in order to avoid missing a survey. Throughout the study, we alternated  
197 the direction that building perimeters were monitored (clockwise on even dates; counter-  
198 clockwise on odd dates) to account for directional effects that could influence carcass detection,  
199 such as shading or physical obstructions. Surveys began at approximately sunrise and took 1.5 to

200 4 hours to complete depending on numbers of birds encountered. On a subset of days, we also  
201 conducted midday surveys (start time: 1000-1500 h) and evening surveys (start time: 1600-1800  
202 h) at all buildings.

203 On all surveys, trained technicians or the authors searched for birds within ~5 m of all  
204 publicly accessible portions of building exteriors. For all carcasses or bird parts encountered, the  
205 location was marked on a building map and carcasses/remains were placed in a plastic bag and  
206 stored in a freezer until species identification was confirmed by the authors. We recorded bird  
207 carcasses with signs of dismemberment because, even though some of these could have resulted  
208 from predation events, we believed some likely represented collision victims that were  
209 scavenged by animals. We also recorded birds found below skyways (i.e., elevated glass  
210 walkways connecting to buildings) if it was uncertain whether the bird had collided with the  
211 skyway or the building itself. As described under “Bias-adjusted fatality estimates,” we  
212 generated separate collision counts that included and excluded these potential predation events  
213 and skyway collisions. When we found an injured bird, we attempted to catch it. Captured birds  
214 were placed in an uncoated paper bag, and those that recovered sufficiently were released later  
215 the same day in parks outside of downtown Minneapolis. Birds that did not recover sufficiently  
216 to be released were submitted to a wildlife rehabilitation center.

217 For the stadium, which experienced a large volume of foot traffic by the public, stadium  
218 staff, and contractors, we implemented an additional protocol for carcasses encountered by staff  
219 and contractors. Specifically, we asked the coordinator of stadium operations to periodically  
220 remind staff and contractors about the collision study and direct that any dead birds encountered  
221 be left in place when possible. In cases where it was deemed necessary to remove a bird, the  
222 carcass was to be submitted to central operations staff and stored in a freezer until collected by

223 the authors. Given the difficulty of communicating this protocol to the hundreds of full-time,  
224 temporary, and touring staff that worked at the stadium over the two years of the study, this  
225 approach undoubtedly missed some human-removed bird carcasses. However, the design of our  
226 carcass removal experiment (see following sub-section) allowed us to account for both scavenger  
227 and human removal of carcasses at all buildings, including the stadium.

228         Because all fieldwork was conducted in publicly accessible areas of building exteriors, no  
229 specific access permissions were required. The study did not involve endangered species but did  
230 include many bird species protected under the U.S. Migratory Bird Treaty Act; therefore,  
231 permission to handle and collect these birds was obtained under U.S. Fish and Wildlife Service  
232 Scientific Collecting Permits (#MB05120C-1 and #MB54075B-1) and a Minnesota Department  
233 of Natural Resources Salvage Permit (#20412). Animal procedures were also approved by the  
234 Institutional Animal Care and Use Committee at Oklahoma State University (#AG-17-6).

235

## 236 **Experimental trials to quantify human and scavenger removal of** 237 **carcasses**

238         To quantify and account for human removal and animal scavenging of bird carcasses  
239 between surveys, we conducted experimental removal trials at all buildings and in all monitoring  
240 seasons. To minimize variation in visual and olfactory cues available to scavengers, the vast  
241 majority of trials used fully intact carcasses that likely resulted from a collision during the  
242 previous inter-survey period; these birds were left in place for trials. A small number of trials  
243 used carcasses that were collected during previous surveys, stored in a freezer, and thawed prior  
244 to the trial; however, these were also fully intact with fresh plumage and no signs of  
245 decomposition. All birds were marked as removal trial carcasses by affixing a tag to one leg. In

246 addition to recording the above data associated with collision surveys, we recorded a unique  
247 alphanumeric code to track the status of each trial carcass on subsequent surveys. Selection of  
248 carcasses for inclusion in removal trials was non-random and based on the need for an adequate  
249 sample of trial carcasses for each building and season. Typically, the first carcass found at each  
250 building in each season was left in place for a removal trial, and additional trial carcasses were  
251 selected on varying schedules for different buildings, depending on observed numbers of  
252 collision fatalities. For example, at buildings with few collision fatalities observed, a higher  
253 proportion of carcasses were left in place than at buildings with many fatalities. Preliminary  
254 observations from Project BirdSafe indicated that bird carcasses in downtown Minneapolis are  
255 primarily removed by humans. Nonetheless, we sought to avoid bias in removal estimates that  
256 arises through “swamping” of animal scavengers (i.e., using more trial carcasses than can be  
257 removed by scavengers) [40] by ensuring there was never more than one trial carcass in place at  
258 any individual building façade or 11 carcasses simultaneously in place across the study area.

259 Notably, this maximum of 11 trial carcasses occurred only once on a morning we documented 48  
260 bird collisions; thus, the number of trial carcasses we used was well below the maximum number  
261 of carcasses the scavenger community could potentially encounter on a single day. Trial  
262 carcasses included a variety of species commonly killed by window collisions and represented a  
263 range of colorations (from drably colored sparrows to brightly colored warblers and buntings)  
264 and body sizes and masses (from hummingbirds and warblers to doves and woodcocks).

265       Once removal trial carcasses were marked, surveyors noted their presence or absence on  
266 each successive morning survey up to seven days after trial initiation, at which point remaining  
267 carcasses were retrieved and stored in a freezer or discarded if the carcass had substantially  
268 decomposed. We followed scavenging definitions in [33]. Specifically, carcasses were

269 considered present if all or some of the carcass remains were detectable in the same place, or if  
270 they had been moved, within the survey area (i.e., within ~5 m of the building). Carcasses were  
271 considered removed if no detectable remains persisted within the survey area.

272

## 273 **Experimental trials to quantify surveyor detection of carcasses**

274 To quantify and account for imperfect detection of bird carcasses present during collision  
275 surveys, we conducted experimental surveyor detection trials for all buildings and seasons. For  
276 each trial, a bird carcass collected in the current study, during Project BirdSafe, or incidentally  
277 outside of formal monitoring, was tagged on one leg with a unique alphanumeric code  
278 identifying it as a detection trial carcass, and placed by the trial coordinator (a technician or one  
279 of the authors) within a building's survey area 0.5-1 hr before the start of a survey. Locations for  
280 trials were selected non-randomly to ensure adequate replication for each season and to capture a  
281 variety of surfaces on which carcasses were found (e.g., rocks, bare soil, pavement). Carcasses  
282 were also selected non-randomly to capture a range of colorations and body sizes/masses similar  
283 to that captured in the removal trials. At each trial location, a carcass was placed on the ground  
284 with the ventral side downward to conceal the tag. Throughout the study, surveyors were  
285 reminded that detection trials could occur at any time, but only the trial coordinator was aware of  
286 the date and location of specific trials. Upon encountering a detection trial carcass, surveyors  
287 picked it up, recorded the identification code, and alerted the trial coordinator that they had  
288 found it. When a detection trial carcass was not found, the trial coordinator returned to the  
289 placement location to determine if it had been removed. If the carcass was still present, we  
290 determined the surveyor had failed to detect it, but if the carcass was removed, we assumed it  
291 was unavailable for surveyors to detect and excluded the trial from detection rate calculations.

