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Wetland Bird Abundance and Safety Implications for Military Aircraft Operations

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ABSTRACT Wetlands with associated avifauna can pose a substantial hazard to aviation safety, potentially increasing bird–aircraft collision (strike) risk when located near air operations areas. We modeled year-round use by wetland avifauna of Drummond Flats Wildlife Management Area (Drummond Flats), a wetland complex located within 10 km of Vance Air Force Base (AFB), Enid, Oklahoma, USA. Our objectives were to 1) quantify seasonal avifauna abundances at Drummond Flats; 2) test *a priori* models reflecting use by bird species recognized as hazardous to aviation safety relative to environmental factors including flooded wetland habitat and vegetation cover; 3) use these models to predict maximal expected abundances of wetland avifauna during flood conditions; and 4) compare our findings with reported bird strikes at Vance AFB. Drought conditions influenced avian use during our study. Of the species expected to respond predictably to flooded wetland habitat, only ducks (Anatinae) occurred in numbers conducive to modeling. Using zero-inflated Poisson models, we found that duck abundance was positively associated with permanent wetland habitat type and, excluding winter, available habitat area (i.e., standing water); whereas, >50% vegetation cover was negatively correlated with abundance. No model predicted >97.2 ducks/ha for any habitat type, except during winter. Our models also identified potential peaks in abundance not evident from raw count data, emphasizing the benefits of this approach. Identifying factors driving abundances also enables targeted management of hazardous species. Further, we found double-sampling to be a practical method for assessing detection bias during avian surveys at wetlands. Restricting to obligate wetland species associated with Drummond Flats, we found 1 strike/184,212 flight-hours, which was an order of magnitude lower than the average for U.S. civil aircraft (1990–2014). Thus, under drought conditions, bird use of Drummond Flats likely did not elevate strike risk for Vance AFB aircraft operations. Published 2017. This article is a U.S. Government work and is in the public domain in the USA

KEY WORDS abundance estimation, avian abundance, bird strikes, bird surveys, double-sampling, ducks, Oklahoma, strike hazard, strike risk, zero-inflated models.

Wildlife management efforts implemented at civil and joint-use airports in the United States since the early 1990s appear to have reduced the number of damaging bird–aircraft collisions (bird strikes) reported to the U.S. Federal Aviation Administration (FAA; Dolbeer 2011). Still, relatively little attention has been directed to mitigating bird attractants originating from the surrounding landscape so as to reduce strike risk (Blackwell et al. 2009, Martin et al. 2011, Coccon et al. 2015). Strike risk in its basic format is composed of an estimate of the effects of the strike (e.g., direct and indirect

costs associated with damage and effects on human health) and corresponding strike probability. As an example of risks posed outside the airport environment, strikes reported to the FAA and occurring at >152 m above ground level have gradually increased with some waterbirds (cormorants [Phalacrocoracidae], ducks and geese [Anatidae], and gulls [Laridae]) and diurnal raptors (including vultures; Accipitriformes and Cathartiformes) contributing most frequently to damaging strikes (Dolbeer et al. 2015, DeVault et al. 2016).

Multiple factors influence strike risk (Dolbeer 2011, Martin et al. 2011, Blackwell et al. 2013, Coccon et al. 2015). A model of strike risk will generally include metrics pertaining to the cost of the strike, some probability of striking particular species or bird groups relative to aircraft

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movements within a particular airspace, and indices of species or group relative abundance within the airspace (Blackwell et al. 2009, Martin et al. 2011). Objective surveys of avian abundances in associated habitats and airspace over time might compose the risk estimate, or serve in concert with the risk estimate to prioritize wildlife management efforts (Blackwell et al. 2009, 2013; Coccon et al. 2015). In the case of military aviation, these data can be used to adjust mission routes, altitudes, and times (Zakrajsek and Bissonette 2005). Military aircraft, for example, often fly at altitudes <300 m above ground level (AGL) and high speeds, which make them more susceptible to strikes (Tedrow 1998, Sodhi 2002, DeVault et al. 2015). Strikes involving U.S. Air Force (USAF) aircraft from 1985 through 2013 resulted, on average, in losses of US\$30 million annually (U.S. Air Force Safety Center 2014).

