

LARGE SCALE AVIAN CONSERVATION ISSUES IN  
THE GREAT PLAINS OF NORTH AMERICA

By

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LARGE SCALE AVIAN CONSERVATION ISSUES IN  
THE GREAT PLAINS OF NORTH AMERICA

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Title of Study: LARGE SCALE AVIAN CONSERVATION ISSUES IN THE GREAT PLAINS OF NORTH AMERICA

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Abstract: Globally many bird populations are declining at a rapid pace due to direct and indirect anthropogenic disturbances. Bird collisions with buildings are one major source of direct mortality. Chapter 1 examined species- and life-history-related variation and correlates of collisions at 40 sites across 3 North American countries. Many of the top 10 most vulnerable species were consistent with other broad scale studies but several emerged for the first time. Building size and glass area were positively correlated for most species and vegetation around buildings was negatively correlated with one species. Life history characteristics of species being migrants, insectivores, and woodland inhabitants also predicted collisions. Chapter 2 assessed the use of radar for predicting numbers of bird-building collisions in Stillwater, Oklahoma. Across the entire night, higher migration traffic rate and lower flight height were associated with increased collisions, and migration variables for periods within the night were also related to collisions. Habitat loss is a major source of indirect mortality to birds, especially in wetland and grassland systems such as the Great Plains. Chapter 3 evaluated broad and fine scale wetland habitat use by different migratory shorebird species in north central Oklahoma. There was variation among broad scale wetland use, with most species selecting for a 500m spatial scale, and most species being fairly similar among fine scale predictors. However, there was variation in effect size across predictors, suggesting that for most shorebirds, efforts to conserve and restore wetlands should focus heterogeneity of wetlands both in terms of habitat availability at both broad and fine scales. Chapter 4 reviewed bird response to fire in North American Grasslands. Most studies focused on prescribed fire and did not evaluate crucial factors that influence ecosystem response to fire. Most studies also only assessed effects of fire during avian breeding seasons. Further most studies were conducted in only prairie or savanna. Overall our findings provide novel insight into important direct and indirect contributions to bird mortality and can be used to help curve global bird population declines.

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## CHAPTER I

### CORRELATES OF BIRD COLLISIONS WITH BUILDINGS ACROSS THREE NORTH AMERICAN COUNTRIES

**Abstract.** Collisions with buildings cause up to 1 billion bird fatalities annually in the United States and Canada. However, efforts to reduce collisions would benefit from studies conducted at large spatial scales across multiple study sites with standardized methods and consideration of species- and life-history-related variation and correlates of collisions. We addressed these research needs through coordinated collection of data on bird collisions with buildings at sites in the United States (35), Canada (3), and Mexico (2). We collected all carcasses and identified species. After removing records for unidentified carcasses, species lacking distribution-wide population estimates, and species with distributions overlapping fewer than 10 sites, we retained 269 carcasses of 64 species for analysis. We estimated collision vulnerability for 40 bird species with  $\geq 2$  fatalities using their North American population abundance, distribution overlap in study sites, and sampling effort. Of 10 species we identified as most vulnerable to collisions, some have been identified previously (e.g., Black-throated Blue Warbler [*Setophaga caerulescens*]), whereas others emerged for the first time (e.g., White-breasted Nuthatch [*Sitta carolinensis*]), possibly because we used a more standardized sampling approach

than past studies. Building size and glass area were positively associated with number of collisions for 5 of 8 species with enough observations to analyze independently.

Vegetation around buildings influenced collisions for only 1 of those 8 species (Swainson's Thrush [*Catharus ustulatus*]). Life history predicted collisions; numbers of collisions were greatest for migratory, insectivorous, and woodland-inhabiting species. Our results provide new insight into the species most vulnerable to building collisions, making them potentially in greatest need of conservation attention to reduce collisions and into species- and life-history-related variation and correlates of building collisions, information that can help refine collision management.

## **Introduction**

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

Bird-building collisions that occur during the day are thought to result from birds mistaking reflections or open areas behind glass as safe flight passages (Klem 1989). At night artificial light (ALAN) (Longcore & Rich 2004) contributes to bird-building

collisions. The ALAN attracts and disorients nocturnally migrating birds, causing them to collide with buildings, become entrapped and later collide, become easy targets for predators, or succumb to exhaustion (Lao et al. 2020; Winger et al. 2019). As human population grows and shifts to urban areas, buildings and ALAN are increasing, which will likely result in increasing numbers of diurnal and nocturnal bird-building collisions if mitigation approaches are not identified and widely implemented.

Many factors influence spatial variation in bird-building collisions, including building size and location, nearby vegetation, and levels of regional urbanization (Hager et al. 2017). When considering total collisions across all bird species, large numbers of collisions occur at buildings with extensive areas of glass (Hager et al. 2008; Klem et al. 2009), with ALAN (Winger et al. 2019), and with nearby trees and shrubs (Hager et al. 2013; Cusa et al. 2015). Local-scale factors also interact with broad-scale factors to influence collisions. For example, a study in the United States, Canada, and Mexico showed that regional urbanization mediates the effect of building characteristics, with large glassy buildings in relatively undeveloped landscapes causing more collisions than similar buildings in urbanized areas (Hager et al. 2017).

Numbers of building collisions may also vary due to factors intrinsic to bird species such as their life history (Cusa et al. 2015; Wittig et al. 2017). Migratory species are thought to collide in greater numbers than nonmigratory species, and nocturnal migrants may collide more frequently than diurnal migrants (Machtans et al. 2013; Loss et al. 2014; Winger et al. 2019). Among-family variation in collisions also is thought to occur. For example, wood warblers (Parulidae) and hummingbirds (Trochilidae) are reported to collide in greater numbers than swallows (Hirundinidae). Some species may

collide with buildings in exceptionally large numbers (e.g., White-throated Sparrow [*Zonotrichia albicollis*]) or may be disproportionately vulnerable, colliding in numbers greater than expected based solely on abundance (e.g., Ruby-throated Hummingbird [*Archilochus colubris*], Ovenbird [*Seiurus aurocapilla*], Yellow-bellied Sapsucker [*Sphyrapicus varius*]) (Arnold & Zink 2011; Loss et al. 2014). These disproportionately vulnerable species are perhaps more likely to be subject to population declines associated with building collision mortality.

Most studies of factors influencing bird-building collisions are descriptive, occur in a single study area, or do not account for factors causing fatality counts to misrepresent collision vulnerability. Only two meta-analyses include evaluation of bird-building collisions across multiple sites and account for abundance and spatial sampling biases to generate vulnerability estimates (Arnold & Zink 2011; Loss et al. 2014). These quantitative syntheses included data from several independent studies with varying sampling protocols, which propagated uncertainty and bias into their meta-analysis results. Further, there are few studies on how avian life histories influence collisions or how correlates of collisions vary among species. One such study suggests forest-inhabiting, foliage-gleaning species collide more frequently at buildings surrounded by extensive vegetation, whereas open woodland-inhabiting, ground-foraging species collide more at buildings surrounded by intense urban development (Cusa et al. 2015). Results of another study show that some collision correlates (e.g., glass area) are relatively consistent among bird species, but there is also among-species variation in correlates (Loss et al. 2019). As with much of the bird-collision literature, these last two studies were conducted at single study sites.

A broad-scale assessment based on a coordinated data-collection approach across multiple sites and considering species- and life-history-related variation and correlates of collisions would help identify bird species and life-history groups most likely to need conservation. Such an analysis would also help identify suites of collision-mitigation approaches that are effective across many bird species. We conducted such an assessment with a bird-collision data set collected under a coordinated sampling protocol at 281 buildings across 40 study sites in the United States, Canada, and Mexico in fall 2014. Our objectives were to assess variation in species' vulnerability to building collisions; identify building and landscape-related correlates of collision numbers for individual species; and identify life history-related correlates of collisions.

## **Methods**

### *Study area and design*

We collected collision data through the Bird-Window Collisions Project under the Ecological Research as Education Network (EREN) (Hager et al. 2017). Collaborators from 40 university or college campuses in the United States ( $n=35$ ), Canada ( $n=3$ ), and Mexico ( $n=2$ ) (Figure. 1.1) collected data during fall migration (August-October) in 2014. At each campus, buildings ( $n=281$  total; range 4–21 per site) were selected by stratifying candidate buildings by size (small, medium, large) and surrounding vegetation cover (high, low) within 50 m, resulting in 6 total building strata (details in Hager et al. 2017).

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

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

Because carcass removal by scavengers and humans varies spatially, temporally, and among bird species, we minimized removal bias by conducting surveys daily (range 5–60 consecutive days/site) between 1400–1600. Carcasses typically persist for multiple days (Hager et al. 2012; Riding & Loss 2018), so daily surveys maximized probability of encountering a carcass before removal. We usually conducted afternoon surveys because some studies suggest that most collisions occur during morning and that most carcass removal by scavengers occurs overnight (Bracey et al. 2016, Hager et al. 2012).

However, surveys at Oklahoma State University were conducted from 0700–0900 due to high numbers of collisions in predawn and early morning hours at this site and removal peaking in the morning (Riding & Loss 2018). Although logistical constraints associated with coordinating research across 40 sites prevented experimental studies of carcass detection and removal at each site, the above protocol likely minimized detection and removal biases (Hager et al. 2012, 2013, 2017; Hager & Cosentino 2014).

All carcasses were collected and identified to species. For all analyses, we removed records for unidentified carcasses, species lacking distribution-wide population estimates, and species with distributions overlapping fewer than 10 sites. We conducted all analyses in R 3.4.4 (R Core Team 2018) unless otherwise noted. Survey protocols were approved by animal care and use committees at each authors' institution, and carcasses were collected under state permits and a U.S. Fish and Wildlife Service Salvage Permit (#MB08907A-0).

### *Measuring potential collision correlates*

Building characteristics, local vegetation, and regional urbanization were computed as described in Hager et al. (2017). Briefly, building metrics included window area (square meters calculated with tape measure or ImageJ [Abramoff et al. 2004]), number of stories above ground-level, and floor space area (square meters [building footprint area]). A single author used high-resolution aerial imagery in ArcMap 10.3 (ESRI 2011) to digitize and calculate local vegetation variables, including percent cover of grass, impervious surface, water, structure, and woody vegetation within 50 m of



buildings. We characterized regional urbanization by using a minimum convex polygon to estimate the proportion of urban cover within 5 km of the edge of the sampled cluster of buildings at each site. Because this study included the same buildings as in Hager et al. (2017), we used the results of their principal components analysis (PCA), which identified principal components capturing characteristics of buildings and their surroundings. To achieve multivariate normality, which improves PCA interpretation (McGarigal et al. 2000), all building metrics were log transformed and all local vegetation variables were logit transformed. The PCA was computed on the correlation matrix and three principal components (PCs) with eigenvalues  $\geq 1$  were retained as collision correlates with axis scores accounting for 70% of variance. The 3 PCs represented building size (e.g., number of stories, window area), local vegetation (within 50 m), and regional urbanization (within 5 km) (Hager et al. 2017).

### *Estimating species' vulnerability to collisions*

We defined species' vulnerability to collisions as the number of collisions relative to population size and geographic distribution overlap with study sites. This definition follows previous studies (Arnold and Zink 2011; Loss et al. 2014) in that it is based on the assumption that species with greater abundance and broader distribution overlap collide more frequently than less abundant or narrowly distributed species. To estimate continent-wide population size, we used the Partners in Flight Population Estimates Database 3.0 (Partners in Flight 2019). To estimate distribution overlap, we used Python 2.7 with ArcGIS 10.3 to count the intersection of our 40 campuses with species

distribution maps (BirdLife International 2016; ESRI 2011). Species distribution maps were visually examined in ArcGIS to ensure all parts of each species' distribution were included, and if portions were missing (usually the migration range), we used information from field guides to fill in missing portions (Sibley 2000; Rodewald 2015). For the subsequent vulnerability analysis, we included only species with  $\geq 2$  fatalities across study sites.

We estimated species' vulnerability with the approach of Arnold and Zink (2011) and Loss et al. (2014), with one modification. Briefly, they estimated vulnerability by using residuals from a fitted regression between species fatality counts and both population size and distribution overlap with study sites. However, we regressed a novel response variable, birds per effort (BPE) on only a single predictor variable (population size) because BPE accounts for species' distribution overlap with sites, as well as varying numbers of surveys at different sites and buildings. We indexed BPE by species ( $i$ ) and calculated  $BPE_i$  by dividing total numbers of fatalities by the total number of days surveyed at all buildings within that species' distribution. We treated species as replicates and fit the relationship between  $BPE_i$  and population size (while fixing regression coefficients to 1) as

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

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

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

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

#### *Identifying collision correlates for individual species*

To identify correlates of collision numbers for individual species, we used generalized linear mixed models (GLMMs) in the glmmTMB package (Brooks et al. 2017) to examine relationships between the three PCA-derived latent variables (predictors) and species' fatality counts (response variable), with individual buildings as replicates ( $n=281$ ). These models were similar to those used by Hager et al. (2017); however, instead of assessing total collisions as the response variable, we conducted separate analyses for 8 species with  $\geq 10$  collisions observed. For each species, we considered models with 14 different combinations of predictor variables: a null model, models for each additive combination of predictors, and models with a single interaction effect and up to one additional predictor (Supporting Information). For each variable combination, we specified one model with a negative binomial (NB) error distribution (to

account for overdispersion) and one model with a zero-inflated negative binomial (ZINB distribution) due to the large number of buildings with no collisions observed. For all 28 resultant candidate models, we specified an offset for log-transformed numbers of surveys (to account for varying effort). We used AIC in the *bbmle* package to rank models (Bolker 2017), eliminated uninformative parameters, and considered models supported when their  $\Delta\text{AIC}=0-2$  and at least 2 above the null model (Arnold 2010). If multiple models were strongly supported, we used conditional model averaging in the *MuMIn* package (Barton 2018) to generate coefficient estimates. Regardless of whether coefficient estimates were from a single model or averaged models, we considered predictor variables meaningful if 95% CIs of coefficient estimates did not overlap zero.

#### *Assessing influence of life history on collisions*

We classified species according to their migratory status and primary habitat (Langham et al. 2015) and their main food resource (González-Salazar et al. 2014, Rodewald 2015). To analyze life-history influence on collision numbers, we merged classifications for these three characteristics into binary categories describing migration status (migratory or nonmigratory), primary food (insectivorous or noninsectivorous), and primary habitat (woodland or nonwoodland). We used GLMMs with a NB error distribution because a preliminary analysis comparing NB and ZINB versions of the below-described full models determined there was greater support for the NB distribution. We specified an offset for log-transformed numbers of surveys and a random effect for building nested within site to account for nonindependence of multiple

replicates for each building and buildings within sites. We included the three PCA-derived latent variables from the species-level correlate analysis as predictors to account for known sources of variance, but because these were not of primary interest for this analysis we did not interpret the significance of these predictors.

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

## **Results**

Surveyors found 324 bird carcasses (said above). After applying our filtering protocol for species with limited information or distributions, we retained for analysis 269 carcasses of 64 species. The most frequently found species were Ruby-throated

Hummingbird and Common Yellowthroat (*Geothlypis trichas*), with 22 and 21 collisions respectively.