292 Trial carcasses that were found were either disposed of, or if still in good condition, collected for  
293 reuse in future detection trials.

294

## 295 **Measuring potential correlates of bird-building collisions**

296 We measured several variables to assess factors influencing bird-building collisions. For  
297 all building façades (i.e., discrete faces of buildings oriented in different directions), we used  
298 ImageJ [41] to measure glass area (including windows and other glass surfaces) based on digital  
299 photographs with a known-length reference object and taken in the daytime at an angle as close  
300 to perpendicular as possible to minimize image distortion. We calculated total glass area for each  
301 building by summing façade-level measurements. We also used ImageJ to estimate the area of  
302 each building’s windows that emitted light at night. We took at least three digital photographs of  
303 each building façade during nighttime hours, with at least one photo taken on a weekday and one  
304 taken on a weekend. All photos were taken at least one hour after sunset between 2045 and 2345  
305 hr from 5 Sep 2017 to 5 Sep 2018. For each image, we calculated the area of windows that  
306 emitted any light. Because we observed night-to-night lighting variation, we averaged lighted  
307 area estimates across all dates for each building. We also generated an estimate of the proportion  
308 of building glass lighted (hereafter “proportion lighted”) by dividing lighted window area by  
309 total glass area. Finally, we characterized building height and horizontal ground area (i.e.,  
310 footprint) because these size-related factors have previously been shown to influence collisions  
311 [14]. For height, we obtained maximum building height from either publicly accessible online  
312 sources (for 18 buildings) or using the 3D Building layer and 3D path ruler in Google Earth Pro  
313 7.3.2.5491 (for 3 buildings). We used a building polygon shapefile in ArcGIS 10.1 [42] to  
314 calculate building footprints.

315 In addition to the above building features, we calculated three variables representing the  
316 interaction between buildings and their surrounding environment. We used ArcGIS 10.1 and 1-m  
317 resolution 2015 land cover data for the Twin Cities region [43] to estimate the distance of each  
318 building to the Mississippi River based on building centroids. We used this same land cover data  
319 to estimate the proportion of land covered by vegetation—including grass, shrubs, and  
320 deciduous and coniferous tree canopy; and excluding bare soil, other buildings, and roads and  
321 other paved surfaces—within 50 and 100 m of the outer edge of each building. These distance  
322 buffers were selected because previous literature has suggested vegetation cover within 50 m can  
323 influence bird-building collisions [14], because we also sought to consider potential effects of  
324 vegetation cover at a scale broader than that captured by the 50 m buffer, and because buffers  
325 larger than 100 m overlapped substantially due to the proximity of many buildings to each other.  
326 Substantial land cover changes have occurred in areas surrounding the stadium since its  
327 construction began in 2015, the most recent year for which high-resolution land cover data were  
328 available. To incorporate these changes in calculations of vegetation cover proportions, we used  
329 ArcGIS’s built-in aerial imagery base map, which reflected land cover in Jan 2018, and we  
330 manually digitized a polygon shape file of new land covers near the stadium. We converted this  
331 shape file to a raster file and merged it with the 2015 land cover layer with the ArcGIS “mosaic  
332 to new raster” tool.

333

### 334 **Bias-adjusted fatality estimates**

335 We generated bias-adjusted collision fatality estimates and conducted statistical analyses  
336 in R version 3.6.1 [44]. For each building, we first calculated raw counts of both fatal and non-  
337 fatal collisions across all morning, midday, and evening surveys. We generated low and high

338 counts based on exclusion or inclusion, respectively, of birds potentially resulting from predation  
339 events (for fatal collisions) or collisions with skyways (for fatal and non-fatal collisions). We  
340 used fatal collision counts to generate adjusted fatality estimates that account for human and  
341 scavenger removal of carcasses between surveys and for observer detection probability of  
342 carcasses present during surveys. We generated these bias-adjusted estimates using the GenEst  
343 statistical estimator [45], which allows modeling of carcass persistence and detection  
344 probabilities as a function of one or more covariates. This estimator also accounts for varying  
345 time intervals between surveys when estimating carcass persistence probability, which allowed  
346 us to account for: (1) missed surveys due to the above-described access issues for some buildings  
347 and days (a survey was considered missed if  $\geq 50\%$  of the building perimeter was not surveyed),  
348 and (2) varying time intervals between successive surveys on days when only morning surveys  
349 were conducted versus days when morning, midday, and evening surveys were conducted.

350       Using GenEst and data from carcass removal trials, we modeled carcass persistence  
351 probability for each building, and we treated the substrate on which trial birds were placed as a  
352 covariate (categories: rocks; natural, including grass, mulch, planters, and bare soil; and  
353 artificial, including concrete, metal, and other artificial surfaces) because the surface a bird lands  
354 on after colliding should influence the rate of detection and removal, especially by humans [33,  
355 46]. Using data from surveyor detection trials, we modeled observer detection probability.  
356 Estimation of observer detection probability in GenEst includes the parameter  $k$ , which is the  
357 change in searcher efficiency with each successive search (0 represents a scenario where  
358 carcasses missed on the first trial cannot be found on a successive survey; 1 represents a scenario  
359 where searcher efficiency stays constant regardless of carcass age and/or the number of times a  
360 carcass was missed). GenEst estimates  $k$  if carcasses are left in place for surveyors to detect on



361 subsequent trials; however, since we collected all carcasses after each trial, we set  $k=0.9$ , which  
362 represents an assumption that carcasses are detectable after each day but with slightly reduced  
363 detectability due to deterioration. We again treated substrate as a covariate but did not generate  
364 building-specific observer detection estimates because we had limited replication at some  
365 buildings, and there was no evidence suggesting that detection was influenced by building-  
366 related factors other than the surrounding substrates. Estimates of carcass persistence and  
367 observer detection probability were combined to model building- and substrate-specific  
368 estimates (along with 95% confidence intervals [CIs]) of the overall probability that a bird  
369 carcass resulting from a fatal collision was detected on the following survey. We generated  
370 adjusted fatality estimates by dividing both low and high raw counts of fatal collisions by the  
371 detection probability estimates for each building, with weighting to account for the proportion of  
372 each substrate in the survey area around each building. This procedure resulted in both low and  
373 high bias-adjusted fatality estimates (and associated 95% CI's) for each building. Data used for  
374 GenEst bias-adjusted fatality estimates are in S1 Dataset; metadata and additional documentation  
375 for GenEst analyses are in S1 Appendix.

376 Notably, bias-adjusted estimates did not incorporate non-fatal collisions because removal  
377 and detection rates for live birds are likely different than for dead birds and it was infeasible to  
378 conduct removal and detection trials with live birds. Nonetheless, to present the full number of  
379 collisions, we summarized low and high raw counts of non-fatal collisions for each building. We  
380 also summarized numbers of carcasses found and submitted by stadium staff; however, we note  
381 that removal trials and bias-adjusted estimates should account for these birds under the  
382 assumption that staff were equally likely to remove birds marked for removal trials and those  
383 that collided but were not included in trials (see Results for validation of this assumption).