To our knowledge, methods to link off-airport, habitat-specific avian survey data to strike risk associated with an airport or airbase are few (but see Coccon et al. 2015). As such, there is little understanding of how the dynamics of land use, weather, and avifauna populations near air operations areas contribute to strike risk or how this risk might be reduced. Our purpose was to understand how bird populations using the federally managed wetland complex Drummond Flats Wildlife Management Area (Drummond Flats), near Vance Air Force Base (AFB), Enid, Oklahoma, USA, might contribute to strike risk for USAF and other aircraft operating from the airbase. As a federally managed wetland area, Drummond Flats offers a contrasting perspective between conservation management and aviation safety efforts.

We conducted a 2.5-year study to determine year-round use of Drummond Flats by avifauna (both obligate and facultative species). We assumed *a priori* that bird abundance would be positively related to area of available habitat within Drummond Flats (Suter 1994, Buler et al. 2007, Hart et al. 2009, Webb et al. 2010, Albanese and Davis 2015). Our objectives were to 1) quantify seasonal avifauna abundances at Drummond Flats; 2) test *a priori* models predicting the probability of use by bird species recognized as hazardous to aviation safety (see Dolbeer et al. 2015) relative to factors such as amount of flooded area, vegetation composition, and season; 3) use these models to predict maximal expected abundances of wetland avifauna; and 4) compare our findings with reported strikes at Vance AFB.

STUDY AREA

Drummond Flats was a wetland complex located west of the town of Drummond, Oklahoma, on an extensive alluvial flat (Barclay 1952). It was managed under the U.S. Department of Agriculture's Wetlands Reserve Easements component of the Agricultural Conservation Easement Program (formerly, the Wetlands Reserve Program; <http://www.nrcs.usda.gov/wps/portal/nrcs/main/national/programs/easements/wetlands/>). Drummond Flats consisted of 97% upland habitat that only flooded occasionally following heavy precipitation events and subsequent overflowing of tributaries. Approximately 10% of the upland area was actively

farmed and 0.5% was forested, while the majority of upland habitat was covered in grassy-herbaceous vegetation interspersed with a few barren saline areas. The area also contained approximately 36 small- to medium-sized natural and manmade ponds and impoundments (including the sewage treatment ponds for the town of Drummond), ranging from 0.1 to 6.5 ha in size. Three creeks (Turkey, Salt, and Elm creeks) flowed through the area, with Salt and Elm creeks classified as ephemeral streams and Turkey Creek as an intermittent stream (U.S. Department of Agriculture 1983). Management efforts at Drummond Flats included moist-soil management through water control structures and dikes, but little to no manipulations of water levels were undertaken during our study. Parts of the upland areas and dry wetland units were disked to promote native food plants for waterfowl and upland game birds, such as ring-necked pheasant (*Phasianus colchicus*) and mourning dove (*Zenaidura macroura*), to provide hunting opportunities. A few food plots were also planted with agricultural crops for upland game bird management. Most of the ponds and impoundments within Drummond Flats were normally flooded, except during extended drought conditions. Significant precipitation events capable of flooding 450 ha of the upland habitat were expected to occur on a yearly basis, whereas precipitation events capable of flooding 800 and 1,100 ha were expected to occur with an average frequency of 2 and 5 years, respectively (Heitmeyer 2012). Temperatures averaged 1.2°C above and precipitation 208 mm below the long-term averages of 14.9°C and 780 mm during our study, respectively (Oklahoma Mesonet 2014; see Supporting Information available online for further details). We experienced 3 significant flooding events during the study, with an estimated 593, 481, and 940 ha being flooded on 25 May 2011, 20 December 2011, and 2 May 2012, respectively.