### *Species' vulnerability to collisions*

After removing species with  $\leq 2$  fatalities, we retained 240 carcasses from 40 species for our estimation of collision vulnerability. Estimated collision vulnerability varied from 1 species 32 times more likely than average to collide to another species 10 times less likely to collide than average (all estimated vulnerabilities in Supporting Information). The 10 most vulnerable species were Black-throated Blue Warbler (*Setophaga caerulescens*), Ovenbird, Ruby-throated Hummingbird, Yellow-bellied Sapsucker, Wood Thrush (*Hylocichla mustelina*), Brown Thrasher (*Toxostoma rufum*), White-breasted Nuthatch (*Sitta carolinensis*), American Goldfinch (*Spinus tristis*), Gray Catbird (*Dumetella carolinensis*), and Common Yellowthroat (Table 1.1). Vulnerability was not correlated with body size ( $r=-0.04$ ,  $p=0.79$ ) or plumage conspicuousness ( $r=0.15$ ,  $p\text{-value}=0.35$ ), suggesting minimal influence of observer detection probability on vulnerability estimates.

### *Collision correlates for individual species*

Collision correlates were evaluated for 8 species with  $\geq 10$  fatalities (vulnerability range +6.2 to -2.5) (Table 1.2). For all species, top models included NB distributions as opposed to ZINB distributions, despite the fact that most counts were zero. The first PC

described building size and included positive loadings of building height, window area, and floor space area. That PC was a positive predictor of collision numbers for 5 of the 8 species (all except Swainson's Thrush [*Catharus ustulatus*], White-throated Sparrow, and Dark-eyed Junco [*Junco hyemalis*]). The second PC represented vegetation cover within 50 m of buildings and included a positive loading of impervious surface and negative loading of woody vegetation. That PC was a negative predictor of collisions only for Swainson's Thrush. Some top models included variables not meaningfully associated with fatalities such as the third PC (which included a positive loading for regional urbanization) and an interaction between the building size PC and local vegetation PC for one species. Other interactions were not included in top models for any species (Table 1.2; Supplementary Information).

#### *Influence of life history on collisions*

The top and only competitive model for the life-history analysis included the building size PC and all 2-way interactions among the 3 life-history variables (Figure 1.2; model rankings in Supporting Information). The interaction terms in our models indicated that migratory species collided more than nonmigratory species, and that this difference was more pronounced for woodland-inhabiting and insectivorous species. Likewise, traits associated with being insectivorous increased collision numbers for woodland-inhabiting species but decreased collisions for species inhabiting other vegetation types (i.e., traits associated with being a woodland-inhabitant were associated with increased collisions for insectivores and decreased collisions for noninsectivores).

However, differences in collision numbers between primary food and primary habitat were small (Figure 1.2c).

## **Discussion**

### *Species' vulnerability to collisions*

Of the 10 bird species most vulnerable to building collisions, 7 (Black-throated Blue Warbler, Ovenbird, Ruby-throated Hummingbird, Yellow-bellied Sapsucker, Wood Thrush, Gray Catbird, Common Yellowthroat) have been documented as highly vulnerable in past multi-site studies (Arnold & Zink 2011; Loss et al. 2014). The other 3 (Brown Thrasher, White-breasted Nuthatch, American Goldfinch) have not been identified previously as highly vulnerable. These novel findings may have arisen due to our coordinated sampling and differences in geographic extent and survey season between our study and previous studies, the more-recent bird population estimates we used, or the more-limited number of species analyzed (i.e., some species may have ranked as highly vulnerable only because of the smaller number of competing species that we ranked).

Estimating collision vulnerability, as opposed to raw fatality counts, may provide insight into the likelihood of population-level effects of building collisions. Of our 10 most-vulnerable species, American Goldfinch, Brown Thrasher, Wood Thrush, and Common Yellowthroat populations have declined since 1970 (Rosenberg et al. 2019), and Wood Thrush is a “bird of conservation concern” in the United States (NABCI 2016). Other human-related factors, such as habitat loss, are undoubtedly driving declines



for these and many other migratory bird species. Nonetheless, our results and those of past studies (Arnold and Zink 2011; Loss et al. 2014) indicate that building collisions are also potentially contributing to declines, especially for the most vulnerable species colliding in greatest numbers relative to their abundance. Further, mortality during migration can affect bird populations, including for species we found to be highly vulnerable to collisions (e.g., Black-throated Blue Warbler, Wood Thrush) (Silllett & Holmes 2002; Rushing et al. 2017). Although specific sources of mortality have not been identified, we suggest building collisions during migration could be a major factor, and further research is needed to analyze the link between collisions and demography for migratory bird species.

Our broad-scale, coordinated sampling approach expands on previous vulnerability analyses (Arnold & Zink 2011; Loss et al. 2014) in part by accounting for biases associated with among-site variation in data collection protocols. That said, our results would have been more robust if we had observed more species with distributions that overlapped  $\geq 10$  sites. As a result of including only 40 such species, some of those we analyzed that had low population sizes or distribution overlap with sites could have artificially high vulnerability estimates if observed in relatively large numbers at a small number of sites. Similarly, incorporating local abundance estimates, rather than continent-wide estimates, would further improve vulnerability estimates (see “Future Directions”). Finally, like all other vulnerability studies, the exact value of indices for species are not comparable with those from other studies. This limitation is especially important to consider for rare species that may collide in low numbers. These taxa are

difficult to detect in short-term collision surveys (Beston et al. 2015), but their populations may be affected by only a few collisions.

*Collision correlates for individual species*

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

Although past studies suggest more collisions occur at buildings surrounded by extensive vegetation and limited impervious surface (Hager et al. 2013; Cusa et al. 2015; Ocampo-Peñuela et al. 2016; Schneider et al. 2018), we only found evidence for such effects for one species, Swainson's Thrush. Since Swainson's Thrush is commonly associated with forested habitat with dense undergrowth (Mack & Yong 2020), this

species may be more likely to frequent areas near buildings with extensive woody vegetation, increasing numbers of collisions.

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

#### *Influence of life history on collisions*

Life history was associated with number of collisions, a finding with important implications for predicting and managing collisions across species with similar traits and for understanding how traits mediate collision risk. Migratory species collided more than nonmigrants (Arnold & Zink 2011; Loss et al. 2014; Wittig et al. 2017). Migrants may collide more because nocturnally migrating species, which comprise the majority of migrants, are more prone to attraction and disorientation from ALAN (Lao et al. 2020; Winger et al. 2019). More generally, migrants could be at greater collision risk as a result

of encountering more buildings over their annual cycle due to traversing a greater area and longer distances (Moore & Aborn 2000).

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

It is possible our classification of life history based on binary predictor variables (e.g., migratory or nonmigratory) resulted in the loss of some potentially valuable information. Future studies with larger numbers of collisions and more species observed may allow assessment of more refined categories (e.g., long, medium, and short distance migrants) to provide greater understanding of how life history influences numbers of collisions. Further, our focus of sampling during fall migration led to an inherent bias

toward migratory species because migrants typically collide more than residents do during migration (Riding 2019). Future studies could assess life-history-related effects across different seasons.

### *Future Directions*

The large spatial extent of our study required sampling during 1 fall migration only; including multiple seasons and years would be an improvement. Related, future studies should attempt to sample more collisions while maintaining a coordinated sampling approach. In addition to a longer sampling period, number of collisions and species could be increased by coordinating citizen science efforts to study bird collisions across multiple cities and using molecular techniques to identify bird carcasses that would otherwise be unidentifiable. Future studies could also quantify and account for bird abundance, which influences collision numbers and varies regionally relative to factors such as latitude, longitude, and proximity to major migration flyways, including those associated with geographical features (e.g., coastlines and mountain ranges). Local species abundance could be estimated with data from public databases (e.g., eBird; Sullivan et al. 2009) or surveys conducted near buildings, and total abundance of migrants could be quantified with weather radar (Van Doren and Horton 2018). Studies should also evaluate sampling bias associated with birds colliding and exiting the survey area before dying and assess risk correlates related to bird vision and morphology, which may influence collision avoidance or the proportion of collisions that are fatal. Finally, future research should attempt to verify species and life-history-related correlates of

collisions because our 16 assessments of 95% CIs of model coefficients to infer variable importance increased probability of type I error (i.e., apparently significant effects arising by chance). We chose to not use the Bonferroni correction to account for multiple assessments (i.e., increasing the CI width used to infer meaningful effects) as it would result in all supported variable coefficient CIs overlapping 0. Many of our documented effects may be biologically important, and Bonferroni correction has been criticized for being overly conservative (i.e., resulting in type II error) (Moran 2003).

### *Implications*

The rankings of vulnerability to building collisions we produced highlighted species with the greatest numbers of collisions relative to population abundance, which are pertinent species on which mitigation steps to reduce building collisions should be focused. Our analyses of species-specific collision correlates at buildings on academic campuses provide further evidence for focusing mitigation on relatively large buildings in these settings and on even larger buildings in urban centers (e.g., skyscrapers in major cities). Our results also support the importance of constructing buildings with smaller expanses of reflective or transparent glass and treating glass on existing buildings. Policies and guidelines to reduce collision risk at new and existing buildings are becoming much more common (San Francisco Planning Department 2019), and there are a growing number of commercially available options to make existing and new glass more bird friendly (e.g., fritted glass, films, decals, netting, or shades) (Klem 2015). Our results also highlight that no single mitigation approach may be effective for all birds and

that species-specific correlates should be considered when managing collisions. Finally, our life-history analysis may aid in developing mitigation approaches that address life-history-related risk factors (e.g., reduction of ALAN during migration to reduce mortality of migrants; Winger et al. 2019).

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## **Supporting information**

Candidate models, coefficients, and CIs from top models for analysis of species-specific collision correlates (Appendix S1), list of participants collecting data (Appendix S2), full candidate model and output for all life-history models (Appendix S3), and estimated collision vulnerability for all species (Appendix S4) are available online. The

authors are solely responsible for content and functionality of these materials. Queries (other than absence of material) should be directed to the corresponding author.



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Table 1.1. Building collision vulnerability estimates for 10 most vulnerable bird species from fall 2014 collision monitoring at 40 sites across North America.

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



Table 1.2. Direction of the relationship<sup>a</sup> of correlates<sup>b</sup> of bird-building collision fatalities for individual species.

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

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

<sup>b</sup>From top supported generalized linear mixed models compared with Akaike's Information Criterion.

<sup>c</sup>Represent principal components derived by Hager et al. (2017).

<sup>d</sup>Variables with 95% CIs of coefficients overlapping zero.

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

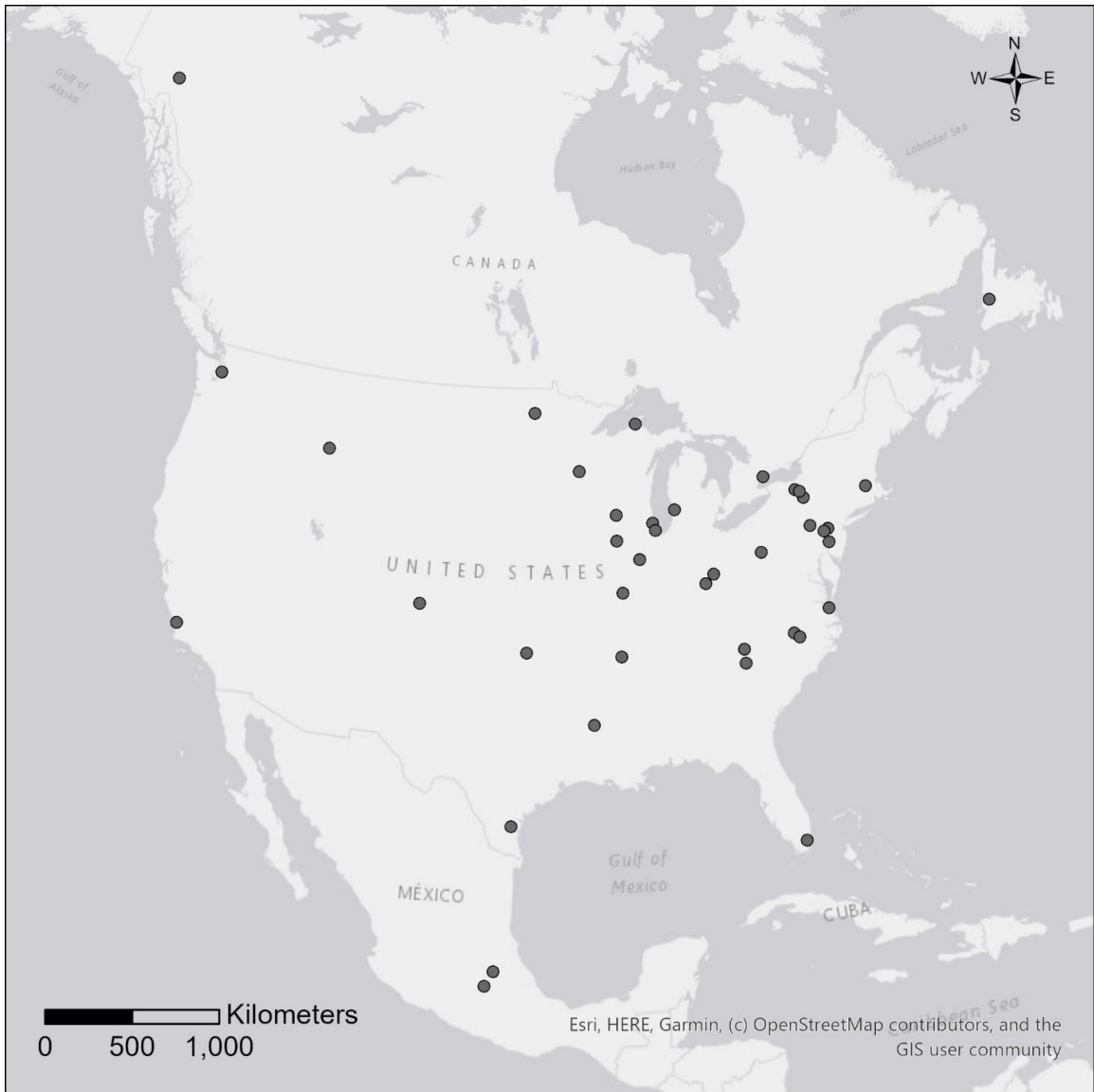


Figure 1.1 Locations in Canada, the United States, and Mexico where bird-building collision monitoring was conducted during Fall of 2014.