384 **Statistical analyses of factors influencing collision fatalities and**  
385 **numbers of species colliding**

386 We only analyzed how fatal collisions were influenced by building-related factors  
387 because there was a strong correlation between low raw counts of fatal collisions and low raw  
388 counts of non-fatal collisions (Pearson's  $r=0.90$ ) and also between high raw counts of fatal and  
389 non-fatal collisions ( $r=0.89$ ). This indicates that results should remain unchanged regardless of  
390 whether fatal or non-fatal collisions are assessed. The low raw count of fatal collisions and high  
391 raw count of fatal collision were also strongly correlated ( $r=0.99$ ), so we based analysis on low  
392 fatal collision counts (i.e., those excluding potential predation events and skyway collisions;  
393 hereafter, low raw counts). We also conducted an analysis using bias-adjusted fatality estimates  
394 to determine if correlates differed from the raw count analysis. We based this analysis on the  
395 high adjusted estimates of fatal collisions (hereafter, high adjusted estimates) because these were  
396 not as strongly related to the low raw counts ( $r=0.85$ ) as the low adjusted estimates were to the  
397 low raw counts ( $r=0.94$ ). For analyses of both low raw counts and high adjusted estimates, we  
398 used generalized linear models (GLMs) with a negative binomial error distribution (function  
399 "glm.nb" in the MASS package) because preliminary analyses indicated that fatality count data  
400 were over-dispersed, and likelihood ratio tests showed that negative binomial models fit the data  
401 significantly better than poisson models. In addition to analyzing factors influencing total  
402 collision fatalities, we also conducted separate analyses for fatalities in spring and fall, and for  
403 total fatalities across seasons for each of the five most frequently colliding bird species (see  
404 Results). These season- and species-specific analyses were also conducted using negative  
405 binomial GLMs, and we used low raw counts because we did not have enough removal and  
406 detection trial replicates at each building to generate bias-adjusted estimates by season and

407 species. Finally, and again using negative binomial GLMs, we assessed factors influencing the  
408 number of species colliding at each building (i.e., counts of numbers of species, not fatalities),  
409 including across the entire study and separately for spring and fall. This analysis combined fatal  
410 and non-fatal collisions because numbers of species fatally colliding was strongly correlated with  
411 total species colliding ( $r>0.99$ ). For all analyses, collision response variables included data for  
412 both 2017 and 2018 because there was no significant difference between years in either fatal  
413 collisions ( $t=-1.86$ ;  $df=20$ ;  $p=0.08$ ) or total collisions ( $t=-1.70$ ;  $df=20$ ;  $p=0.11$ ) at each building.

414 For all analyses, we began with an initial set of eight predictor variables (building height,  
415 glass area, lighted window area, proportion lighted, footprint, distance to Mississippi River, and  
416 proportion of land covered by vegetation within 50 m and 100 m). Preliminary analyses  
417 indicated strong correlations ( $r>|0.7|$ ) between three variable pairs: glass area and building  
418 height ( $r=0.75$ ); lighted window area and footprint ( $r=0.84$ ); and percent vegetated cover  
419 within 50 and 100 m ( $r=0.80$ ) (S1 Table). To avoid multicollinearity, we only retained the  
420 variable from each pair that was more strongly correlated to the response variable of interest.  
421 Glass area and lighted window area were correlated with each other, but just below the 0.7  
422 criterion ( $r=0.698$ ); we retained both variables for analysis because few previous studies have  
423 separately considered the role of these two factors. Following removal of correlated variables,  
424 we used the “stepAIC” function in the R package “MASS” to implement a backwards  
425 elimination approach to model selection, beginning with a global additive model (i.e., containing  
426 all uncorrelated variables), which retained variables when their removal resulted in an increase of  
427  $\Delta AIC \geq 2$ . For variables included in the top model following this procedure, we also assessed  
428 model coefficients, and we only drew inferences from variables that had non-standardized  
429 coefficient estimates with 95% confidence intervals that did not overlap zero. All data used for

430 statistical analyses are in S2 and S3 Datasets, and R code for analyses is in S2 and S3  
431 Appendices.

432

## 433 **Results**

### 434 **Raw counts and species composition of collisions**

435         Across all buildings, seasons, and species, the low raw count (excluding possible  
436 predation events and skyway collisions) was exactly 1,000 fatal and non-fatal bird collisions (per  
437 building range=2-305 total collisions) (Table 2). The vast majority of these (86.8%) were found  
438 during morning surveys, of which we conducted far more (372 surveys) than midday (58  
439 surveys; 7.8% of collisions) and evening surveys (57 surveys; 5.4% of collisions). Four buildings  
440 including the stadium caused 74.3% (743) of collisions. Of all collisions, 22% (220) were non-  
441 fatal (i.e., birds we found stunned and/or saw fly away; per building range=0-70 non-fatal  
442 collisions) and 78% (780) were fatal (i.e., carcasses or remains; per building range=1-254 fatal  
443 collisions); the same four buildings caused 74.0% (577) of all fatal collisions. Across both years,  
444 we observed nearly four times more collisions in fall (758) than spring (209), with only 33  
445 collisions in June. Including an additional 167 collisions (153 fatal; 14 non-fatal) that were  
446 potential predation events and skyway collisions resulted in a high raw count of 1,167 collisions;  
447 the same building rankings and seasonal patterns also emerged for high counts.

448 **Table 2. Collision counts, results of removal and detection trials, and bias-adjusted fatality estimates for all buildings.**

Building Id <sup>a</sup>	Raw counts <sup>b</sup>			Bias trials <sup>d</sup>			Bias-adjusted fatalities <sup>e</sup>	
	Fatal	Non-fatal	# of species <sup>c</sup>	Removal	Detection	Detection prob.	Low	High
17	254-264	51-51	44	43	5	0.59 (0.48-0.69)	431 (370-525)	448 (384-545)
4	91-113	27-30	38	32	6	0.31 (0.18-0.45)	297 (202-493)	369 (251-613)
1 (Stadium)	155-159	70-70	42	27	23	0.70 (0.56-0.8)	222 (192-274)	228 (197-281)
3	77-112	18-20	35	33	1	0.48 (0.36-0.61)	158 (126-211)	231 (184-307)
8	4-8	0-1	4	5	2	0.04 (0-0.62)	114 (6-4000)	228 (12-8000)
9	59-64	8-10	24	24	14	0.70 (0.58-0.81)	83 (72-102)	90 (78-111)
19	29-34	4-4	17	14	3	0.43 (0.25-0.62)	67 (46-115)	79 (54-135)
12	25-26	5-7	13	10	4	0.53 (0.33-0.72)	47 (34-76)	48 (36-79)
20	23-28	9-10	15	9	2	0.51 (0.28-0.72)	45 (32-83)	54 (39-101)
15	11-15	5-5	9	11	1	0.29 (0.14-0.5)	37 (21-76)	51 (29-104)
13	6-8	4-4	9	8	4	0.24 (0.08-0.5)	24 (12-72)	32 (16-96)
2	9-18	1-3	9	6	3	0.39 (0.18-0.64)	22 (13-50)	45 (27-101)
6	14-45	4-4	10	14	4	0.64 (0.48-0.79)	21 (17-29)	70 (57-94)
16	1-1	1-1	1	6	1	0.05 (0-0.61)	20 (1-1000)	20 (1-1000)
21	5-7	2-2	5	8	9	0.45 (0.24-0.69)	11 (7-20)	15 (10-29)
5	5-11	5-6	6	8	6	0.65 (0.44-0.81)	7 (6-11)	16 (13-24)
10	4-4	3-3	6	5	6	0.56 (0.24-0.8)	7 (4-16)	7 (4-16)
11	3-6	2-2	5	7	2	0.51 (0.24-0.74)	5 (4-12)	11 (8-24)
14	1-6	1-1	2	3	3	0.18 (0.02-0.65)	5 (1-58)	33 (9-350)
7	2-2	0-0	2	5	3	0.57 (0.29-0.78)	3 (2-7)	3 (2-7)
18	2-2	0-0	2	8	3	0.61 (0.37-0.79)	3 (2-5)	3 (2-5)
Totals	780-933	220-234	75	286	105	-	1629 (1170-7235)	2081 (1413-12022)