METHODS

Habitat Assessment

We used Environmental Systems Research Institute's ArcGIS 9.0 (1999–2004) Geographic Information System (GIS) software to assemble base data layers for Drummond Flats from U.S. Geological Survey topographical image mosaics of 1.0-m resolution 1:12,000 digital ortho-image quarter quadrangles (DOQQs). We assembled base layer data for 6 years, including 3 years with above (2004, 2008, and 2010) and 3 years with below (2003, 2005, and 2006) average precipitation. We visually examined the entire Drummond Flats area of each year's DOQQ at the 1:2,500 scale. When we located a discrete patch of wetland habitat (defined as saturated substrate or standing water), we delineated the broadest contiguous extent of the habitat that we could identify among the DOQQs as a polygon. We classified discrete wetland habitat patches ≥ 0.1 ha in size and with a maximum width of ≥ 10 m that held water during ≥ 4 of the 6 years as permanent wetland habitat (i.e., including classes Permanently Flooded, Intermittently Exposed, Semipermanently Flooded in Cowardin et al. [1979], $n = 36$). We classified the remainder of the area (including

creeks and drainage ditches) as temporary wetland habitat. We further classified permanent wetland habitat patches into large (≥ 1.0 ha; range = 1.3–6.5 ha) and small (< 1.0 ha; range = 0.1–0.8 ha) units. Four sewage treatment ponds for the town of Drummond were located within Drummond Flats and we treated them as a single large wetland unit because of their similarity in physical attributes and close proximity to each other. Most ($> 97\%$) of the wetland habitat at Drummond Flats consisted of habitat classified as temporary wetland habitat. This habitat area was not naturally divided into smaller discrete units; therefore, we used UTM gridlines spaced 200 m apart to create a 200×200 -m grid over the area and defined the temporary wetland habitat within each grid unit as a temporary wetland habitat survey unit.

Wetland Surveys

We documented abundance and wetland use by wetland avifauna (see Supporting Information available online for definition of wetland avifauna) during October 2010–March 2013. We used a stratified sampling design (outlined below) based on our previous knowledge that waterfowl generally tend to be most abundant on larger permanent wetland units at Drummond Flats (K. Andersson et al., unpublished data). We performed surveys on a weekly basis, with permanent and temporary wetland habitat surveyed on alternate weeks. During each consecutive 2-week period, all 10 large permanent wetland units (LPUs), 5 (20%) of the small permanent wetland units (SPUs), and 40 (10%) of the temporary wetland units (TUs) were surveyed. We randomly selected a set of SPUs and TUs at the onset of each astronomical season and surveyed them throughout that season. The exact start and end dates of each astronomical season varied by year, but were approximately 21 December–19 March for winter, 20 March–20 June for spring, 21 June–21 September for summer, and 22 September–20 December for autumn. With few exceptions, we surveyed each wetland unit both during morning (first 4 hr following sunrise) and evening (last 4 hr prior to sunset) during each survey event (2-week period).

All surveys were area counts and conducted either on foot or from an all-terrain vehicle, using a combination of 10×40 binoculars and $20\text{--}60 \times 80$ spotting scopes to observe birds. To estimate detection bias, we used a double-sampling approach (Cochran 1977, Eberhardt et al. 1979, Bart and Earnst 2002, Farmer and Durbian 2006), whereby we conducted an intensive count on a randomly selected subsample of units ($n = 77$) immediately following a regular count. Regular surveys were conducted by a single surveyor, while 2 surveyors worked in conjunction during double sampling. During a regular survey, the surveyor traversed the wetland unit or travelled along the edge of the wetland unit until an unobstructed view of all parts of the wetland unit was obtained. If the view of any part of a wetland unit was obstructed by vegetation, the surveyor traversed the vegetated part of the unit at least once in an attempt to flush any birds present.