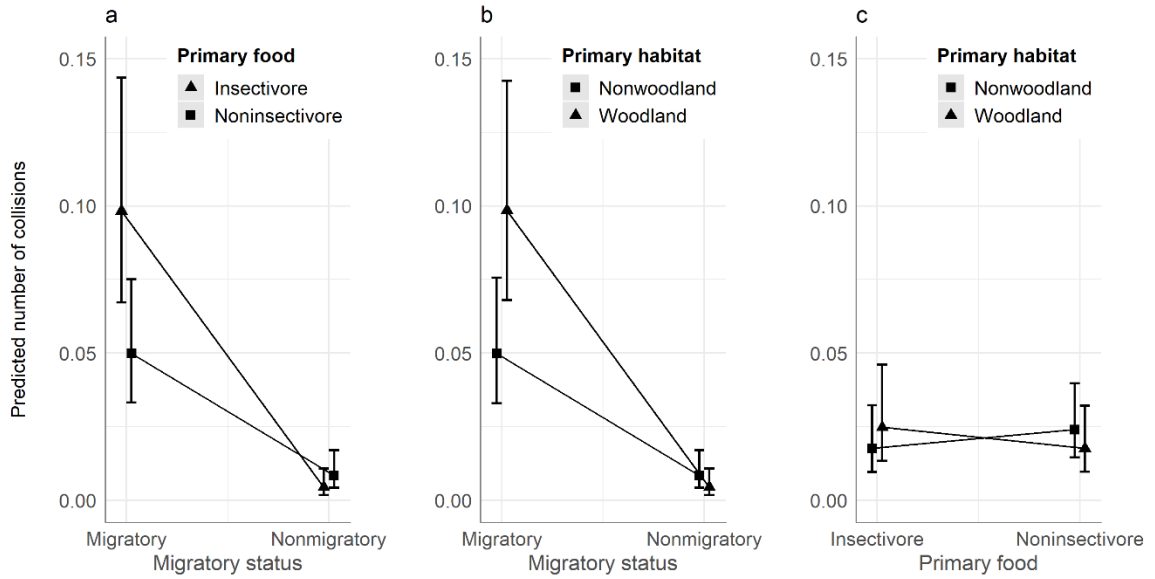


Figure 1.2 Associations of life-history characteristics with numbers of bird-building collisions per replicate (predicted effects based on the fitted generalized linear mixed model): (a) interaction between migratory status and primary food, (b) interaction between migratory status and primary habitat, and (c) interaction between primary food and primary habitat (bars represent 95% CIs).

## CHAPTER II

### PREDICTING MIGRATORY BIRD-WINDOW COLLISIONS USING WEATHER RADAR

#### **Abstract**

1. Up to one billion birds die annually in the U.S. from window collisions; most of these casualties represent migratory native species. Because this major mortality source likely contributes to the decline of the North American avifauna, mitigation tools are needed that accurately predict real-time collision risk, allowing hazards to be minimized before mortality occurs.
2. We assessed the use of weather surveillance radar, a developing and increasingly used tool for studying and predicting bird migration, to provide an invaluable early warning system to reduce collisions.
3. Based on bird-window collision monitoring in Oklahoma, USA, we show that radar-derived migration variables are associated with daily collisions. Across the entire night, higher migration traffic rate and lower flight height were associated with increased collisions, and migration variables for periods within the night were also related to collisions.

4. Our results suggest radar can predict bird-window collisions and help refine mitigation efforts that reduce collisions (e.g., reducing nighttime lighting).

## **Introduction**

Human structures and activities are increasingly encroaching into the aerosphere, the aerial habitat used by volant animals (Lambertucci et al. 2015). Collisions with human-built structures (e.g., buildings, communication towers, energy infrastructure) are a major threat in the aerosphere, causing up to 1.5 billion avian fatalities annually in the United States (Loss et al. 2015). Collisions with buildings, especially their windows, cause up to 1 billion of these annual fatalities and primarily affect migratory native bird species during migration periods (Loss et al. 2014). Nocturnal migrants comprise the majority of these casualties and are the most frequent collision victims at buildings and many other structures (e.g., communication towers), partly due to attraction and disorientation caused by artificial lighting at night (ALAN) emanating from and near buildings (Lao et al. 2020, Winger et al. 2019). Collisions may occur when birds are ascending to migration cruising height during time periods near dusk or dawn, or during other times of night when birds are forced to lower altitudes due to changing weather conditions (Lao 2019).

Mitigation to reduce bird collisions (e.g., reducing nighttime lighting), including the hundreds of millions of window collisions, would be improved if collision risk could be related to numbers of migratory birds aloft. This relationship would provide a mechanism to use migration forecasts as a proxy for collision risk. Nocturnally migrating birds are extremely difficult to monitor because direct visual observation of birds flying

under cover of darkness and at high speed and altitude is often impossible. Acoustic monitoring can help identify species composition of migratory birds aloft but is severely constrained by species' behavior and factors influencing detection (e.g. distance, signal-to-noise ratio) (Farnsworth 2005, Sanders and Mennill 2014). Weather surveillance radar (WSR) is a proven tool for monitoring nocturnally migrating birds and other organisms in the aerosphere (Horton et al. 2016). Recent studies have used radar to examine how abiotic variables (e.g., wind, barometric pressure, precipitation) influence flying animals (e.g., flight timing, speed, orientation, direction, and altitude) (Dokter et al. 2013). Radar-derived estimates of migration traffic rate, speed, and heading have shed unprecedented light on bird migration and could be valuable for predicting collisions with manmade structures (Shamoun-Baranes et al. 2016).

Recent technological advances using radar—including machine learning approaches that enhance the ability to discern biological signatures from precipitation (Lin et al. 2019) and continent-scale prediction of bird migration (Van Doren and Horton 2018)—suggest the possibility of characterizing broad-scale relationships between collisions and radar-derived estimates of aerial migration activity. However, only small-scale applications of mobile, low-powered, marine surveillance radar units (Gauthreaux and Besler 2003) have been investigated. The larger, higher-powered WSR-88D (NEXRAD) network, which includes 143 units across the continental U.S., has been employed for near real-time, broad-scale monitoring and forecasting of bird migration (Horton et al. 2016, Van Doren and Horton 2018), and could allow broad-scale prediction of bird-structure collisions.

To test the use of NEXRAD to predict bird collisions more broadly, we conducted bird-window collision monitoring in Stillwater, Oklahoma, USA, and related daily-observed fatalities to radar-derived measures of nocturnal bird migration. We considered radar derived bird migration traffic rate, speed, and height averaged across entire nights preceding collision surveys and variables for particular periods of the night.

## **Materials and methods**

### *Collision data*

We conducted collision monitoring six days/week at 17 buildings in Stillwater, Oklahoma, a small urban area with only three buildings taller than five floors. Stillwater covers a geographic area of approximately 76.51 km<sup>2</sup>, has an estimated human population of 50,299 in 2019 (United States Census Bureau), and is located in the cross-timbers ecoregion (a transitional zone where eastern deciduous forests interlace with grasslands of the Great Plains). Study design and collision surveys are fully described in Riding et al. (2020), and surveys were conducted during spring migration (April-May) 2015-2017 and fall migration (September-October) 2015-2016. Monitored buildings were selected based on size and amount of surrounding vegetation; selected buildings were less than 27 m tall and included residences, commercial and university office buildings, and an athletics facility. Authors, technicians, and citizen scientists conducted surveys, which began between 0700-0900 CST. Surveyors walked around each building (alternating directions on successive days) searching for bird carcasses within two meters of the base

of buildings and documenting species or descriptions of all carcasses/remains (Figure 1). When a carcass was discovered, we took photographs, documented location and descriptive information, and collected remains in sealable plastic bags. We summed total fatal collisions across all buildings for each day, only considering individual birds that were likely migrants based on species and collision date. Residency status (e.g., resident, migrant, or unknown) was determined for individual birds based on the date of collision occurrence, bird age (e.g., hatch year birds unlikely to migrate in late spring or early summer), seasonal occurrence data from eBird (Sullivan et al. 2009), and specific dates associated with arrival, migration, and departure for our study area (Oklahoma Bird Records Committee 2014). We used information from experimental carcass removal and surveyor detection trials, conducted at the same buildings and time, to generate nightly adjusted fatality estimates that account for carcass removal by humans and animals and imperfect detection by surveyors (Riding & Loss 2018).

#### *Radar-derived migration data*

We collected radar data from level-II NEXRAD archived on the Amazon Web Services cloud (Amazon Web Services, Ansari et al. 2017), which scans the airspace every 5-10 minutes, collecting data in each 250 m-radius horizontal distance band centered on the radar. The radar also collects elevation-specific information within each distance band, allowing characterization of the distribution of birds' flight heights. Because our study area was >85 km from all NEXRAD installations, estimates of migration variables were averaged among three Oklahoma radar sites (KTLX in Oklahoma City, KVNK in Jet, KINX in Inola) (Figure 2). We averaged measures across all scans for the entire night preceding each collision survey (civil dusk to civil dawn,



with times shifting seasonally, i.e., inclusive of times when the sun is  $\geq 6^\circ$  below horizon), and for four time periods within the night associated with different intensities of bird migration and varying effects of weather conditions on collisions (Lao 2019). These periods included: (1) civil dusk until one hour later, (2) one hour after civil dusk until the nightly midpoint between civil dusk and dawn, (3) the nightly midpoint until one hour before civil dawn, and (4) one hour preceding civil dawn.

We used the bioRad package (Dokter et al. 2018) in R version 3.5.3 (R Core Team 2019) to extract bird migration variables for each scan 5-25 km from each radar. We used recommended settings of algorithm parameters in the ‘calculate\_vp’ function to filter out precipitation (correlation coefficient threshold set to 0.95) and insects (standard deviation of volume velocity profiling technique threshold set to one m/s) (radar cross-section of individuals=11 cm<sup>2</sup>; Dokter et al. 2018). We calculated three specific radar-derived migration variables (averaged across all horizontal bands and heights for each radar, then averaged across radars): migration traffic rate (MTR), speed, and height. We define MTR as number of birds hr<sup>-1</sup> within the elevation layer of interest crossing a one km line perpendicular to migratory direction. The unit for MTR was birds km hr<sup>-1</sup> calculated as: MTR=bird density (birds km<sup>-3</sup>) x bird speed (km hr<sup>-1</sup>) for each layer (height in km above ground). We define speed as distance covered over time at ground level (groundspeed) and height as average height above ground level at each radar location (since height above sea level varies among these).

## *Statistical Analyses*

We used generalized linear models with a normal error distribution (adjusted fatality estimates were continuous, not counts) to relate nightly adjusted fatality estimates (replicate=night) with MTR, speed, and height. For highly correlated predictors ( $|r| \geq 0.7$ ), we used variable importance rankings from the party package (Strobl et al. 2008) to determine which to retain for analysis. Highly correlated variables were never included in the same model. For analyses with migration variables averaged across the entire night (three analyses, one each for spring and fall and one for both seasons combined), no predictors were highly correlated, thus candidate models included all additive combinations of predictors along with all combinations of two- and three-way interactions. For analyses with migration variables calculated for separate periods of night (two analyses, one each for spring and fall), candidate models included all additive combinations of predictors and two-way interactions of each radar-derived predictor variable with MTR from each time period (MTR was determined extremely important in variable importance rankings, but was often highly correlated across different times periods within a night). Although most buildings were surveyed 6 days/week, we occasionally missed surveys at one or a few buildings and only one building was surveyed on Sundays. These differences in surveys were incorporated into the estimation of carcass removal used to generate nightly adjusted fatality estimates (Riding and Loss 2018). This variation in survey effort was further accounted for in our modeling approach by including an offset for number of buildings surveyed in all models. We used Akaike's information criterion (AIC) in the bbmle package (Bolker 2017) to rank models and considered models competitive when  $\Delta AIC = 0-2$  and at least two less than the null model,

after elimination of uninformative parameters (Arnold 2010). Variables in supported models were considered meaningfully associated with collisions when 95% confidence intervals (CIs) of coefficient estimates did not overlap zero. When there were multiple competitive models, we used model averaging in the MuMIn package (Barton 2018) to recalculate beta coefficients and CIs.

## Results

We conducted 3857 collision surveys (i.e., a survey entailed one building being surveyed once) with 2246 surveys in spring, 1582 in fall. We collected 304 total carcasses of which 227 carcasses (54 different species) were considered migratory for our study area. Our total adjusted fatality estimate across all buildings, considering only migrant individuals and accounting for carcass removal and detection, was 270 birds (spring=163; fall=107). At least one collision occurred on 85 days in spring and 42 days in fall; the greatest daily collision count in each season was seven birds.

For analyses with radar-derived migration variables averaged throughout the night, top models for both spring (n=179 days) and fall (n=122 days) included an MTR\*height interaction; however, 95% CIs of coefficients for these variables overlapped zero (Supplementary Tables). When pooling spring and fall (n=301 days), the top model again included an MTR\*height interaction, and 95% CIs did not overlap zero, indicating a meaningful effect. This suggests sample size limited the apparent importance of the MTR\*height interaction in separate-season analyses, and that this factor may be important regardless of season. The negative coefficient for this interaction term (Figure

3a) indicates collision fatalities increase with increasing MTR, and that this effect is strongest when migration heights average lower.

For the spring analysis with migration variables calculated for different periods of night, the best model included two-way interactions between MTR at civil dusk and three other factors (speed at civil dusk, speed at civil dawn, MTR at civil dawn; Supplementary Tables). The first two interactions indicate fatalities increase with MTR, especially when migration speed is lower at dusk or higher at dawn (Figure 3b, c). The other interaction indicates fatalities increase when MTR is high at either civil dusk or dawn, but not at both times (Figure 3d). For the fall analysis for different periods of night, top models were averaged and included MTR at civil dawn and an interaction between MTR for the first half of night and speed at civil dawn (Supplementary Tables). The positive coefficient for this interaction indicates collision fatalities increase with increasing MTR during the first half of night, and that this effect is strongest when flight speeds are higher at dawn (Figure 3e). This model also indicates fatalities decrease with increasing MTR at dusk (Figure 3f). All above-mentioned variables were meaningful as indicated by 95% CIs not overlapping zero.

## **Discussion**

The ability to predict bird-window collisions would greatly benefit efforts to mitigate this substantial threat to birds, and thus contribute to halting and reversing widespread declines of avian populations (Rosenberg et al. 2019). We show that radar-derived migration variables were associated with daily numbers of bird-window collisions in Stillwater, Oklahoma, USA. Although further research in multiple study

areas is needed to confirm the broad-scale predictive capability of the NEXRAD network across North America, our findings show that radar has strong potential to help refine management approaches that reduce bird collisions with buildings, and perhaps other human-built structures.

For both spring and fall analyses of radar-derived variables averaged throughout the night, daily collisions were positively associated with MTR, especially when migration heights were lower. Migrating birds are thought to fly at high altitudes to gain beneficial wind currents that aid migration (Dokter et al. 2013), but another benefit of higher migration may be avoidance of human-built structures in the airspace and/or light pollution associated with buildings and cities (Horton et al. 2019). Other studies have speculated that when large numbers of birds migrate at low heights, collisions with human-built structures (e.g., wind turbines) likely increase (Drewitt and Langston 2006, Furness et al. 2013). However, these studies have focused on risk prediction, and no research has validated the predicted relationship between flight height and collisions. Thus, even in our study area where the tallest monitored buildings were not above 27m, our results support the riskiness of low flight, at least in the context of bird-building collisions. Bird migration heights vary temporally in association with time of year, time of day/night, and multiple interacting weather conditions, including presence of low cloud ceilings, headwinds, and precipitation (Bruderer et al. 2018, Dokter et al. 2013, Lao 2019). Further, ALAN “sky glow” is exacerbated by low clouds and precipitation (Kyba et al. 2015), conditions which may make light even more likely to attract low-migrating birds near buildings, where they immediately collide or collide later when making smaller-scale movements near buildings.