449 Collision counts, results of removal and detection trials, and bias-adjusted bird fatality estimates for 21 buildings, including U.S. Bank  
 450 Stadium, monitored in downtown Minneapolis, Minnesota, 2017-2018. Table includes raw counts of fatal and non-fatal collisions;  
 451 information about bias trials that were used to generate detection probability estimates accounting for both carcass removal and  
 452 imperfect detection of window-killed bird carcasses; and bias-adjusted fatality estimates based on application of detection probability  
 453 estimates to raw fatal collision counts. Buildings are ranked in descending order based on the low bias-adjusted fatality estimate  
 454 (parentheses indicate 95% confidence intervals).

455 <sup>a</sup>Unique numeric code for each building used for purposes of current study

456 <sup>b</sup>Raw counts for fatal and non-fatal collisions at each building; low and high values are counts that respectively exclude and include birds  
457 potentially resulting from predation events (for fatal collisions) and collisions with skyways between buildings (for fatal and non-fatal collisions)  
458 <sup>c</sup>Number of species observed as collision casualties across the entire study, including both fatal and non-fatal collisions  
459 <sup>d</sup>Number of carcass removal trials conducted to quantify animal scavenger and human removal of carcasses, number of detection trials conducted  
460 to quantify surveyor detection probability for carcasses present in search area (excludes detection trials where trial carcasses were removed before  
461 surveyors had a chance to encounter them), and estimated probability of detecting a window-killed carcass that falls in the survey area (detection  
462 probability accounts for both removal and detection probability)  
463 <sup>e</sup>Bias-adjusted fatality estimates based on application of detection probability estimates to raw fatal collision counts; low and high adjusted  
464 estimates were generated using the low and high fatal collision counts

465 In addition to a few buildings causing the majority of collisions, a small number of  
466 façades caused most of the collisions at several buildings. For example, we documented  
467 collisions around the stadium's entire perimeter, but 52% of all collisions occurred at the ~6,000  
468 m<sup>2</sup> expanse of glass on the northwest façade, 17% occurred at one glass surface on the southwest  
469 façade, and 11% occurred at one glass surface on the northeast façade (Fig 2). In addition to  
470 collisions observed at the stadium during surveys, 62 bird carcasses (20 in 2017; 42 in 2018)  
471 were submitted by stadium staff. Supporting our assumption that staff removed birds marked for  
472 removal trials at a rate similar to carcasses not in trials—and therefore that removal trials  
473 accounted for staff-removed birds—5 of the 62 submitted carcasses were removal trial birds.  
474

475 **Fig 2. Bird collisions at U.S. Bank Stadium.** (a) Locations of 229 bird collisions (159 fatal  
476 collisions; 70 non-fatal collisions; 95 collisions in 2017; 134 in 2018) observed during  
477 monitoring at U.S. Bank Stadium in downtown Minneapolis, Minnesota, USA, 2017-2018;  
478 Points include carcasses potentially resulting from predation events and bird collisions with  
479 skyways (i.e., the high raw counts described in the text). (b, c) the largest unbroken span of glass  
480 (~6,000 m<sup>2</sup>) where 52% of all collisions at the stadium occurred; (d) a glass surface on the  
481 northeast façade where 11% of collisions occurred; (e) a glass surface on the southwest façade  
482 where 17% of collisions occurred. ~~(f)~~ Image sources: USGS National Map Viewer NAIP Plus  
483 aerial imagery ~~{(a)}~~; the authors ~~{(b-e)}~~.

484

485 Among the 1,000 collision records that excluded possible predation events and skyway  
486 collisions, we identified 75 bird species as collision casualties (per building range=1-44; Table  
487 2), including 72 fatally injured species (per building range=1-37). Five species accounted for

488 48.9% of all collisions: White-throated Sparrow (*Zonotrichia albicollis*) (14.1%), Nashville  
489 Warbler (*Leiothlypis ruficapilla*) (10.8%), Ovenbird (*Seiurus aurocapilla*) (9.8%), Common  
490 Yellowthroat (*Geothlypis trichas*) (7.4%), and Tennessee Warbler (*Leiothlypis peregrina*) (6.8%)  
491 (Table 3; see S2 and S3 Tables for counts of all species overall and by season). The same species  
492 were the top colliders in fall, although Ovenbird and Common Yellowthroat switched the third  
493 and fourth rankings. During spring, Ovenbird, White-throated Sparrow, Tennessee Warbler and  
494 American Woodcock (*Scolopax minor*) were the top four colliders, followed by three species tied  
495 for fifth: Black-billed Cuckoo (*Coccyzus erythrophthalmus*), Northern Waterthrush (*Parkesia*  
496 *noveboracensis*), and Dark-eyed Junco (*Junco hyemalis*).

497 **Table 3. Top ten most frequently colliding bird species**

All seasons		Spring (15 Mar-31 May)	
Species	Count	Species	Count
White-throated Sparrow	141	Ovenbird	37
Nashville Warbler	108	White-throated Sparrow	34
Ovenbird	98	Tennessee Warbler	15
Common Yellowthroat	74	Unknown bird <sup>a</sup>	13
Tennessee Warbler	68	American Woodcock	8
Dark-eyed Junco	33	Black-billed Cuckoo	7
Unknown bird <sup>a</sup>	32	Northern Waterthrush	7
Black-and-white Warbler	29	Dark-eyed Junco	7
Ruby-throated Hummingbird	26	Black-and-white Warbler	6
Northern Waterthrush	22	Yellow-bellied Sapsucker	5
Summer (1-30 Jun)		Fall (15 Aug-31 Oct)	
Species	Count	Species	Count
House Sparrow	6	White-throated Sparrow	107
Black-billed Cuckoo	5	Nashville Warbler	104
Yellow-billed Cuckoo	4	Common Yellowthroat	66
House Finch	4	Ovenbird	61
Common Yellowthroat	3	Tennessee Warbler	53
Unknown bird <sup>a</sup>	2	Dark-eyed Junco	26
Chipping Sparrow	1	Ruby-throated Hummingbird	23
Virginia Rail	1	Black-and-white Warbler	23
Mourning Warbler	1	Lincoln's Sparrow	19
Red-eyed Vireo	1	Red-breasted Nuthatch	18