During double-sampling, 1 of the 2 surveyors (Surveyor A) was positioned for an unobstructed view of any birds entering

or leaving the survey unit before the other surveyor (Surveyor B) initiated the regular survey. Immediately after concluding the regular survey, Surveyor B performed the intensive survey. Specifically, Surveyor B followed the entire perimeter of the habitat in the survey unit and traversed any part of the habitat in the survey unit not consisting of unvegetated standing water so that no point within it was passed at a distance > 10 m. We suspect that few, if any, birds of interest to this study were likely to remain in place when passed at such close distance (Rodgers and Smith 1995, Blumstein et al. 2003). Further, throughout both the regular and intensive surveys, Surveyor A carefully noted any birds entering or leaving the survey unit. Upon completion of the intensive survey, surveyors met and, if necessary, adjusted the counts from the intensive survey according to observations by Surveyor A of any birds entering or leaving the survey unit that went undetected by Surveyor B. This approach allowed us near certainty that no birds that left or entered the unit during the surveys were missed or incorrectly included. We therefore believe counts from intensive surveys to be close to 100% accurate.

We recorded only birds present in wetted habitat within the wetland unit at the onset of the survey (i.e., any birds entering the wetted habitat within the wetland unit during the course of the survey were not included); thus, count samples were instantaneous. If any birds were flushed during surveys, we attempted to visually follow the birds and determine where they landed so as to not count them again at subsequent survey units. In most cases, it was obvious where the birds landed or that they left the area entirely. We therefore believe the frequency of double counting to be low. We identified all birds to species or lowest possible taxonomic group if species was not identified.

We grouped some species of wetland avifauna into guilds for the purpose of analysis (see Supporting Information) because of similarities in their behavior and habitat requirements. Still, many avian species and guilds were rarely encountered or recorded in very low numbers. In fact, only ducks (Anatinae), shorebirds (Charadriidae, Recurvirostridae, and Scolopacidae), and blackbirds (*Agelaius*, *Xanthocephalus*, *Euphagus*, *Quiscalus*, and *Molothrus*) were observed in numbers and frequencies that would allow for model development (Table S1, available online in Supporting Information). Only ducks, however, primarily use a habitat type (i.e., standing water) that was expected to increase linearly with increased area of flooding (basically, a measure of area covered in standing water). Our goal was to develop models that could be used to predict abundances during flood events (characterized by area of flooding); therefore, we only modeled duck abundances (see below).

In addition to bird data, we visually estimated the proportion of the survey unit composed of wetted habitat; wetted habitat consisting of mud (saturated substrate not covered by water), shallow water (≤ 20 cm deep), and deep water (> 20 cm deep), as well as wetted habitat covered by emergent vegetation (i.e., canopy cover [Daubenmire 1959]) being $< 50\%$ or $\geq 50\%$, and slope of habitat edge (incline where wetted habitat meets nonwetted habitat) being $< 20^\circ$

or $\geq 20^\circ$. We collected all habitat variables concomitant with bird surveys. All percentage estimates, other than for vegetation cover, were made on an interval scale with the following intervals: 0, 1–5, 6–25, 26–50, 51–75, 76–95, and $\geq 96\%$. Interval midpoints were used in all analyses. To calculate estimates of the area of standing water for each unit survey, we multiplied the percentage values with the total area of the survey unit, as estimated from GIS data.

Aircraft Movements

Vance AFB provided information on flight patterns and data on flight-hours and sorties for the study period, a sortie being an operational flight by one aircraft, starting at initial takeoff and ending when the aircraft has landed and been on the ground for ≥ 5 min or the engines have been stopped (U.S. Department of the Air Force 2001). We used all available data on bird strikes concurrent with our study that included a reported strike location < 10 km from Vance AFB and a strike altitude $< 1,000$ m AGL. Bird-aircraft strike data for Vance AFB were provided by D. P. Sullivan and Lt. T. M. Robertson, USAF Bird/Wildlife Aircraft Strike Hazard Team.