Analyses for separate periods of night provide further insight into how collision mitigation may be effectively targeted toward particular time periods and/or weather conditions. Spring collisions increased when MTR was high at dusk, especially when flight speed was low at dusk or high at dawn. Fall collisions increased when MTR was high in the first half of night, especially when flight speed was high at dawn. In spring, high MTR and low flight speeds at dusk could indicate unfavorable conditions (e.g., headwinds) causing difficulty in migration exodus and ascending to cruising height. This could increase collisions directly (e.g., collisions at dusk for low-flying departing individuals) or indirectly—including later at night and toward dawn—by affecting numbers of migratory birds forced to return to or stay in terrestrial habitat, discontinuing migration in aerial habitat. For both spring and fall, the enhanced effect of early-evening (i.e., civil dusk and first half of night) MTR when dawn flight speeds are high may reflect that large volumes of birds in early portions of night are responding to conditions that facilitate high speeds later in the night or at dawn. Fall collisions also decreased when MTR was high at civil dusk; this may reflect favorable conditions early that hold steady throughout the night, leading to a large exodus at dusk rather than later and continuation of migration throughout the night. Spring collisions were high with high MTR at dusk or dawn, but not both. This effect of high MTR at dawn in association with low MTR at dusk, or vice versa, may reflect poor conditions at one time of night and favorable conditions at another time. For example, headwinds and precipitation followed by tailwinds and clear skies, or tailwinds and clear skies followed by inclement weather, could respectively cause birds to initiate or discontinue migration in the middle of the night. The observation that spring collisions do not increase when MTR is either high or

low at both dusk and dawn suggests that conditions favoring consistently high or low MTR throughout the night reduce collision risk.

Although the above results strongly suggest the utility of radar for predicting bird collisions, increased predictive understanding of collisions requires studies that merge radar and meteorological data to assess how birds alter migration in response to the interaction between weather and lighting at different times of night. Our study was in a small urban area with few tall buildings and less ALAN area compared to larger urban areas. We expect patterns exhibited by our results to be even more pronounced in areas with numerous tall structures and more area or higher intensity of ALAN because large amounts of lighting projected into the aerosphere greatly alters MTR, flight height, and speed, attracting migrants (Horton et al. 2019, Van Doren et al. 2017) and elevating window collision rates in urban areas (Lao et al. 2020, Winger et al. 2019). Further, even though our study was >85 km from the three radar installments, radar derived variables from 5-25 km were still associated with collisions. This suggests using distant radars is still a valid approach and that study areas closer to radar sites are likely to more strongly predict collisions.

### *Conclusion*

Bird-window collisions are an increasing threat to migratory birds due to urban expansion, infrastructure growth, and increasing ALAN (Cabrera-Cruz et al. 2018, Horton et al. 2019, Kyba et al. 2016, Seto et al. 2012). We show that collisions are associated with radar-derived measurements of migration, including migration traffic rate, height, and speed. In addition to high MTR and low migration height being

associated with collisions based on nightly measurements of these migration variables, measurements for particular periods of night were also related to collisions, which suggests potential for these measurements to help refine collision predictions. Our study highlights the importance of using radar data to inform mitigation such as lighting reduction policies and guidelines (e.g., Audubon’s “Lights Out” program), which may decrease avian attraction, increase flight height, and reduce collisions for migratory birds. Implementation of such mitigation may be particularly important on nights when bird migration is forecast to be intense with low flight heights, when migration traffic rate is expected to be high at dusk and low at dawn (e.g., when storm fronts are forecasted to drastically alter migration conditions overnight), or when migration speed is high at dawn. Our results indicate the potential for near-real time, continent-scale prediction of bird collisions based on modification of algorithms used in existing bird migration forecasts such as BirdCast (Van Doren and Horton, 2018). Although further studies should be conducted across multiple sites at broader spatial scales, radar has potential to predict bird collisions at a wide variety of human-made structures, and thus contribute to reducing human-caused mortality that affects North American bird populations.

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### **Data availability**

All radar data used in this analysis is open access and archived on the Amazon Web Services cloud (cited in text). The full dataset of bird collisions used in this analysis is currently being used in ongoing research but will be made available upon acceptance.

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Figure 2.1. Collisions with building windows annually cause up to 1 billion bird fatalities in the United States. This (a) Ruby-throated Hummingbird (*Archilochus colubris*) and (b) Yellow-breasted Chat (*Icteria virens*) were both collision casualties found at our study site in Stillwater, Oklahoma, USA where we conducted (c) near-daily surveys of building perimeters to document bird collisions during migration periods.

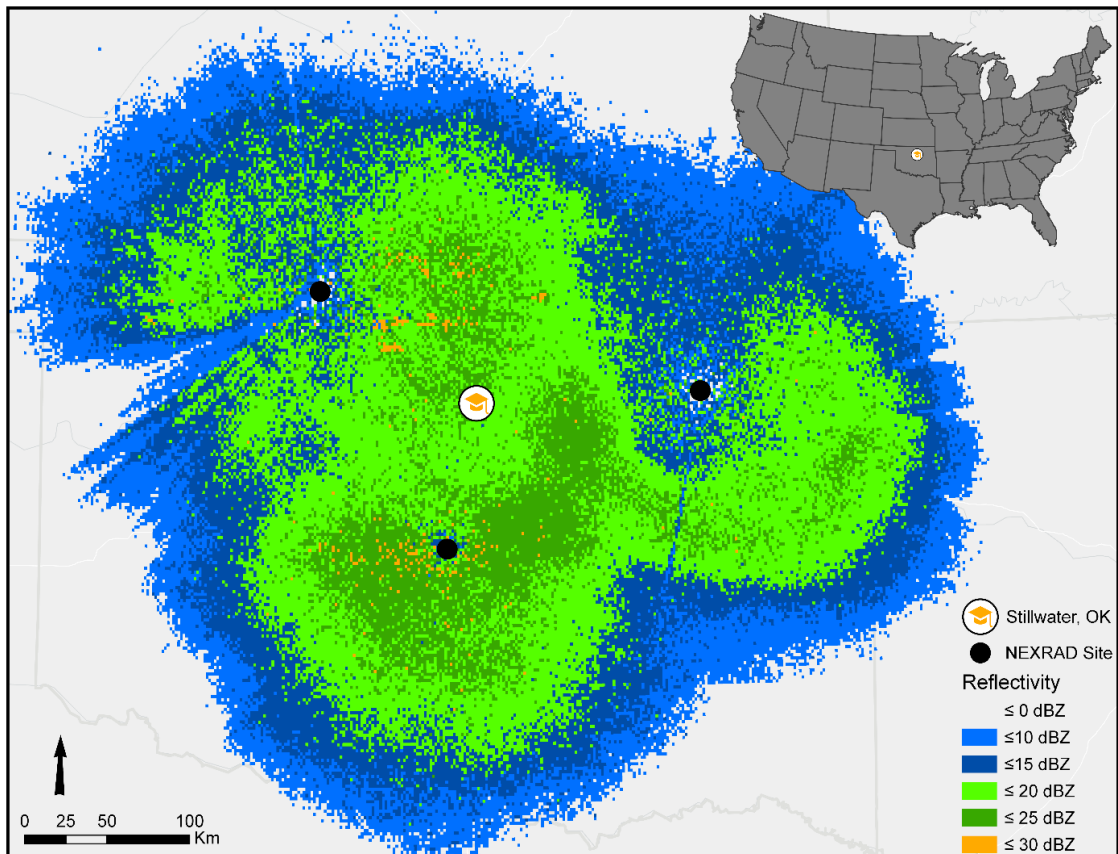


Figure 2.2. Map of Stillwater, Oklahoma, USA, with three surrounding NEXRAD sites used for data analysis (color overlay represents radar-derived reflectivity; estimated numbers of birds aloft increases with increasing reflectivity). Because NEXRAD sites were >85 km from Stillwater, data were averaged across these three radars (although



image shows reflectivity beyond 25 km from each radar, but we only used data 5-25 km from each radar to generate migration variables; see text for details).

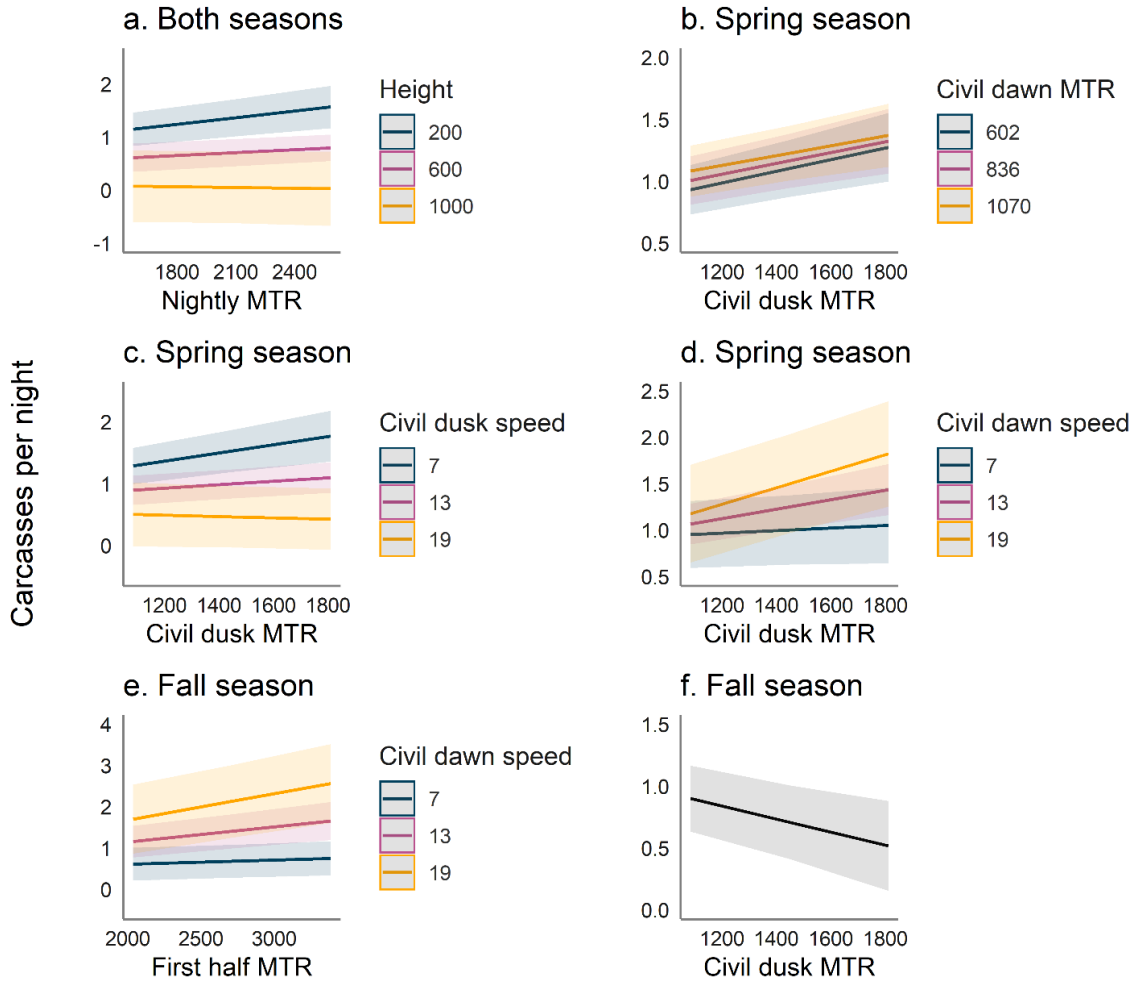


Figure 2.3. Predicted number of migratory bird collisions per night based on radar-derived migration variables averaged throughout the night for both spring and fall migration (a) and during different time periods within the night for spring (b & c) and fall (d, e, & f). MTR ranges shown reflect the actual distribution of three standard errors of the mean MTR for each time period.

## CHAPTER III

### HABITAT USE BY MULTIPLE SHOREBIRD SPECIES DURING MIGRATORY STOPOVERS IN THE NORTH AMERICAN GREAT PLAINS

**Abstract.** Wetlands are crucial ecosystems that provide many ecosystem services and functions, yet habitat loss has reduced wetlands in the United States (U.S.) by >50% since European settlement. Shorebirds are one group of species that are in decline due to wetland loss, especially since they often have very specific habitat requirements due to their complex, morphology-driven life histories. Some migratory species travel great distances and rely on migratory stopover sites in the Great Plains to refuel along their perilous journeys, and research is needed to better understand how different species respond to extent and connectivity of wetlands at broad spatial scales, as well as features at fine, individual wetland spatial scales. We addressed this research need using data from >14,000 wetlands in north-central Oklahoma using zero-inflated generalized linear mixed models to examine the influence of wetland availability at multiple broad spatial scales and of fine scale wetland characteristics on 14 different shorebird species. We found some variation in species response to broad scale habitat availability, with most species using a 500m spatial scale. We also noted some variation in strength of response across species both in comparison to broad scale habitat availability and to fine scale

features. Species responded fairly similarly to fine scale features but again there was variation in effect size. Our results help to improve the understanding of species specific habitat needs, which may lead to different conclusions than for all shorebirds combined, which informs best management practices for restoring and conserving crucial shorebird wetland habitat, especially for species of conservation concern.

## **Introduction**

Wetlands provide important ecosystem services and functions to human societies, including flood and erosion control, sediment and nutrient retention, groundwater recharge and discharge, biodiversity hotspots, education and recreation opportunities, and cultural values (Henley and Harrison 2000, Turner et al. 2000, Woodward and Wui 2001). Human-caused habitat loss has reduced the extent of U.S. wetlands by >50% since European settlement (Davidson 2014, Mitsch and Gosselink 1993, Henley and Harrison 2000), and most remaining wetlands are highly degraded. The North American Great Plains have experienced the most severe wetland loss of anywhere in the U.S. in recent years (Dahl 2011), and remaining wetlands are imperiled by increasing temperatures, evapotranspiration, and precipitation variation caused by climate change (Kloesel et al. 2018). These factors, along with agricultural intensification, land cover change, and increasing human demand for water (Johnson et al. 2010, Moomaw et al. 2018) may further reduce the extent and hydroperiod of wetlands in the Great Plains and beyond.

Gains in wetlands has been primarily focused on benefits to migratory waterfowl (e.g., ducks and geese) habitat through conservation funding programs (e.g., North

American Wetlands Conservation Act, Wetlands Reserve Easement Program). These types of programs can be counterproductive as they do not address specific habitat needs for other wetland dependent wildlife, including migratory shorebirds (Rosenberg et al. 2019), although some programs have more focused efforts on shorebirds (e.g., Western Hemispheric Shorebird Reserve Network and some Joint Venture Programs). Shorebirds (e.g., sandpipers and plovers) often have specific habitat needs (e.g., specific water depths and substrate types) due to their specialized food preferences and morphology-driven life histories. Many migratory shorebirds travel great distances, with some in the Western Hemisphere breeding as far north as the Arctic Ocean and wintering as far south as Patagonia (Haig et al. 2008, Amezaga et al. 2002, Skagen 2006). Globally, many shorebird species are in decline (Andres et al. 2012, U.S. Shorebird Conservation Plan 2004, Morrison et al. 2000, Rosenberg et al. 2019), largely due to loss of high-quality wetlands across their annual cycles (Carlisle et al. 2009, Dahl 2011, Kirby et al. 2008, Galbraith et al. 2014), including migratory stopover sites (McGowan et al. 2011, Studds et al. 2017). Loss, degradation, and variability in occurrence of wetlands used as stopover sites can cause a higher density of migratory birds to use habitat that results in greater competition and associated effects on migration timing and success, as well as survival and reproductive fitness (Newton 2006, McGowan et al. 2011, Studds et al. 2017). Research is still needed to understand habitat relationships of wetland dependent species other than waterfowl (such as shorebirds) to develop more integrated and broad conservation plans addressing the needs of all wetland dependent species.