498 Top ten most frequently colliding bird species (includes fatal and non-fatal collisions) across all  
499 collision surveys at all 21 monitored buildings, including U.S. Bank Stadium, in downtown  
500 Minneapolis, Minnesota, USA, 2017-2018. The “All seasons” count excludes mid-summer and  
501 winter periods when no collision monitoring occurred (see S2 and S3 Tables for counts of all  
502 species observed as collision casualties, including overall and by season, respectively).  
503 <sup>a</sup>Birds that could not be identified to any taxonomic level, typically due to dismemberment and/or severe  
504 decomposition, distant viewing and/or poor quality documentation photos  
505

## 506 **Bias-adjusted fatality rates and comparisons among buildings**

507 We conducted 286 removal trials and 105 surveyor detection trials, not counting  
508 detection trials where a carcass was removed before a surveyor could detect it. Combining  
509 GenEst-derived estimates of carcass persistence probability (which was modeled for each  
510 building and as a function of substrate) and observer detection probability (which was modeled  
511 across buildings and as a function of substrate), resulted in overall estimates of detection  
512 probability that varied among buildings from 4% to 70% (mean=45%). When applying building-  
513 specific detection probabilities to fatal collision counts, we generated bias-adjusted fatal collision  
514 estimates that varied among buildings from 3 to 431 (median=24; mean=78) based on low  
515 fatality counts and 3 to 448 (median=48; mean=99) based on high fatality counts. Based on low  
516 adjusted estimates, the stadium had the third highest fatality estimate behind buildings #4 and  
517 #17. Based on the high adjusted estimates, the stadium ranked fourth behind buildings #3, #4,  
518 and #17. When adding non-fatal collisions (either low or high counts) to any bias-adjusted  
519 estimates, the stadium always ranked third in total collisions behind #4 and #17.

## 520 **Factors influencing collision fatalities and numbers of species**

### 521 **colliding**

522           After excluding variables that appeared in top models but had non-standardized  
523 coefficients with 95% CI's overlapping zero, the top model for most collision variables included  
524 only glass area and proportion of vegetated cover within 50 m (standardized coefficient estimates  
525 for strongly supported variables in Table 4). In all instances, these factors had a positive effect  
526 (i.e., increasing collisions with increasing glass area and vegetation), including for total low  
527 fatality counts, high adjusted fatality estimates (Fig 3), spring and fall fatalities, and fatalities for  
528 the three most frequently colliding species (White-throated Sparrow, Nashville Warbler,  
529 Ovenbird). For Common Yellowthroat, the top model included positive effects of glass area and  
530 vegetation within 100 m, and for Tennessee Warbler, the top model included only a positive  
531 effect of vegetation within 50 m. For total numbers of species colliding, the top model included  
532 positive effects of glass area and vegetation within 50 m, as well as a positive effect of the  
533 proportion of glass lighted at night (Fig 4). The top model for numbers of species colliding in  
534 spring and fall also included positive effects of glass area and vegetation (within 100 m for  
535 spring; 50 m for fall), and the model for spring also included a positive effect of lighting  
536 proportion. For most response variables, standardized coefficient estimates (Table 4) illustrated  
537 that effects of glass area and vegetation were of approximately similar magnitude when both  
538 factors were supported. The effect of lighting proportion was slightly less than effects of glass  
539 area and vegetation for the response variables with all three factors supported.

540 **Table 4. Standardized coefficient estimates for variables in supported models for analyses including all 21 buildings.**

	Height	Glass area	Prop. light	Area light	Footprint	Distance to river	Prop. vegetation	
							50 m buffer	100 m buffer
<i>Collision fatalities (all)</i>								
Total low raw count <sup>a</sup>	-	0.012	-	-	-	-	0.012	-
Total high adj. estimate <sup>b</sup>	-	0.005	<i>0.003</i>	-	-	-	0.003	-
Spring low raw count <sup>c</sup>	-	0.036	-	-	-	-	0.048	-
Fall low raw count <sup>d</sup>	-	0.019	-	-	-	-	0.016	-
<i>Collision fatalities (species)<sup>e</sup></i>								
White-throated Sparrow	-	0.051	-	-	-	-	0.089	-
Nashville Warbler	-	0.113	-	-	-	<i>-0.054</i>	0.107	-
Ovenbird	-	0.096	-	-	-	-	0.093	-
Common Yellowthroat	-	0.110	<i>0.041</i>	-	-	-	-	0.169
Tennessee Warbler	-	-	-	-	-	-	0.230	-
<i>Number of species<sup>f</sup></i>								
All seasons	-	0.066	0.033	<i>-0.042</i>	-	<i>-0.020</i>	0.039	-
Spring	-	0.120	0.090	<i>-0.075</i>	-	-	-	0.117
Fall	-	0.049	-	-	-	-	0.049	-

541 Standardized coefficient estimates for variables included in strongly supported models for analyses of building-related variables  
 542 associated with bird collisions based on monitoring at 21 buildings, including U.S. Bank Stadium, in downtown Minneapolis,  
 543 Minnesota, USA, 2017-2018. Analyses were conducted for total collision fatalities across all seasons and for spring and fall, for total  
 544 fatalities for the five species most frequently observed as collision casualties, and for numbers of species observed to collide across all  
 545 seasons and for spring and fall. For results based on subset of 17 buildings with potential outliers excluded (stadium, #3, #4, and #17),  
 546 see text and S4 Table. Coefficients in italics had non-standardized coefficient estimates with 95% CI's that overlapped zero.

547 <sup>a</sup>Analysis response variable was raw counts of total fatal collision casualties excluding birds potentially resulting from predation events and  
 548 collisions with skyways connecting buildings

549 <sup>b</sup>Analysis response variable was bias-adjusted estimates of fatal collisions adjusted to account for removal of bird carcasses by humans and animal  
 550 scavengers and for imperfect detection of carcasses present during surveys (this version of the bias-adjusted estimate was based on the high raw  
 551 count of fatal collisions, which included birds potentially resulting from predation events and collisions with skyways connecting buildings)

552 <sup>c</sup>Analysis response variable was raw counts of spring fatal collision casualties excluding birds potentially resulting from predation events and  
 553 collisions with skyways connecting buildings

554 <sup>d</sup>Analysis response variable was raw counts of fall fatal collision casualties excluding birds potentially resulting from predation events and  
 555 collisions with skyways connecting buildings

556 <sup>e</sup>Analysis response variables were low raw counts of fatal collision casualties for individual species, excluding birds potentially resulting from  
557 predation events and collisions with skyways connecting buildings  
558 <sup>f</sup>Analysis response variables were total numbers of identifiable species observed as fatal and non-fatal collision casualties at each building

559 **Fig 3. Correlates of numbers of collision fatalities (all buildings).** Relationships between high  
560 bias-adjusted estimates of bird collision fatalities (see text for description of this fatality  
561 estimate) and (a) glass area, and (b) proportion of land covered by vegetation within 50 m. The  
562 four buildings estimated to cause the greatest numbers of fatalities, including the stadium, are  
563 labelled (numbers represent unique numeric codes used for purposes of current study); For  
564 results based on 17 buildings with these 4 potential outliers removed, see text and S1 Fig.