Data Analysis

We predicted *a priori* that duck abundance would be positively related to available habitat area (i.e., standing water) within a survey unit (Tuite et al. 1984, Suter 1994, Hart et al. 2009, Webb et al. 2010). Furthermore, we assumed that a steeper slope would negatively influence abundance for ducks because it would generally impede the visibility for the birds and therefore, increase risk of predation (Metcalf 1984, Lima 1998, Whittingham and Evans 2004, Albanese and Davis 2015). For similar reasons, emergent vegetation cover $\geq 50\%$ was also hypothesized to influence bird abundance negatively for ducks (Metcalf 1984, Helmers 1992, Lima 1998, Whittingham and Evans 2004, Webb et al. 2010). Temporal abundance patterns are known to vary among seasons, but are expected to remain stable among years; therefore, we analyzed each season separately across all years.

Duck abundance data exhibited marked zero-inflation (74–88% zeros among seasons) and overdispersion in the nonzero data (variance-to-mean ratios in nonzero counts among seasons: 6.7–59.1), so we considered the following model types: negative binomial, quasi-Poisson, zero-inflated Poisson, and zero-inflated negative binomial models (Potts and Elith 2006, Zuur et al. 2009). To select the best overall model for each season, we used a 3-step approach, with Steps 1 and 2 focused on model assumptions (i.e., distributions) given the data. Specifically, we first fitted a fully parameterized model of each model type. Explanatory variables included intercept, area of available habitat, vegetation cover, slope, time within season (measured in weeks from the onset of each season), year, and primary wetland type (i.e., permanent or temporary). Here, we also allowed for 2 different relationships between bird numbers and area of available habitat (untransformed and square-root transformed; independently in both model components for zero-inflated models). This first step yielded 12 different overall models for each season

(4 for each zero-inflated model and 2 for each of the other model types; Table S2, available online in Supporting Information).

In Step 2, we plotted Pearson residuals against fitted values and all explanatory variables. We discarded any models that showed obvious patterns (Burnham and Anderson 2002, Zuur et al. 2009). We also examined plots of observed against fitted values, and discarded models that were poor predictors of nonzero counts (*cf.* Potts and Elith 2006, Zuur et al. 2009). For all seasons, these 2 steps excluded all models except the zero-inflated Poisson models.

In Step 3, we assessed the actual fit of our remaining models, given the observational data. We used the second-order variant of Akaike's Information Criterion (AIC_c , i.e., AIC corrected for small sample size; Burnham and Anderson 2002) to select the best-approximating model among the remaining fully parameterized models for each season (Burnham and Anderson 2002, Zuur et al. 2009). This approach allowed us to avoid the problem with AIC_c often giving preference to models that were notably poor at predicting nonzero counts but successful in predicting zeros; our data reflected considerable zero-inflation. The primary purpose of the models was to predict bird numbers under ideal conditions (i.e., nonzero counts); therefore, the capability of predicting nonzero data was an essential model characteristic. We recognize that it is possible that emphasis placed on nonzero prediction capability could bias final predictions upward, but this is not necessarily undesirable where great costs (both in terms of economic damage and possible loss of human lives associated with strikes) are at stake.

We used only one count (i.e., morning or evening) per survey unit and event for modeling. Early data exploration showed, on average, a slight tendency toward greater numbers during morning surveys; we therefore used data from morning surveys whenever possible. If no morning survey was available for a particular survey unit and event, data for the corresponding evening survey were used instead. We included survey unit ID as a random intercept in the models to account for the repeated measures design. During the summer and autumn seasons, there was no variability in duck abundance (i.e., all zeros) for 1 of the 2 categories for the variable vegetation cover. Thus, it was not possible to include vegetation cover in these 2 cases.

For summer data, variable slope caused considerable convergence problems during model fitting, while at the same time model evidence suggested this was more than likely a nuisance parameter (i.e., the ratio of the parameter estimate to its standard error was always very low). Thus, we excluded slope from the set of possible explanatory variables for the summer data.