Migratory shorebirds rely on wetland connectivity at multiple spatial scales, from the transcontinental network of connected wetlands along their migratory routes to

complexes of wetlands used in individual stopover locations. Research has shown that fine-scale habitat features, such as water depth and vegetation height and cover, can influence shorebird species richness, total abundance, and stopover duration during migration (Skagen and Knopf 1994, Skagen et al. 2008, Webb et al. 2010). Migrating shorebirds also respond to extent and connectivity of floodwater and wetland habitat at broader spatial scales (e.g., 1.5-10 km) (Albanese et al. 2012, Albanese and Davis 2013, Farmer and Parent 1997). Notably, most studies of shorebird habitat use and selection during stopovers either consider all shorebird species together (Albanese and Davis 2013, 2015, Albanese et al. 2012, Webb et al. 2010) or focus on one or a few individual species (Baker et al. 2004, Hovick et al. 2017, Morrison et al. 2004, Tozer et al. 2010).

Understanding how multiple individual shorebird species respond to broad-scale wetland availability and fine-scale wetland features during migratory stopovers during the same temporal span at the same study sites can help identify species-specific limiting factors during this crucial period of the annual cycle. This information can inform wetland protection and management strategies that benefit multiple shorebird species (Albanese and Davis 2013, Albanese and Davis 2015, LaGrange and Dinsmore 1988, Skagen and Knopf 1993), including species of conservation concern (i.e., threatened or endangered) that may require more specific habitat requirements.

To assess wetland habitat use for multiple shorebird species migrating through the North American Great Plains, we conducted shorebird surveys at more than 14,000 points in Oklahoma, USA, and measured wetland availability at multiple broad spatial scales, as well as finer-scale characteristics within wetlands (e.g., water area, vegetation height). Our specific objectives were to (1) identify and compare the scale at which different

shorebird species respond to wetland availability on the landscape and (2) identify and compare the relative importance of broad-scale wetland availability and fine-scale wetland characteristics.

## **Methods**

Shorebird abundance data were collected by conducting shorebird surveys on wetlands during migration seasons from fall 2007 through spring 2009 (spring migration: March-May; fall migration: July-October) in ten counties in north-central Oklahoma, USA (Figure 1). The study area, totaling 24,372 km<sup>2</sup>, is primarily grasslands, agricultural areas, small woodlands, and urbanized areas interspersed with numerous wetland types (Albanese et al. 2012, Albanese and Davis 2013, Henley and Harrison 2000, ODWC 2006). The study area experiences highly variable seasonal and annual weather patterns, which influences wetland extent, temporal hydroperiod, and spatial pattern and connectivity. During spring and fall study periods, average monthly temperature was 14.4 degrees and 23.0 degrees, respectively, and average monthly precipitation was 10.1 cm and 8.8 cm, respectively (Oklahoma Climatological Survey).

Full details of study design and data collection are in Albanese et al. (2012) and Albanese and Davis (2013, 2015). Here, we provide a brief description of key methods relevant to the current study. We used a hierarchical habitat sampling design consisting of broad-scale experimental units (BSUs) in which each contained multiple individual wetlands (hereafter, fine-scale units; FSUs; Figure 3.1). We randomly placed 10 BSUs (each a circle with 10-km radius) within the study area boundaries using ESRI ArcGIS

software. We identified FSUs as discrete, contiguous areas of wetland/water surrounded by non-wetland areas that could potentially provide shorebird habitat within each BSU. We grouped 14,444 total FSUs into hydroperiod categories (CAT)—including permanent, semi-permanent, and temporary—using summaries of long-term weather data and assessment of wetland persistence across a time series of satellite images. Within each hydroperiod category, we used in-field assessments to further designate wetland types (TYPE), including lacustrine, palustrine, riverine, sheet-water, and water treatment ponds (Cowardin et al. 1979). We also calculated three additional fine-scale wetland characteristics for each FSU: (1) proportional cover of shallow water (<16 cm) and saturated substrate (hereafter, WAT); (2) shorebird habitat area (AREA), which is the product of WAT and the total area of each FSU; and (3) vegetation cover/height (VEG), the multiplicative interaction between proportional cover and dominant height category of emergent vegetation in the portion of each FSU captured by the WAT variable.

We conducted shorebird surveys using a sampling approach that separated each migration season into 4, 23-day periods. During each period, we sampled 13-15% of the FSU's in each BSU, and subsequent sampling periods for any given BSU were never closer than 10.5 days apart. This 10.5 day inter-survey interval was based on known stopover lengths of migratory shorebirds; specifically, previous research indicates that the longest stopover for individual shorebirds averages 10.5 days (based on the highest value of the average residency period calculated across multiple individual shorebirds in a stopover site; Skagen and Knopf 1994, Farmer and Durbian 2006, Skagen et al. 2008). The use of 23 day intervals therefore ensures independence among surveys because it was unlikely that we double-counted any individual shorebirds across multiple sampling

bouts for a BSU (we conducted 166 total bouts across all BSU's). All shorebird surveys were conducted from vehicles or on foot during daylight hours on randomly chosen dates within each 23-day period. After arriving at an FSU, surveyors waited for several minutes before starting counts to allow shorebirds to resettle following any disturbance caused by the surveyor's presence. Each FSU with area  $\leq 1$  ha was surveyed for 5 minutes, and for FSUs  $>1$  ha in size, an additional 5 minutes of surveying was conducted for each additional 1 ha. Surveyors used binoculars and/or a spotting scope to locate, identify, and count all shorebirds seen within each FSU.

For analyses described below, we only considered shorebird species occurring at  $>80$  FSUs and with  $>400$  individuals observed across all surveys, which resulted in 14 species remaining for analysis (Table 3.1). The included species represented a range of migratory strategies, including short-distance, intermediate-distance, and long-distance passage migrants (i.e., species that only occur in the study region during migration), and residents (i.e., migratory species that breed in the study area) (Albanese and Davis 2013). Selected species were also characterized by a variety of morphological traits such as body mass and bill length.

To capture extent and connectivity of shorebird habitat at multiple broader spatial scales, we calculated the h-index, a metric reflecting the percent area covered by shorebird habitat at different radii (500m, 1000m, 2000m, 3000m) from the centroid of each FSU (see Albanese and Davis 2012). The h-index is similar to the above calculation of the WAT variable, but at larger spatial scales surrounding FSU's rather than within FSU's. To calculate h-index, the above-calculated WAT layer was converted to a  $10 \text{ m}^2$  raster grid layer. We then estimated shorebird habitat incidence ( $p$ ) as the proportion of



sampled FSUs in each BSU that contained shorebird habitat during a survey period, and we used a kernel density estimation program (Seaman and Powell 1996) to generate smoothed density averages for each FSU. A kernel function  $h$  (i.e., smoothing parameter for each of the above radii) was placed in each grid cell, with height determined by values of  $p$  for each FSU and survey interval. Thus, the kernel density value at distance  $x$  from an FSU centroid with probability  $p$  was  $fn(x) \times p$ . Estimates of  $p$  were constant across different values of  $h$  and different radii. The above process resulted in kernel density estimates being assigned to each 10 m<sup>2</sup> grid cell in each BSU. H-index estimates ranged from 0-1 with values of 1 being complete shorebird habitat cover within the circle surrounding an FSU centroid, and 0 being no shorebird habitat cover.

All analyses were conducted in R version 3.6.3 (R Core Team 2020). To identify the scale at which h-index best predicted abundance for each shorebird species, we used generalized linear models in the glmmTMB package (Brooks et al. 2017). For this analysis, we treated abundance of individual shorebird species as response variables, individual survey counts at FSU's as replicates ( $n=14,444$ ), h-indices at each spatial scale as predictors, and a zero-inflated negative binomial error distribution (because most counts were zero). We used Akaike's Information Criterion (AIC) in the bbmle package to rank models (Bolker 2017), considering only the top model and only when it had a  $\Delta$ AIC value at least two less than the null model. To identify associations between fine-scale wetland characteristics and shorebird abundance, we used generalized linear mixed models, again in the glmmTMB package. We used a similar modeling framework as above, except we also included a random effect for wetland type nested within hydroperiod category (to account for variation among wetland types and hydroperiod

categories). No random effect was included to account for FSUs nested within BSUs because the above-described sampling design minimized chances of double-counting individual shorebirds on successive sampling bouts in each BSU. For predictor variables, we included the h-index for the scale that was best-supported in the prior analysis and considered all additive combinations of h-index, AREA, VEG, and WAT. These four predictors were scaled prior to modeling to standardize coefficient estimates, allowing direct comparisons of effect sizes for different variables within and among species. We again used AIC in the *bbmle* package to rank models, considering models competitive when  $\Delta AIC=0-2$  and at least two less than the null model, after elimination of uninformative parameters (Arnold 2010).

## **Results**

Across the entire study, total abundance by species ranged from 432 (Spotted Sandpiper) to 8558 individuals (Least Sandpiper), and frequency of occurrence (i.e., number of surveys with  $\geq 1$  individual) ranged from 82 to 1122 (out of 14,444 surveys/FSU's) (Table 3.1). For most species (9 of 15), abundance was most closely associated with the h-index (i.e., the metric for broad-scale habitat availability) calculated at the 500 m spatial scale, but abundance of American Avocet, Least Sandpiper, and Snowy Plover were associated with the h-index at the 1000 m scale, and Wilson's Phalarope abundance was associated with the h-index at the 2000 m scale (Table 3.2).

For the analysis combining the top h-index with local wetland characteristics, the top model included all 4 predictors (h-index, WAT, AREA, VEG) for eight species:

American Avocet, Greater Yellowlegs, Least Sandpiper, Long-billed Dowitcher, Pectoral Sandpiper, Snowy Plover, Western Sandpiper, and Wilson's Phalarope (Table 3.2).

AREA, h-index, and VEG were each supported as predictors of abundance for 13 of 14 species (all except Semipalmated Sandpiper for AREA, Killdeer for h-index, and Lesser Yellowlegs for VEG). WAT was supported as a predictor for 11 species (all except Baird's Sandpiper, Spotted Sandpiper, and White-rumped Sandpiper).

Regarding the direction and magnitude of effects (Table 3.2), regardless of the scale at which shorebird abundance was associated with h-index, this factor almost always had a positive effect when it was supported (abundance of only Spotted Sandpiper was negatively associated with h-index), and this effect was greatest for American Avocet, White-rumped Sandpiper, and Semipalmated Sandpiper. WAT (i.e., proportional cover of shallow water and saturated substrate) was positively associated with abundance for 8 of 11 species for which it had a supported effect. Even for species with abundances positively associated with this factor, the strength of response was variable, with the strongest relationships for White-rumped Sandpiper, Lesser Yellowlegs, and American Avocet. For the 3 species that had negative associations with WAT (Snowy Plover, Killdeer, and Least Sandpiper), the magnitude of response was relatively similar. AREA (i.e., product of WAT and total area of each FSU) was positively associated with abundance for all 13 species for which it had a supported effect, and the magnitude of this effect was variable, with the strongest relationships for Killdeer, Long-billed Dowitcher, and American Avocet. Finally, VEG (i.e., vegetation cover/height) was negatively associated with abundance for 12 of 13 species for which it had a supported effect (abundance of only Pectoral Sandpiper was positively associated with VEG), and

this effect was strongest for Semipalmated Sandpiper, Snowy Plover, and Western Sandpiper.

## **Discussion**

We found that most species responded most strongly to broad scale habitat availability at the 500 m scale but a few species at broader scales. Most species also respond to broad scale habitat availability positively, however species varied in their strength of response. Broad scale habitat area and fine-scale wetland features are both important for all species, but there is species variation in the relative effects of broad versus fine scale factors and among different fine-scale factors. Together these results indicate the importance of managing for both broad scale wetland extent and fine scale features for most shorebird species during migratory stopovers, and also the importance of considering species-related variation in responses to wetland habitat. Our method of selecting broad scale habitat availability estimates was limited by the inclusion of only one scale per model since estimates at different scales were highly correlated. This is likely an over simplified way of evaluating broad scale habitat availability and selection is likely a hierarchical process. Shorebirds probably do not perceive discrete scales and future studies should attempt to evaluate habitat density at more continuous scales.

Abundances for most species were most closely associated with estimates of broad scale shorebird habitat availability at the 500 m spatial scale. However, varying response to h-indices by some species such as American Avocet, Least Sandpiper, Snowy Plover, and Wilson's Phalarope suggest that at least some species select more strongly for

larger spatial scales. Our findings provide further support that broad scale patterns of wetland availability on the landscape are important drivers for determining stopover sites used by shorebirds during migration. These patterns may arise from varying combinations of life history or other factors influencing habitat selection. A similar study found that habitat density at a 1.5 km scale had the most influence on overall shorebird occurrence (Albanese et al. 2012). Migrants likely use characteristics seen at broad spatial scales such as habitat availability, selecting for stopover sites with higher amounts of perceived wetland areas, and thus reducing the energy costs needed to make finer scale movements during refueling before reinitiating migration (Farmer and Parent 1997; Albanese and Davis 2013). Further, different shorebird species exhibit different migration distances and strategies which influence habitat selection, likely reflecting a variety of different habitat needs at stopover sites (Skagen and Knopf 1993). Habitat management for shorebirds focused at 500m may work for most shorebirds, but not all species or life histories respond similarly and that some species may need management focused at larger spatial scales. Conservation management plans should be flexible and recognize the importance of variability (i.e., heterogeneity) in broad scale habitat availability.

For all but 1 shorebird species responding to broad scale habitat availability, the effect of h-index was positive. However, there was variation in effect sizes for these species with positive responses (i.e., some responded more positively than others), perhaps related to variation in species- or life-history traits. Spotted Sandpiper exhibited a negative response to habitat density, possibly meaning they select for availability of wetland habitat not captured well by our definition of wetlands; we lumped all wetlands together, so birds such as Spotted Sandpiper utilizing riparian areas and edges of

shorelines, which make up a small percentage of wetlands in our study area, may not be captured as well. Future research is needed to test hypotheses related to the effects of these traits on the scale at which shorebirds respond to habitat availability.

For most species, both broad scale wetland availability and fine-scale features were important, with the relative effects of each varying by species. For most species, at least one fine scale factor had stronger effects than broad scale wetland availability. Alternatively, for most species some fine scale factors had weaker effects than broad scale wetland availability, a finding similar to prior studies considering all shorebirds (Albanese and Davis 2015). This provides further evidence that broad scale factors are often more important than fine scale factors, and that the relative importance is species dependent. This suggests that for most shorebirds, efforts to conserve and restore wetlands should focus on heterogeneity of wetlands both in terms of habitat availability at broad scales which influence wetland connectivity and fine scale characteristics that define wetlands.