565  
566 **Fig 4. Correlates of numbers of species colliding (all buildings).** Relationships between total  
567 numbers of species observed as casualties (including both fatal and non-fatal collisions) and (a)  
568 glass area, (b) proportion of window area with lighting emitted at night, and (c) proportion of  
569 land covered by vegetation within 50 m. The four buildings estimated to cause the greatest  
570 numbers of collisions, including the stadium, are labelled (numbers represent unique numeric  
571 codes used for purposes of current study); For results based on 17 buildings with these 4  
572 potential outliers removed, see text and S2 Fig.

573  
574 Visual inspection of the above relationships (Figs 3 and 4) suggests that four large  
575 buildings with extensive glass area and/or nearby vegetation (#3, #4, #17, and the stadium)  
576 largely drove the importance of these factors for nearly all analyses. To determine if additional  
577 factors influence collisions for a set of buildings more representative of most of those in  
578 downtown areas, we removed the above four buildings and re-ran analyses (data used for these  
579 analyses are in S3 Dataset, and R code is in S3 Appendix). For this subset of 17 buildings, only  
580 glass area and lighted window area were correlated ( $r=0.77$ ); because there was another variable  
581 that captured lighting (proportion lighted), we removed lighted window area from these analyses

582 to avoid multicollinearity. For the subset of 17 buildings, and after setting aside variables that  
583 had non-standardized coefficients with 95% CI's overlapping zero, the top model for total low  
584 fatality counts included positive effects of glass area and vegetation within 100 m (S1 Fig;  
585 standardized coefficient estimates in S4 Table). The model for the high adjusted estimates did  
586 not converge, even when manually changing the number of model iterations (possibly due to low  
587 replication relative to the broad range of fatality estimates); therefore, we were unable to identify  
588 correlates for this response variable for the subset of 17 buildings. The top model for spring  
589 fatalities included positive effects of proportion lighted and vegetation within both 50 m and  
590 100m. The top model for fall fatalities included glass area and vegetation within 100 m. For both  
591 White-throated Sparrow and Ovenbird, the top model included only positive effects of glass area,  
592 and the top model for Common Yellowthroat contained this same effect and positive effects of  
593 vegetation within 50 and 100 m. The top model for Nashville Warbler included positive effects  
594 of building height, building footprint, and vegetation within 50 m, and for Tennessee Warbler,  
595 the null model ranked highest, indicating that none of the variables we measured explained  
596 collision fatalities for this species. The top model for total numbers of species colliding included  
597 positive effects of glass area, lighting proportion, and vegetation within 100 m (S2 Fig). The top  
598 model for species colliding in spring included positive effects of lighting proportion and  
599 vegetation within 100 m, and the model for fall included positive effects of glass area and  
600 vegetation within 100 m.

601

## 602 **Discussion**

603 In a study of 21 buildings over four migration seasons in downtown Minneapolis,  
604 Minnesota, we documented substantial variation among buildings in numbers of bird collisions,

605 with four large buildings causing the majority of collisions, including a large multi-use stadium,  
606 which ranked third for most estimates. These same four buildings drove the positive effects of  
607 glass area and the proportion of surrounding land covered by vegetation on nearly all collision  
608 response variables. Focusing on 17 buildings more representative of most of those in major  
609 downtown areas resulted in slightly different predictors of collisions emerging, which suggests  
610 that factors leading some buildings to cause exceptionally high numbers of bird collisions are not  
611 the exact same factors causing collision variation among a more typical set of buildings. Across  
612 both analyses, we also found evidence that the proportion of windows lighted at night influences  
613 bird collision fatalities in spring, as well as the number of species colliding overall and in spring.  
614

## 615 **Collision comparisons among buildings**

616 Collision numbers varied greatly among buildings, with four buildings (three high-rise  
617 office buildings and U.S. Bank stadium) causing 74% of observed collisions (based on low raw  
618 fatality counts) and 68% of estimated fatalities (based on low bias-adjusted estimates). Estimated  
619 fatality rates for these top buildings, which ranged from 79 to 216 fatalities/yr (111 fatalities/yr at  
620 the stadium), not only exceeded other buildings in this study, but also exceed the estimated range  
621 of fatality rates at the majority of U.S. high rise buildings (5-77 birds/yr as estimated with  
622 collision data from 11 cities) [4]. Fatality rates exceeding those of our top buildings have in some  
623 cases been shown at other extremely large and/or glassy buildings such as: the McCormick Place  
624 Convention Center in Chicago, Illinois (four inter-connected buildings along the Lake Michigan  
625 shoreline with an average of 1,028 fatalities/yr from 1978 to 2012) [4, 47]; the Yonge Corporate  
626 Centre in Toronto, Canada (three office buildings with >800 fatalities in 2010) [48], and the  
627 vehicle assembly building at the John F. Kennedy Space Center in Florida (a 160 m tall,

628 32,376m<sup>2</sup>, mostly windowless structure with an average of 421 fatalities/yr from 1980 to 1991)  
629 [49]. These examples, as well as the top-ranked buildings in our study, seem to represent the  
630 upper extreme of bird collision fatality rates; indeed, these types of buildings were excluded  
631 from a U.S. estimate of bird-building collision mortality due to their high outlier status [4]. Ours  
632 and the above studies indicate that major bird collision reductions can be achieved by focusing  
633 mitigation efforts on a small number of especially problematic buildings.

634         We are unaware of other collision studies at stadiums; thus, direct comparisons between  
635 U.S. Bank Stadium and other similar structures are not yet possible. Nonetheless, given research  
636 showing that large, glassy buildings nearly always cause large numbers of bird collisions, we  
637 expect that similar glassy stadiums would also cause substantial collision mortality. Even less-  
638 glassy stadiums with extensive lighting may cause numerous collisions because intense  
639 nighttime lighting confuses nocturnally migrating birds, altering their flight paths, bringing them  
640 closer to the ground, and elevating collision risk [27]. Recognizing the risk posed to birds, there  
641 have been some efforts to incorporate bird-friendly design elements into new stadiums. For  
642 example, the Fiserv Forum basketball arena in Milwaukee, Wisconsin, was designed to reduce  
643 bird collisions by minimizing the use of reflective and see-through glass [50]. Retroactive  
644 treatment of existing stadiums should also reduce collisions, and regardless of the approach  
645 used—whether it be installation of bird-friendly glass, application of film on existing glass, or  
646 some other approach—in-field monitoring and validation of the effectiveness of different  
647 approaches is needed to clarify which mitigation steps work best for different types of glass,  
648 buildings, and surroundings (e.g., heavily vegetated vs. non-vegetated). Notably, our results for  
649 U.S. Bank Stadium suggest that a major reduction in collisions can be achieved by focusing  
650 mitigation on one or more particularly problematic spans of glass (Fig 2).