The number of possible combinations of the explanatory variables for the zero-inflated Poisson models (1,024–16,384, depending on season) made fitting all possible submodels impracticable. Hence, model selection or model-averaging (Burnham and Anderson 2002) on all possible submodels was not a viable option. Instead, we used a step-wise backward selection based on AIC_c until model fit no

longer improved (i.e., $\Delta AIC_c > 0$; Burnham and Anderson 2002, Zuur et al. 2009, Arnold 2010). We used PROC NLMIXED (SAS 9.3, SAS Institute, Inc., Cary, NC, USA) for all statistical modeling.

Maximal abundances are important in understanding a site's potential contribution to strike risk. Thus, one of our goals was to predict maximal abundances at Drummond Flats during flood stage. To avoid extrapolating predictions beyond the range of data, we numerically found the combination of parameter values that yielded maximal abundance within the range of observed values for each wetland type (temporary and permanent), except for area of available habitat and slope for temporary habitat (due to slope $\geq 20^\circ$ being unrealistic during flood stage for this habitat type). We then used these parameter values in PROC NLMIXED to predict maximal abundance values with 95% confidence intervals at maximal observed area of available habitat for each habitat type (i.e., 6.46 ha for permanent wetland habitat and 4.00 ha for temporary wetland habitat). These maximal abundance estimates were then converted to maximal densities and used to calculate maximal abundance estimates for ducks at Drummond Flats under conditions equivalent to a 2-year flood event (i.e., all permanent [39.1 ha] and 800 ha temporary wetland habitat flooded; Heitmeyer 2012). Confidence intervals for predictions were based on standard errors approximated by the Delta Method and truncated at 0 (Cox 2005, SAS Institute Inc. 2013).

As a result of low temperatures during early winter in 2010–2011, most of the wetted habitat was frozen at Drummond Flats, making it unavailable for use by ducks. As a result, the few ducks that were present in the general area concentrated in the small pools of open water that still existed (chiefly at the Drummond sewage treatment ponds). This caused a contradictory relationship between duck abundance and area of available habitat in our best approximating model for winter (Tables 1 and 2). It is unreasonable to expect the corresponding density during these extreme conditions (when birds are concentrated together) to be representative of larger areas of Drummond Flats under completely different conditions (i.e., when the site is not frozen and birds have the opportunity to be more dispersed). Therefore, we could not make any realistic model predictions for duck abundance at flood stage during winter. Additionally, we only encountered ducks in temporary wetland habitat on 3 occasions during 2 summers for 10 total

ducks. Thus, no model predictions were possible for temporary wetland habitat during summer because of lack of data. The predicted maximal duck abundance for the entire Drummond Flats for summer was therefore based on permanent wetland habitat only.

RESULTS

Wetland Surveys

In total, we conducted 6,834 individual unit surveys during October 2010–March 2013. Of these, 1,915 were surveys of permanent habitat units and 4,919 were surveys of temporary habitat units. During these surveys, we counted 35,371 birds of 74 wetland species, including 17 species of ducks, 11 species of wading birds (Ardeidae and Threskiornithidae), 26 species of shorebirds, 5 species of blackbirds, and 15 other wetland-associated bird species (Table S3, available online in Supporting Information). Only 4 guilds (ducks, wading birds, shorebirds, and blackbirds) occurred with any regularity and in significant numbers during the study (i.e., estimated abundance based on proportional area surveyed in each habitat class ≥ 50 individuals on ≥ 10 occasions). Blackbirds, shorebirds, and ducks were the most abundant avian guilds, with greatest estimated numbers of blackbirds and shorebirds being approximately twice as high as for ducks (Table S1); ducks were >6 times as numerous as any other avian species or guild.