In relation to particular fine scale features within wetlands, we found that for most species effect sizes increased for WAT (i.e., proportional cover of shallow water and saturated substrate) and AREA (i.e., product of WAT and total area of each FSU), but strength of response varied across species. Habitat area is often positively associated with shorebird abundance in wetland areas (Albanese and Davis 2015, Taft et al. 2002, Skagen et al. 2005, Webb et al. 2010). Studies have also found that shallow water is often an important predictor for shorebird species abundance (Davis and Smith 1998) but others found lack of importance on total shorebird abundance and richness (Albanese and Davis 2015). Our results suggest that species specific analyses may yield different conclusions

than analyses based on all species. Higher amounts of shorebird habitat area and shallow water results in a larger feeding area, a feature likely selected for by shorebirds to maximize the available substrate area for feeding and refueling along migratory routes. For most species, conservation efforts should focus on increasing shallow water and saturated substrate, as well as the proportion of this cover within potential habitat. However, response by different species to these predictors, especially those of conservation interest, should also be taken into consideration when developing restoration or conservation plans.

We also found that for most shorebird species, abundance decreased with increasing VEG (all except Pectoral Sandpiper). Prior studies have reported similar findings, that total shorebird abundance and richness decrease with increasing vegetation cover in and around wetland habitat (Albanese and Davis 2015, Weber and Haig 1996, Davis and Smith 1998, Niemuth et al. 2006). Notably, Farmer and Durbain (2006) found that increased vegetation structure in wetlands increases the likelihood of detection bias (i.e., shorebirds are more difficult to detect in wetlands with high amounts of vegetation). Our study design minimized this bias (only 13.6% of area surveyed contained similar habitat structure to that found by Farmer and Durbain 2006 to influence detection; Albanese and Davis 2015). It is possible that larger bodied shorebirds are more easily detectable than smaller bodied shorebirds in wetlands with more vegetation. However, we found no strong correlation between effect sizes for VEG and different body size metrics (tarsus length  $r=0.41$ ,  $p=0.17$ ; body mass  $r=0.39$ ,  $p=0.19$ ; wing chord  $r=0.57$ ,  $p=0.04$ ) for each species. Further, the effect sizes for VEG were variable across species relative to variation in body size, suggesting that species exhibit a higher probability of driving of

this variability than detection bias. Nevertheless, some caution should be taken when interpreting our results. For most species, VEG had the highest effect size of any predictor in top models, but there was some variation in effect size across species. For example, the effect sizes for Semipalmated Sandpiper and Western Sandpiper were -4.368 and -3.494 respectively, implying a strong selection against VEG, but the effect sizes for Pectoral Sandpiper and Greater Yellowlegs were relatively close to 0, implying they are not selecting strongly for or against VEG. Overall, these findings broadly suggest that VEG is an important predictor of shorebird species abundance, and that decreasing vegetation cover/height in wetlands will likely increase abundance for most species (Albanese and Davis 2015, Davis and Smith 1998). However, the variation in species response suggests that this action will benefit some species much more than others. Future studies should attempt to document and evaluate the variation in shorebird species response to vegetation in wetlands.

For shorebird species that we evaluated, there is some variation in the scale of response to broad scale habitat availability (i.e., some species respond stronger to estimates of habitat availability at 500m scale while others respond stronger at 1000m), and there is variation in response within a specified scale (i.e., species responding to 500m scale exhibit a range of effect size). Species also varied in their relative effect sizes of broad scale features compared to fine scale features. For fine scale features, the direction of effect was fairly consistent across species but there was still some species related variation in effect size. Our results help us understand how different shorebird species respond to broad scale wetland availability and fine scale wetland characteristics at migratory stopover sites. These results also suggest testable hypotheses for future



research to explain species level variation in habitat associations (e.g., certain life history traits that may explain patterns). Considering individual species is important as results vary for species and considering species may lead to different conclusions than for all shorebirds combined. This informs management that can be more refined for particular species of conservation concern such as Lesser Yellowlegs, Pectoral Sandpiper, and Semipalmated Sandpiper, all of which have experienced population declines since 1970 (Rosenberg et al. 2019) and are US Birds of Conservation Concern (NABCI 2016).

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Table 3.1. Species included in analyses, their abundance (total individuals observed across all surveys) and frequency of occurrence (total surveys with  $\geq 1$  individual observed).

Common Name	Scientific Name	Abundance	Frequency of Occurrence
American Avocet	<i>Recurvirostra americana</i>	1549	132
Baird's Sandpiper	<i>Calidris bairdii</i>	4078	289
Greater Yellowlegs	<i>Tringa melanoleuca</i>	573	269
Killdeer	<i>Charadris vociferous</i>	5159	1122
Least Sandpiper	<i>Calidris minutilla</i>	8558	554
Lesser Yellowlegs	<i>Tringa flavipes</i>	1109	246
Long-billed Dowitcher	<i>Limnodromus scolopaceus</i>	2877	126
Pectoral Sandpiper	<i>Calidris melanotos</i>	728	97
Semipalmated Sandpiper	<i>Calidris pusilla</i>	3756	219
Snowy Plover	<i>Charadrius nivosus</i>	1053	252
Spotted Sandpiper	<i>Actitis macularius</i>	432	268
Western Sandpiper	<i>Calidris mauri</i>	1784	82
Wilson's Phalarope	<i>Phalaropus tricolor</i>	3899	128
White-rumped Sandpiper	<i>Calidris fuscicollis</i>	4602	165

Table 3.2. Relative standardized effect sizes (based on model coefficient estimates) for associations between abundance of individual shorebird species and broad-scale availability of shorebird habitat at multiple scales (h-index; scales indicate radius at which h-index was calculated), and fine-scale characteristics of individual wetlands (WAT – define; AREA – define; VEG – define). Empty spaces indicate variables that were not included in the top model for a species.

Common Name	h-index scale	h-index estimate	WAT estimate	AREA estimate	VEG estimate
American Avocet	1000	0.973	0.752	0.517	-1.185
Baird’s Sandpiper	500	0.668		0.275	-3.041
Greater Yellowlegs	500	0.146	0.521	0.480	-0.432
Killdeer	500		-0.154	0.569	-0.698
Least Sandpiper	1000	0.681	-0.121	0.335	-2.436
Lesser Yellowlegs	500	0.731	1.040	0.393	
Long-billed Dowitcher	500	0.880	0.427	0.561	-1.292
Pectoral Sandpiper	500	0.884	0.630	0.426	0.474
Semipalmated Sandpiper	500	0.911	0.277		-4.368
Snowy Plover	1000	0.770	-0.181	0.445	-3.881
Spotted Sandpiper	500	-0.354		0.461	-1.184
Western Sandpiper	500	0.643	0.312	0.402	-3.494
Wilson’s Phalarope	500	0.732		0.340	-2.022
White-rumped Sandpiper	2000	0.944	1.232	0.403	-0.526

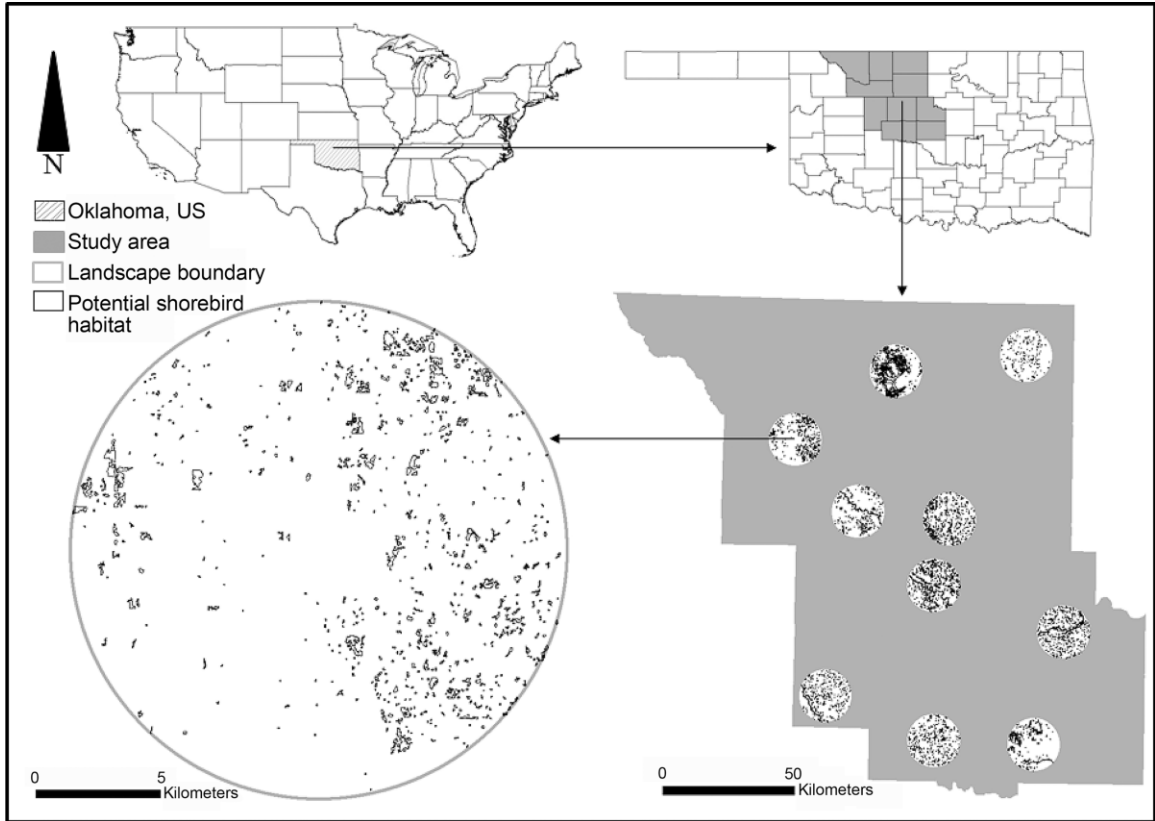


Figure 3.1. Study area and landscapes in north-central Oklahoma, USA. Reproduced from Albanese and Davis 2015.

## CHAPTER IV

### A REVIEW OF BIRD RESPONSE TO FIRE IN NORTH AMERICAN GRASSLANDS

**Abstract.** Fire is a key ecological process influencing the structure, function, and biodiversity of most grass-dominated ecosystems globally. In North America, broad-scale wildfire suppression, lack of prescribed fire, and loss of grasslands to agricultural intensification, energy development, and urbanization, have greatly impacted grassland biodiversity, causing declines of many wildlife species including grassland-dependent birds. Many studies have evaluated how birds respond to fire in grasslands, but research gaps remain and a systematic review of the literature on fire effects on birds is lacking. We conducted such a systematic review of 1098 peer-reviewed studies to assess overarching patterns in the literature and research gaps related to: (1) types of fire regimes studied (prescribed vs. wild fire) and fire-related aspects of study design (e.g., which fire-related predictors are considered, like time since fire and fire intensity); (2) avian life history periods and response variables studied (e.g., abundance, species richness); and (3) characteristics of ecosystems studied (e.g., ecosystem types and whether other vegetation management approaches are evaluated). Our review illustrates that most studies have focused on prescribed fire (not wildfire) and have not evaluated effects of important factors known to influence ecosystem responses to fire (e.g., fire

intensity and season). Most studies also have only assessed effects of fire during avian breeding seasons (not during migration and non-breeding seasons) and only evaluated species-specific responses (i.e., few studies evaluating bird community responses). Further, most research has been conducted in prairies or savannas (i.e., limited research in steppe and multiple ecosystems). Our review provides a summary of the state of the science on fire effects on birds in grasslands, information that can provide a roadmap for future research evaluating how fire affects grassland birds and ecosystems.

## **Introduction**

Grass-dominated ecosystems (e.g., prairies, savannas, steppes; hereafter “grasslands”) are highly threatened worldwide, including in North America (Curtin and Western 2008, Henwood 1998, Hoekstra et al. 2005). In most grasslands, fire is a dominant ecological process that affects vegetation structure, biodiversity, and ecosystem functioning and services (Anderson et al. 2006, Briggs et al. 2002, Frank et al. 1998, Samson et al. 2004). Yet, public attitudes about fire in North American grasslands are often negative, which has resulted in widespread loss of fires on the landscape, including suppression of wildfires and only limited use of prescribed fire (Donovan and Brown 2007, Twidwell et al. 2013). Disruption of fire regimes has caused habitat degradation and fragmentation, as well as ecosystem and biome transitions, due to pervasive processes like biological invasions and woody plant encroachment (Archer et al. 2017, Ratajczak et al. 2012). Such changes greatly affect abundance, diversity, and species composition of grassland-dependent wildlife (Ceballos et al. 2010, Grant et al. 2004).

Birds are an important component of grassland biodiversity and key contributors to grassland-mediated ecosystem services (e.g., through their control of insect pests, seed dispersal, and provision of recreational opportunities). However, many bird species that depend on North American grasslands during breeding, migratory, or wintering periods have experienced steep population declines (Askins et al. 2007, Hoekstra et al. 2005, Knopf 1994, Rosenberg et al. 2019, Sauer et al. 2013). These declines are caused by many factors operating throughout birds' annual cycles; however, a key driver of decline is the massive loss of grassland habitat throughout much of North America (Brenna and Kuvlesky 2012, Samson and Knopf 1994, Vickery and Herkert 2001). For example, only ~1-18% of all tallgrass prairie remains in the U.S. (Samson and Knopf 1994), and other grassland ecosystems have also experienced severe losses (e.g., desert grasslands of the southwestern U.S., sagebrush steppes, and mixed grass prairies of North America's interior west) (Van Auken 2000). In addition to loss of grassland habitat, a lack of grassland heterogeneity, largely attributable to lack of fire, has driven local and regional declines of grassland bird populations and species diversity (Burgess and Maron 2016, Powell 2006, Rienking 2005, Walk and Warner 2000). Reversing declines of grassland-dependent birds requires a comprehensive understanding of how major disturbances such as wild and prescribed fire influence bird populations and communities (Brawn et al. 2001).

Although avian responses to fire in grasslands have been widely studied, there appear to be limitations in the literature related to the ecosystems, fire regimes, and avian life history stages and response variables studied. For example, studies appear to predominantly evaluate how birds respond to prescribed fire (i.e., controlled fire

purposefully used to manage grassland ecosystems) as opposed to wildfire (i.e., both low-intensity, wildfires and high-intensity, highly damaging wildfires that are often anthropogenically caused) (Limb et al. 2016, Fuhlendorf et al. 2006, 2009; but see Pastro et al. 2014), and to principally evaluate effects of the presence or frequency of fire, but not effects of important factors that influence ecosystem responses to fire (e.g., fire intensity and season) (Duchardt et al. 2016, Limb et al. 2016, McNew et al. 2015, Pillsbury et al. 2011, Wood et al. 2004). Related to avian life history, most studies appear to evaluate bird responses to fire only during the breeding season (Coppedge et al. 2008, Flesch et al. 2016) even though fire can affect bird populations and communities in other seasons (e.g., migration and wintering periods; Hovick et al. 2014, 2017, Soehren et al. 2018). Finally, most studies conducted to date have been limited to assessing avian responses to fire in one or a few study areas. These limitations prevent generalized understanding of how fire affects bird populations and communities within the context of other factors contributing to avian population declines, and of fire's effects on ecosystems more broadly.