651           Although we accounted for removal of carcasses by humans and scavengers, as well as  
652 imperfect detection of carcasses present during surveys, the true number of fatalities was greater  
653 than our bias-adjusted estimates. These estimates only represent the monitoring period (15 Mar-  
654 30 Jun; 15 Aug-31 Oct), and although collisions are less frequent in other seasons [16, 37],  
655 additional collisions undoubtedly occurred during unmonitored seasons at most buildings. We  
656 also missed an unknown number of non-fatal collisions where birds flew away before the next  
657 survey. An unknown number of these birds, and of non-fatal collisions we did observe, likely  
658 died later or experienced sublethal effects that impaired their behavior, susceptibility to  
659 predation, and/or ability to continue migration and eventually reproduce [51]. Notably, the  
660 percentage of such birds that survive is virtually unknown in the scientific literature due to  
661 difficulties of tracking birds after non-fatal collisions. Finally, at most buildings, additional bird  
662 carcasses likely fell in inaccessible locations, such as above-ground platforms and areas of roofs  
663 beneath windows.

664

## 665 **Factors influencing collision fatalities and numbers of species**

### 666 **colliding**

667           When considering all 21 buildings, glass area and vegetation within 50 m were included  
668 in top models for most collision response variables. Because buildings with extensive glass area  
669 also tended to be tall, and because buildings with extensive vegetation within 50 m also tended to  
670 have abundant vegetation within 100 m, we were unable to isolate the effects of these factors.  
671 Our results nevertheless suggest that large glassy buildings with extensive nearby vegetation or  
672 park space cause the greatest numbers of collisions. Past studies at a variety of building types  
673 have also shown increases in bird collisions with greater building height [4, 19], area and/or

674 percentage of windows or glass [7, 19, 25], and vegetation near buildings [7, 11-12]. The effect  
675 of glass area likely arises due to several factors, including greater confusion of birds due to larger  
676 amounts of reflective and/or see-through surfaces, especially in large unbroken expanses [52],  
677 and an increase in light emission increasing numbers of nocturnal migrants attracted to buildings  
678 (see lighting discussion below). The effect of vegetation likely occurs due to its attractiveness to  
679 birds as a source of food and cover, especially for migratory birds resting and refueling during  
680 stopovers in an otherwise heavily urbanized landscape. Vegetation may also exacerbate  
681 reflection effects; birds may be less able to perceive glass as a barrier when it reflects vegetation  
682 and/or more likely to fly toward glass if they perceive they are flying toward vegetation [10].

683         Nearly all studies of bird-building collision correlates have assessed collisions across the  
684 entire monitoring period (usually spring and fall, or fall only) and for all birds combined. We  
685 provide evidence that collision correlates can vary among seasons and species, a conclusion  
686 supported by the limited past research that has assessed species-specific correlates [25]. When  
687 outlier buildings were excluded, spring fatalities were best predicted by lighting proportion and  
688 vegetation within 50 and 100 m, while fall fatalities and total fatalities were best predicted by  
689 glass area and vegetation within 100 m. For species analyses including all buildings, glass area  
690 and vegetation within 50 m were each supported for 4 of 5 species; however, Common  
691 Yellowthroat fatalities were predicted by vegetation within 100 m. A unique pattern also  
692 emerged for Nashville Warbler when outlier buildings were excluded; fatalities for this species  
693 were positively influenced by building height, footprint, and vegetation within 50 m. These  
694 results suggest that Nashville Warbler habitat use, flight behavior, and/or collision avoidance  
695 may be more closely tied to factors associated with building size than other species, and that  
696 Common Yellowthroat may be more likely to be attracted near buildings when nearby vegetation

697 covers an area larger than that captured by a 50 m distance buffer. Finally, Tennessee Warbler  
698 was the only species for which fatalities were not associated with glass area and for which no  
699 variables predicted fatalities in the outlier-excluded analysis. These results suggest that factors  
700 other than glass area, and indeed other than most factors we measured, could influence collisions  
701 for this species. More broadly, the above types of species-specific collision correlates could also  
702 arise due to other biological and ecological factors that vary among species, including  
703 morphology (e.g., wing-loading) and flight maneuverability, migration timing (relative to both  
704 time of day and season), and visual capacity to detect reflective and transparent surfaces at  
705 different distances, during different times of day, and under different lighting conditions.  
706 Regardless of the mechanisms, our findings suggest that results of studies focused on one  
707 migration season, all seasons combined, and/or all birds combined should not necessarily be  
708 extrapolated across all seasons and species. Further, management measures based on correlates  
709 identified in such studies may not be equally effective for all species and seasons, and species-  
710 and season-specific approaches may be necessary to achieve the greatest reduction in collisions.

711 Factors explaining total numbers of species colliding were nearly identical to those  
712 influencing total collision fatalities. Both glass area and vegetation were associated with both  
713 response variables regardless of whether outlier buildings were included, although as discussed  
714 below, a positive effect of lighting proportion was also supported for numbers of species  
715 colliding. We are uncertain if these factors independently influence both numbers of fatalities  
716 and numbers of species colliding, or if they only explain number of species colliding because  
717 more species are represented with increasing fatalities. We hypothesize that glass area and  
718 vegetation could directly influence numbers of species colliding; this could occur if large  
719 buildings with extensive glass and nearby vegetation attract a greater diversity of birds as a result

720 of being surrounded by a greater diversity of land covers and/or vegetation that provides diverse  
721 food and cover. Past research provides evidence for this explanation; a study in Toronto found  
722 that forest-dwelling bird species collided more at buildings surrounded by extensive greenspace  
723 while open woodland-dwelling species collided more at buildings surrounded by extensive  
724 urbanization [25]. Thus, greater variation in land cover at large, glassy buildings could result in  
725 attraction and collision of a larger diversity of species with varying habitat affinities.

726 Notably, habitat loss is one of the greatest threats to bird populations, and as human  
727 development and urbanization expand, urban vegetation and greenspaces provide many benefits  
728 to birds, including resident birds and migratory birds passing through urban areas. However, our  
729 results are consistent with past research suggesting that vegetation near windows elevates  
730 collision rates. Taken together, these conclusions stress the need to prioritize mitigation  
731 strategies related to reducing window collisions (e.g., window films) versus those reducing urban  
732 vegetation. Further, such collision mitigation steps may be most important for buildings and  
733 glass surfaces surrounded by extensive vegetation and greenspace.

734 Caution should be taken in interpreting our results, as the large number of analyses with  
735 assessment of variable importance based on 95% confidence intervals of coefficient estimates  
736 increases the risk of Type I error (i.e., apparently significant effects arising by chance alone).  
737 Further, although characteristics of the outlier buildings appear to influence which collision  
738 correlates were identified and therefore provide insight into collision risk factors for these  
739 structures, greater replication of large, glassy, and irregularly shaped buildings (including  
740 stadiums) would more conclusively identify bird collision risk factors that are generalizable to  
741 multiple contexts. This increased replication could be achieved through coordinated and  
742 standardized collision monitoring in multiple cities (e.g., following [14]), meta-analyses of

743 published and unpublished datasets, and creation of a bird collision database to facilitate data  
744 sharing among researchers, conservation organizations, and building designers (see also [53]).