Given these apparent limitations in the literature on avian responses to fire in grasslands, a systematic literature review would help explicitly identify and quantify such limitations and highlight research gaps to be addressed in the future. We conducted such a systematic review of peer-reviewed studies that evaluate bird population and community responses to fire in grasslands of North America. Specifically, we assessed research gaps and overarching patterns in the literature related to: (1) types of fire regimes studied (wild vs. prescribed fire) and fire-related aspects of study design (e.g., which fire-related predictors are considered, such as time since fire and fire rotation



interval and intensity); (2) avian life history periods (e.g., breeding, non-breeding, migration) and level of ecological organization (species or community); and (3) characteristics of ecosystems studied (e.g., ecosystem types and whether studies assessed vegetation management approaches other than fire, like grazing and woody plant removal).

## **Methods**

We used the Scopus database to perform a literature search for studies of bird responses to fire in grasslands of North America. We searched article titles, keywords, and abstracts with the search terms “avian and fire”, “avian and burn”, “bird and fire”, and “bird and burn”. We included only studies published as peer-reviewed articles and excluded technical reports and conference presentations. The Scopus database contains studies published since 1970, and we included studies published from that year through December 2019 when the search was conducted. A full list of 1098 resulting publications was exported to a CSV file for further review. We only included studies for in-depth review if they were conducted in North America, were in grasslands—including prairie (e.g., tallgrass, mixed-grass, and shortgrass prairie, coastal and mesquite grasslands), savanna (e.g., pine and oak savanna), sagebrush steppe, or multiple cover types (typically a gradient including at least one of these grasslands types)—and had ecological relevance to our objectives related to effects of fire on wild birds (one example of an irrelevant, non-ecological study that we excluded evaluated skin lesions on broiler chickens in slaughter houses). We included studies evaluating avian response variables at all levels of

taxonomic classification (e.g., species, genus, family, order, class) and ecological organization (e.g., population or community). If a paper lacked information needed to evaluate whether it met inclusion criteria, we excluded it; for example, we excluded studies in pine forests that did not report if the understory was grass-dominated.

For all 1098 publications, we used a tiered approach to review, starting with the title; for studies not excluded as irrelevant following title review, we then reviewed the abstract, and if necessary, the article's full text. This approach resulted in elimination of 711 articles following title review, 114 articles after abstract review, and 108 articles after full-text review. For the remaining 165 articles used in this review, we extracted data related to three broad types of information (details and rationale for extracted information provided in following paragraphs): (1) types of fire regimes studied and fire-related aspects of study designs; (2) avian life history periods and response variables studied; and (3) characteristics of ecosystems studied. For each of the below-described data types within the three broad categories, we calculated summary statistics, including numbers and percentages of the total number of studies ( $n=165$ ).

Related to types of fire regimes and fire-related aspects of study design, we recorded the type of fire studied (prescribed fire or wildfire) and whether or not one or more unburned control areas was included as part of the evaluation. We also recorded whether studies evaluated effects of fire intensity (i.e., energy output from fire) and fire season because season of fire influences its intensity, and because both fire season and intensity are related to fire behavioral characteristics (e.g., fuel load and flammability influence flame length and scorching heights) that affect vegetation regeneration and thus bird populations and communities (Govender et al. 2006, Hewett Ragheb et al. 2019,

Howe 1994, Keeley 2009). If studies evaluated fire intensity, we also recorded the metric used to estimate this factor. Regardless of whether fire season was explicitly evaluated as a predictor variable, we extracted information about the season of fire whenever it was provided; seasons included dormant season (winter), growing season (summer), and transition season (spring or fall). We also recorded whether studies evaluated time since fire (i.e., number of years since the most recent fire), reported fire frequency (i.e., number of fires per unit time in a specified area), and reported fire rotation interval (i.e., average time in years to burn entire designated area) because past studies indicate that these factors can independently influence vegetation and birds (Dickmann & Cleland 2002, Govender et al. 2006).

Related to avian life history periods and response variables, we recorded the period of the avian annual life cycle studied, including breeding, in transit (i.e., migration), and stationary non-breeding seasons (following definitions in Marra et al. 2015). We tracked this information because bird populations and communities may have seasonally variable responses to fire, because these different periods of the annual cycle have varying importance in contributing to regulation of population demography, and because there is known bias in the broader avian ecology literature toward the breeding season (Marra et al. 2015). We also documented the level of ecological organization evaluated for birds in each study—including species-level (i.e., responses of one or more single species evaluated separately at either the population or individual level) and community-level (i.e., responses of two or more species evaluated in combination, for example using metrics like total bird abundance and species richness and diversity). This information was tracked because understanding the effect of fire on different levels of

ecological organization gives insight into the magnitude of its effects on ecosystems and can help inform conservation efforts focused at particular levels (e.g., species vs. community-focused conservation).

Related to characteristics of ecosystems, we recorded the type of ecosystems studied (corresponding to the grassland ecosystem types defined above). We also recorded if studies evaluated vegetation management techniques other than fire (e.g., grazing, woody plant removal, herbicide application), since these management steps influence vegetation and bird populations and communities, both in tandem with and independent of fire (Duchardt et al. 2016, Fuhlendorf et al. 2006, Vickery et al. 1999).

## **Results**

### *Fire regimes and fire-related aspects of study design*

Of the 165 studies meeting our inclusion criteria, most evaluated only how birds were influenced by prescribed fire ( $n=138$ , 84%), and relatively few examined effects of natural or anthropogenically caused wildfire ( $n=20$ , 12%) or of both prescribed fire and wildfire ( $n=7$ , 4%) (Figure 4.1a). Most studies included one or more unburned control areas as part of their evaluation ( $n=110$ , 67%; compared to 55 [33%] studies with no unburned controls). Time since fire was evaluated as a predictor variable in 87 studies (53%), fire frequency was reported in 77 studies (47%), and fire rotation interval was reported in 79 studies (48%); further, 44 (27%) studies only reported one of these fire-

related predictor variables, 49 (30%) reported two, and 34 (21%) reported all three. Fire intensity was not explicitly evaluated as a predictor variable for most studies ( $n=156$ , 95%), and the studies that did evaluate this factor ( $n=9$ , 5%) used highly variable metrics to quantify it (including Byram's equation [ $n=1$ ], MTBS database [ $n=4$ ], and arbitrary intensity scales [ $n=4$ ]). Although the vast majority of studies ( $n=160$ , 97%) were not designed to explicitly evaluate the effect of fire season, most studies ( $n=109$ , 66%) did report the season of fire, and most of these focused on bird responses to growing season fire ( $n=48$ , 29%), followed by fire during the dormant seasons ( $n=21$ , 13%) and during two or more seasons ( $n=40$ , 24%) (Figure 4.1b).

#### *Avian life history periods and response variables*

Most studies ( $n=114$ , 69%) documented bird responses to fire during the avian breeding season only; fewer studies evaluated the stationary non-breeding season only ( $n=18$ ; 13%), none evaluated migration only, and 19 (12%) evaluated two or more of these periods of the annual cycle (Figure 4.2a). Most studies ( $n=112$ , 68%) evaluated bird responses to fire only at the species level, as compared to 42 (25%) documenting responses at both the species and community level, and 11 (7%) at the community level only (Figure 4.2b).

### *Characteristics of ecosystems*

Most studies were conducted in either prairie ( $n=77$ , 47%) or savanna ( $n=54$ , 32%), whereas fewer studies were in sagebrush steppe ( $n=18$ , 11%) or multiple ecosystem types ( $n=17$ , 10%) (Figure 4.3). The majority of studies ( $n=90$ , 55%) explicitly evaluated vegetation management techniques other than fire (including studies that looked at these other techniques either separate from or in tandem with fire); these management techniques included grazing ( $n=42$ , 26%), woody plant removal ( $n=38$ , 23%), herbicide ( $n=19$ , 12%), mowing or disking ( $n=12$ , 7%), but only 17 of these studies (10%) included >1 vegetation management technique other than fire.

## **Discussion**

### *Fire regimes and fire-related aspects of study design*

Most studies evaluated how grassland birds respond to prescribed fire, and few addressed responses to natural or anthropogenically caused wildfire. Although fire suppression has occurred for decades in North American grasslands, prescribed fire is still frequently used to manage some grassland ecosystems, which likely explains the large proportion of studies evaluating its use. Due to fuel accumulation, fire suppression causes many wildfires to burn at unnaturally high intensity and to cover a larger spatial area than most prescribed fires (Archibald et al. 2013, Fernandes and Botelho 2003, Steele et al. 2015) and most naturally occurring wildfires, which historically burned at

lower-intensity across smaller spatial extents (Latta et al. 2000). These differences between prescribed fire and wildfire related to spatial scale, timing, and intensity, cause differential effects on vegetation structure and composition, which also likely leads to different effects on birds (e.g., Jones et al. 2016, Minney 1994; Sparks 1999). Further, prescribed fire can interact with wildfire to influence birds and their habitat because the use of the former affects the frequency, intensity, and extent of the latter (Fernandes and Botelho 2003). Fully understanding how grassland birds respond to fire, and developing best management strategies related to both prescribed fire and wildfire, requires additional research evaluating how different types of fire affect birds and comparing independent and interactive effects of wildfire and prescribed fire.

Comparing bird responses between fire treatments and unburned control areas allows estimation of absolute effects of fire; studies lacking a control can only compare relative effects of different fire treatments. Although most studies in our review included an unburned control, a sizable minority (33%) did not. An example of how inference is limited by not including a control is provided by Augustine and Derner (2015). This study found that density of Lark Buntings (*Calamospiza melanocorys*) did not vary significantly with time since fire across three treatments (recent burn, 2 years, and 3 years since fire); however, density was significantly lower in all burn treatments compared to an unburned area. Although some management-relevant research objectives do not require a control (e.g., studies evaluating fire treatments in a landscape with no unburned areas), understanding relative and absolute effects of different types of fire will usually require reference points for bird population and community metrics in the absence of fire.

The effect of time since fire was evaluated slightly more often than not. This factor is an important driver of grassland bird abundance, habitat selection, and species richness and composition (e.g., Augustine and Derner 2015, Baldwin et al. 2007; Bechtoldt & Stouffer 2005, Korosy et al. 2013). For example, Henslow's Sparrow (*Ammodramus Henslowii*), a declining species of significant conservation concern, avoids recently burned areas in tallgrass prairies during the breeding season, instead preferring areas that were burned 2-4 years prior and thus have tall, dense grass and deep leaf litter (Herkert & Glass 1999, Brawn et al. 2001). Large-scale variation in time since fire also creates spatial heterogeneity in vegetation successional stages, which provides a variety of habitats that support high bird diversity, as well as species requiring different successional stages in different parts of their annual cycle (Holcomb et al. 2014, Hovick et al. 2015, Fuhlendorf et al. 2006). Fire frequency and rotation interval (reported in 47% and 48% of studies, respectively) are also important to consider because they interact with time since fire to affect vegetation structure and composition. For example, vegetation structure and species composition 1 year post-fire differs between 2 and 10 year fire rotation intervals or fire frequency as a result of varying levels of fuel accumulation in years intervening fires. Given that only half of studies reported the combined effects of two, or all three, of these interacting factors, there is substantial room for future research addressing the interacting effects of time since fire, fire frequency, and fire rotation interval, including in interaction with below-described factors like fire season and intensity.

Most studies did not explicitly evaluate how variation in fire intensity (i.e., energy output from fire) affected birds, or even report intensity of the fires studied. Fire intensity



is often directly related to fire behavioral characteristics (e.g., flame length, scorching heights) that affect vegetation regeneration, structure, and species composition (Keeley 2009). Because fire intensity greatly affects vegetation, it is also likely to have a substantial impact on bird populations and communities (Bock and Block 2005). Compared to low-intensity fires, high-intensity fires typically affect broader areas, leave lower fuel loads, remove more woody vegetation, and in ecosystems with ladder fuels that allow flames to reach the tree canopy (e.g., savannas), have greater likelihood of resulting in stand replacement. In combination, these effects of intense fires also typically lead to reduced spatial heterogeneity of vegetation on the landscape (Cassell et al. 2019). These differences in the ecological effects of low and high-intensity fires are likely to lead to differential effects on bird populations and communities (e.g., greater changes in abundance and in species composition and diversity). Future studies evaluating effects of fire intensity on birds could estimate this factor using remote sensing techniques that capture post-fire spectral characteristics of vegetation and soil (Lentile et al. 2006) or more traditional ground-based measurements like flame length, degree of bark char, or Byram's equation (Byram 1959).

While most studies reported the season of the fire(s) studied, but very few (5) explicitly evaluated how birds respond to the season of fire. Fires in different seasons have varying effects on ecosystems as a result of different weather conditions and varying species composition and moisture content of fuel, which also vary within season, all of which influence fire behavior and intensity in ways that influence vegetation (Miller et al. 2019). Moreover, fires in different seasons affect different bird species assemblages and periods of avian annual cycles (see following sub-section). For example,

a spring transition season fire could affect winter resident species that have not yet migrated, in-transit spring migrants, and summer and permanent resident species at the onset of their nesting season, or a late-summer growing season burn could affect permanent resident and summer resident species at the conclusion of their nesting season, as well as in-transit fall migrants, or any birds inhabiting the burned areas at subsequent times. As an example of the importance of fire season, a study in pine savannas showed that non-breeding season survival of Henslow's Sparrow was higher in sites that were burned during the growing season, as compared to those burned in the dormant season, a pattern likely emerging as a result of greater seed availability and more-favorable vegetation structure in association with growing season fire (Thatcher et al. 2006). Understanding fire effects on birds—and therefore leveraging the use of seasonal prescribed fire and season-specific strategies of wildfire management to optimally manage bird populations and communities—will require much further research explicitly evaluating the effects of different seasons of fire.

#### *Avian life history periods and response variables*

Most studies only evaluated how fire affected birds during their breeding season. This collective bias toward the breeding season mirrors a larger trend documented for a wide variety of animal taxa across the ecology literature (Marra et al. 2015). The breeding period is crucial for bird populations because it is the time when young are produced; however, in-transit and stationary non-breeding periods can also drive population dynamics and declines, especially in migratory species (Morrissette et al.

2010, Saino et al. 2004, Rushing et al. 2016). Fire can clearly influence avian life history periods other than the breeding season, for example, including survival, abundance, and habitat use of in-transit migrants and wintering birds (Bechtoldt & Stouffer 2005; Korosy et al. 2013; Hovick et al. 2014, 2017). There are also community-level implications of disproportionately focusing on the breeding season, as this approach can overlook a large proportion of the bird species that use a location during the course of a year, especially in lower latitude areas where peak avian diversity often occurs during the non-breeding season. Finally, in addition to the need for future research addressing how fire effects all portions of avian annual cycles, research is needed to evaluate time lag effects that extend beyond the time and season of burning—for example, as illustrated by the above Henslow’s Sparrow example in which winter survival was affected by prescribed fires implemented during previous growing seasons.

Most studies only evaluated how fire affects individual bird species. This species-level approach can serve a crucial purpose, as conservation efforts often focus at the species level. This pattern may also arise partly as a result of studies addressing basic ecological questions that require a focus on species (e.g., what aspects of population demography or behavior are affected by fire?). Species-focused assessments may in some cases be useful for making community-level inferences because fire-associated effects on multiple individual species can result in discernible changes at the community level. However, species-level responses do not always manifest in such changes to communities (e.g., if abundances of two different species have opposing responses to fire, total abundance may remain unchanged) (Supp and Ernest 2014). Further research focused on community-level metrics of bird responses to fire will be crucial because conservation

focused on communities is often more efficient and cost-effective than species-focused conservation, and because fundamental research into bird community responses will broaden our general understanding of the ecological effects of fire.