745

## 746 **Evidence for effects of nighttime lighting on bird-building collisions**

747         The proportion of glass emitting light at night appeared in top models for spring collision  
748 fatalities (analysis excluding outliers) and numbers of species colliding overall and in spring  
749 (both all-building and outlier-excluded analyses). Lighted window area was not supported for  
750 any collision variables in the all-building analysis, and we did not include this factor in the  
751 outlier-excluded analysis because it was correlated with glass area. However, we expected  
752 lighted window area to also be associated with collisions because it was correlated with glass  
753 area—which predicted most collision variables—and because past studies have shown a positive  
754 relationship between bird-building collisions and a light emission index that is similar to lighting  
755 area in combining building size with the percentage of buildings or windows emitting light [18,  
756 54]. We tested this possibility by re-running all analyses either with glass area removed (all-  
757 building analysis) or replaced by lighted window area (outlier-excluded analysis); this resulted in  
758 lighted window area being included in the top model for nearly all collision variables.

759 Nevertheless, we are unable to isolate the effects of these two factors because the buildings in  
760 our study that had extensive glass area also had an extensive area of lighted windows at night.

761         We expected lighted window area to be relevant to bird collisions, as this factor should  
762 indicate the amount and/or brightness of light pollution birds experience near buildings, and thus  
763 the degree to which they are confused, disoriented, and/or attracted to buildings [29]. However,  
764 the apparent effect of proportion of glass lighted on some collision response variables was  
765 somewhat surprising because any given proportion value represents a different amount of light

766 emission depending on building size and glass area. The lighting proportion variable could  
767 indirectly capture the contiguousness of lighted area on buildings; in other words, lighted areas  
768 may be closer together and/or occur in larger unbroken spans when lighting proportions are  
769 greater. This increased contiguity of lighting could pose greater perceptual challenges to birds,  
770 such that they experience greater disorientation or attraction or have greater difficulty detecting  
771 and avoiding glass, an effect analogous to that of contiguous expanses of glass [52]. Future  
772 research could isolate effects of glass area, lighted window area, and proportion of glass lighted  
773 by monitoring buildings that vary independently in regard to these factors or by experimentally  
774 changing amounts of light emitted from buildings with different amounts of glass area and  
775 measuring collision rates with different treatments. Even in lieu of research clearly documenting  
776 causation, we argue there is sufficient circumstantial evidence regarding nighttime lighting  
777 effects on bird-building collisions to expand efforts to reduce light pollution in downtown areas  
778 and other settings.

779         We are uncertain why lighting proportion was associated with numbers of species  
780 colliding but not total collision fatalities, and with fatalities in spring but not fall. The former  
781 pattern could occur if lighting has the greatest effect during migration periods (e.g., particular  
782 times of the night or year) with a high diversity, but not necessarily the greatest number, of  
783 migrating birds. Lighting could disproportionately influence spring fatalities if this season has a  
784 higher frequency of weather conditions that exacerbate light pollution effects (e.g., low cloud  
785 ceilings; heavy precipitation) and/or if the mix of species migrating during spring is collectively  
786 more sensitive to light pollution. Further research into the mechanisms behind light pollution  
787 effects on migratory birds, including for different seasons and species, would help clarify the role  
788 of lighting in bird collisions.

## 789 **Conclusions**

790 We illustrated substantial variation in bird collision rates in a major U.S. downtown area.  
791 A few large, glassy buildings with extensive surrounding vegetation—including a stadium and  
792 three high-rise office buildings—caused the majority of collisions and drove the importance of  
793 glass area and vegetation in explaining collision fatality rates. Excluding these buildings revealed  
794 slightly different collision correlates. Although glass area and vegetation still predicted several  
795 collision variables, this result suggests that factors causing some buildings to cause exceptionally  
796 large numbers of collisions are not the exact same factors causing more modest collision  
797 variation among buildings that are more representative of most of those in downtown areas.

798 Our results suggest management approaches that can reduce bird collisions at both new  
799 and existing buildings. Reducing numbers of collisions and numbers of species colliding should  
800 be achievable by reducing light emission at night, reducing the area of untreated glass, and  
801 avoiding the use of vegetation near glassy surfaces. Mitigation strategies for existing buildings  
802 include treatments that provide visual markers and/or reduce reflective and see-through effects of  
803 glass (e.g., window film applications); such treatments are likely to be especially important for  
804 buildings that emit extensive lighting at night and are in close proximity to extensive vegetation  
805 and greenspaces. Collisions should also be reducible by considering such features in the design  
806 and construction of new buildings, including stadiums and the many other large, glassy  
807 structures that are otherwise likely to cause large numbers of bird collisions. Finally, further  
808 field-testing and peer-reviewed research is needed to provide rigorous validation of bird-friendly  
809 construction approaches and measures to reduce collisions at existing buildings. Such  
810 management and research regarding approaches to reduce bird-building collisions will be crucial  
811 for mitigating this major threat to bird populations.

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817

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955

956 **Captions for Supporting Information**

- 957 **S1 Table. Correlation matrix.** Correlation matrix for all predictor variables assessed
- 958 **S2 Table. Total species collision counts.** Total collision counts, including both fatal and non-  
959 fatal collisions, for all species observed as collision casualties
- 960 **S3 Table. Seasonal species collision counts.** Collision counts by monitoring season, including  
961 both fatal and non-fatal collisions, for all species observed as collision casualties
- 962 **S4 Table. Supported variables (outliers excluded). Standardized** coefficient estimates for  
963 variables in supported models for analyses excluding outlier buildings

964 **S1 Fig. Correlates of numbers of collision fatalities (outliers excluded).** Relationships  
965 between low raw counts of collision fatalities and supported variables for analysis excluding  
966 outlier buildings

967 **S2 Fig. Correlates of numbers of species colliding (outliers excluded).** Relationships between  
968 total numbers of species colliding and supported variables for analysis excluding outlier  
969 buildings

970 **S1 Dataset. Data used for GenEst fatality estimates.** Input data for GenEst analysis to generate  
971 estimates of fatal collisions adjusted to account for removal of bird carcasses by humans and  
972 animal scavengers and for imperfect detection of carcasses present during surveys (metadata and  
973 analysis description in S1 Appendix); U.S. Bank Stadium is building 991.

974 **S2 Dataset. Data used for analyses including all buildings.** Input data for analyses of building-  
975 related variables associated with bird collisions (based on all 21 buildings); U.S. Bank Stadium is  
976 building 991.

977 **S3 Dataset. Data used for analyses with outliers excluded.** Input data for analyses of building-  
978 related variables associated with bird collisions (based on 17 buildings with 4 outliers excluded);  
979 U.S. Bank Stadium is building 991.

980 **S1 Appendix. Metadata for S1 Dataset.** Metadata for S1 Dataset used to estimate bias-adjusted  
981 fatality rates with GenEst, and additional documentation for GenEst analysis.

982 **S2 Appendix. R code for analyses including all buildings.** R code for analyses of building-  
983 related variables associated with bird collisions (based on all 21 buildings; data in S2 Dataset).

984 **S3 Appendix. R code for analyses with outliers excluded.** R code for analyses of building-  
985 related variables associated with bird collisions (based on 17 buildings with 4 outliers excluded;  
986 data in S3 Dataset).