### *Characteristics of ecosystems*

Most studies were either in prairie ecosystems such as tallgrass, mixed grass, or shortgrass prairie, or in pine or oak savannas with grass-dominated understory; relatively few studies were in sagebrush steppe or included multiple grassland types (e.g., studies assessing fire effects across a gradient from open prairie to savanna to closed forest). Fire plays a critical role in maintaining all grass-dominated ecosystems, but prescribed fire—the type of fire studied in the majority of studies—is generally more frequently applied in prairies and savannas than in steppes, as a result of steppes having drier climates and lower fuel accumulation, conditions that limit the capability of this ecosystem type to withstand frequent fire (Lauenroth et al. 1999, Scheintaub et al. 2009). These differences in fire frequency may partly explain the lower number of studies in steppe ecosystems. Of the few studies that considered multiple ecosystem types, more than one-third were review articles that contained no original data. Because bird assemblages vary across ecosystem gradients (e.g., varying bird abundance, species composition, and representation of life history guilds across a gradient from savanna to woodland) (Roach et al. 2019), and because characteristics of fire also vary across these gradients (e.g., lower fire frequency with progression from tallgrass to mixed grass to shortgrass prairie), bird responses to fire are likewise expected to vary among ecosystem types and along

ecosystem gradients. Future studies should consider evaluating and comparing bird responses to fire across multiple grassland ecosystem types to improve ecosystem-specific approaches to avian conservation management (Hartung and Brawn 2005, Mabry et al. 2010).

Most studies evaluated how birds responded to vegetation management techniques either in addition to or in interaction with fire. Some of these strategies (grazing, herbicide, and timber harvest) have similar effects as fire by creating heterogeneity, are often conducted in tandem with fire and each other, and likely influence fire characteristics (e.g., grazing could moderate fire intensity or frequency) and effects of fire on birds (Augustine and Derner 2012, Duchardt et al. 2016, Fuhlendorf et al. 2006, Peterson and Reich 2001, Roach et al. 2019, Vickery et al. 1999, Yeiser et al. 2015). Future studies should explicitly consider effects of other vegetation management practices when applicable, to parse apart the independent and interactive effects of these processes with fire and improve conservation and management plans for grassland birds.

### *Limitations*

Our study was designed to generate a representative sample of recent literature on bird responses to fire in grasslands of North America, but it was not exhaustive. Due to limited institutional access to literature databases, our search used Scopus, which does not include publications prior to 1970 or access to some ecological journals containing important studies of bird responses to fire. For example, despite its title containing our search terms, Vickery et al. (2005)<sup>a</sup> was not returned in our search because it was

published in a journal (*Studies in Avian Biology*) not included in the Scopus database. In addition to this limitation of the literature database, our search terms may have overlooked some studies of bird groups traditionally referred to by names other than “bird” (e.g., ducks, geese, quail, turkey) (e.g., Renwald et al. 1978, Sasmal et al. 2018); this limitation highlights the importance of future studies of these bird groups including “bird” as a keyword. Further, this issue may have affected our evaluation of some factors related to the portion of the avian annual cycle studied (e.g., all North American quail and turkey species are non-migratory, and thus, perhaps more likely to be studied year-round due to their relatively sedentary life history) and characteristic of ecosystems studied (e.g., missing studies of ducks could have caused us to miss studies of relevant wetlands if they did not report the studied wetlands as grass-dominated ecosystems). Likewise, some studies that evaluated ecological disturbances more broadly may not have included “fire” as a keyword and therefore may have been overlooked. However, we believe this limitation would not contribute systematic bias to our comparisons (e.g., relative to particular characteristics of fires, ecosystems, and birds studied).

### *Conclusion*

Grasslands and birds utilizing them have experienced declines at least partly attributable to fire exclusion. We show that prescribed fires were studied more often than wildfires and that most studies do not evaluate important fire factors, such as fire intensity and season, that influence vegetation, ecosystems, and birds. We also show most studies evaluated birds during the breeding season (as opposed to migration and non-

breeding seasons) and species-specific bird response (as opposed to community response) in prairie or savanna grasslands. While research concerning these particular areas should not be reduced, they do highlight gaps that should receive more research attention in future studies in order to fully understand how bird populations and communities respond to fire in grasslands. A comprehensive understanding of how fire affects birds has the potential to benefit declining bird populations through optimal management of fire in North American grasslands and other ecosystems and biomes more broadly. These types of information are also crucial for returning and continuing the use of fire in grasslands to restore their structure, function, and biodiversity.

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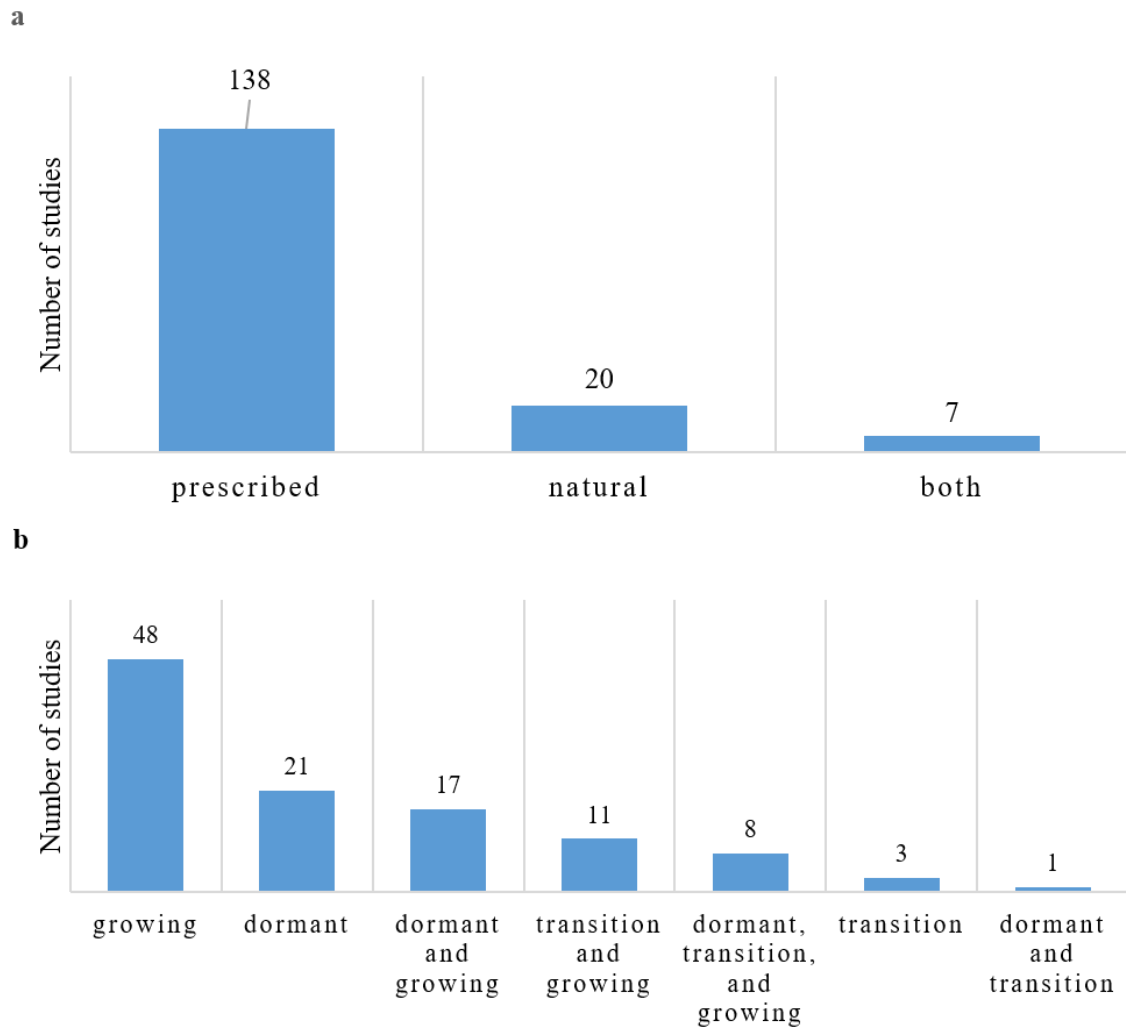


Figure 4.1. Number of studies conducted for (a) types of fire and (b) season of fire.

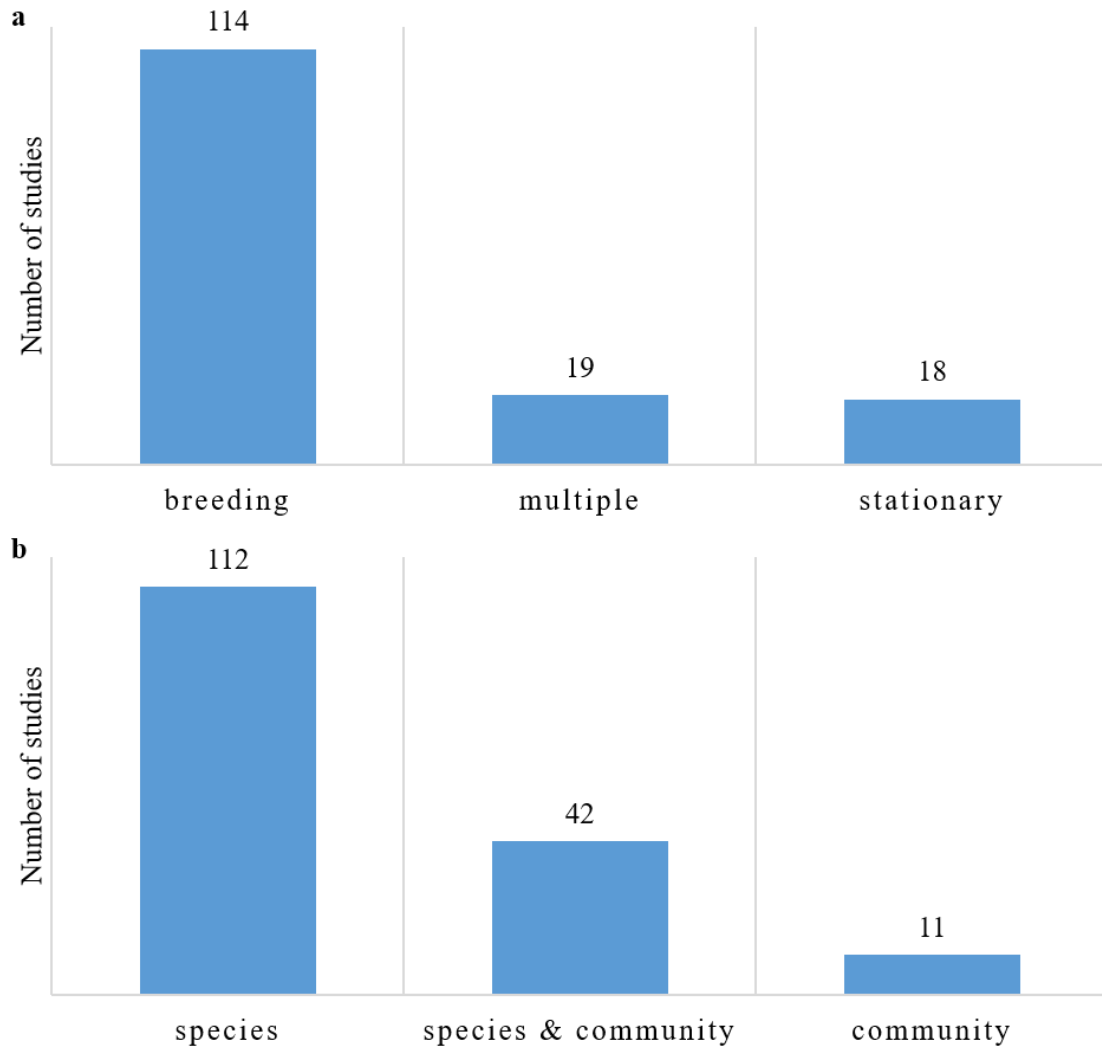


Figure 4.2. Number of studies conducted for different (a) avian life history periods and (b) levels of ecological organization for birds.



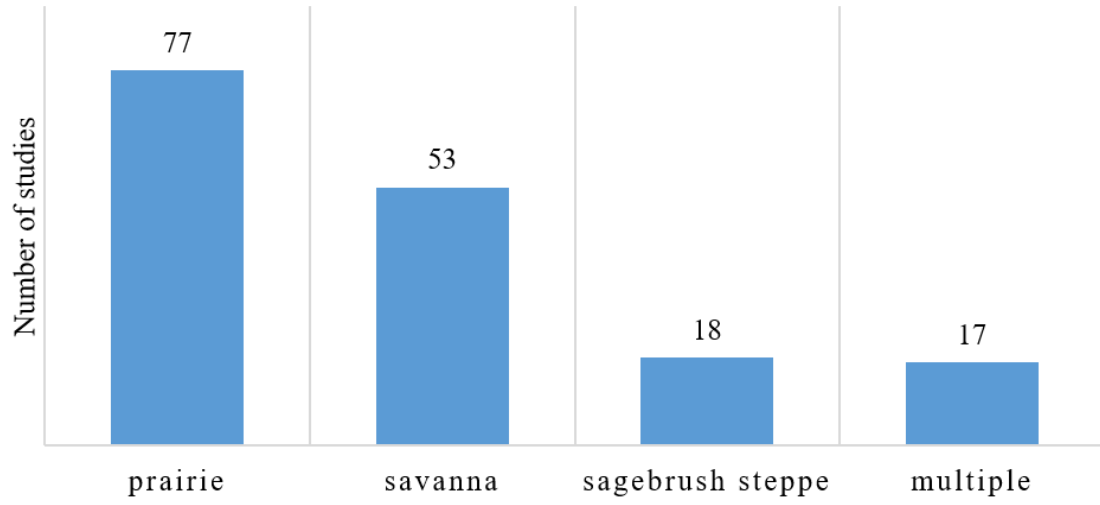


Figure 4.3. Number of studies conducted in each ecosystem type.

## APPENDICES

Chapter 1. Candidate models, coefficients, and CIs from top models for analysis of species-specific collision correlates (Appendix S1), list of participants collecting data (Appendix S2), full candidate model and output for all life-history models (Appendix S3), and estimated collision vulnerability for all species (Appendix S4) are available online at the following link:

<https://conbio.onlinelibrary.wiley.com/doi/abs/10.1111/cobi.13569>. The authors are solely responsible for content and functionality of these materials. Queries (other than absence of material) should be directed to the corresponding author.

Chapter 2. Webtables for model rankings for radar-derived migration variables averaged across the entire night for different migration seasons (WebTable 1), for different time periods throughout the night for both spring and fall (WebTable 2), and top model coefficients and confidence intervals for models averaged across the entire night (WebTable 3) and different time periods throughout the night (WebTable 4) are available online at the following link: [https://d509cb3c-48f3-4aff-abda-86ce7a6c6b10.filesusr.com/ugd/c6fb62\\_7cf9665504c54fc582a1a75acce5f663.pdf](https://d509cb3c-48f3-4aff-abda-86ce7a6c6b10.filesusr.com/ugd/c6fb62_7cf9665504c54fc582a1a75acce5f663.pdf).

VITA

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