Our detection probabilities during wetland surveys were 0.87 for shorebirds, 0.99 for ducks, 0.99 for wading birds, and 0.95 for blackbirds. However, the lower detection probability for shorebirds was due to a few instances with no shorebirds detected during the regular survey and a single Wilson's snipe (*Gallinago delicata*) detected during the intensive survey, giving a detection probability of 0 for those surveys. If Wilson's snipe was excluded, the detection probability for the shorebird guild increased to 0.98. As a result of the relative rarity of all other avian wetland species at Drummond Flats, detection rates were either unobtainable (i.e., due to no individual of the species being encountered during any intensive survey or, in the case of sora [*Porzana carolina*], a single encounter during an intensive survey resulting in a detection rate of 0) or 1. Because all detection probabilities were either close to 1 or unobtainable, we used uncorrected survey counts in all analyses.

Table 1. Final best models for duck abundance at Drummond Flats Wildlife Management Area, Oklahoma, USA, during October 2010–March 2013, for each astronomical season. All models were zero-inflated Poisson models and therefore had 2 model components: the count model and the zero model, each with an independent set of explanatory variables. Possible model parameters were as follows: area of available habitat in ha (AAH or \sqrt{AAH} ; continuous), year (YEAR; nominal: 2010–2013), time within season in weeks (WEEK and (WEEK)²; continuous), slope at the edge surrounding wetted habitat (SLOPE; nominal: $<20^\circ$ or $\geq 20^\circ$), vegetation cover in wetted habitat (VCOV; nominal: $<50\%$ or $\geq 50\%$), and habitat type (TYPE; nominal: permanent or temporary). See main text for greater detail on model development, as well as Supporting Information, available online.

Season	Count model	Zero model
Winter	AAH + YEAR + WEEK + (WEEK) ² + SLOPE + TYPE	\sqrt{AAH} + YEAR + (WEEK) ² + SLOPE + VCOV + TYPE
Spring	AAH + YEAR + WEEK + SLOPE + VCOV	\sqrt{AAH} + WEEK + (WEEK) ² + SLOPE + VCOV + TYPE
Summer ^a	AAH + YEAR + WEEK + (WEEK) ²	AAH + WEEK + (WEEK) ²
Autumn	\sqrt{AAH} + YEAR + WEEK + (WEEK) ² + SLOPE	\sqrt{AAH} + YEAR + SLOPE + TYPE

^a Abundance was modeled for permanent habitat only because of lack of nonzero data for temporary habitat during the summer period.

Table 2. Estimated model coefficients (β) and associated standard errors for final models (see Table 1) of duck abundance at Drummond Flats Wildlife Management Area, Oklahoma, USA, during October 2010–March 2013, for each astronomical season. All models were zero-inflated Poisson models and therefore had 2 model components: the count model and the zero model, each with an independent set of explanatory variables. $\text{Var}_{\text{intercept}}$ denotes the variance of the random intercept term.

Variable	Winter		Spring		Summer		Autumn	
	β	SE	β	SE	β	SE	β	SE
Count models								
Intercept	-0.669	0.598	2.601	0.256	-6.173	0.924	-2.323	0.890
AAH	-1.036	0.060	0.280	0.049	0.601	0.117		
$\sqrt{(\text{AAH})}$							0.838	0.215
YEAR = 2013	-0.034	0.099						
YEAR = 2012	-0.365	0.070	-0.152	0.065	0.476	0.292	2.465	0.283
YEAR = 2011							2.228	0.291
WEEK	1.026	0.069	-0.223	0.009	1.167	0.183	0.304	0.065
(WEEK) ²	-0.052	0.004			-0.041	0.011	-0.018	0.004
SLOPE $\geq 20^\circ$	0.154	0.087	-0.695	0.107			1.266	0.153
VCOV $\geq 50\%$			-0.342	0.165				
TYPE = temporary	-3.463	0.997						
$\text{Var}_{\text{intercept}}$	4.383	1.349	1.787	0.464	1.633	0.938	4.351	2.285
Zero models								
Intercept	2.743	0.607	2.084	0.543	-4.597	3.130	3.312	0.784
AAH					-1.547	0.569		
$\sqrt{(\text{AAH})}$	-1.267	0.323	-1.545	0.243			-1.114	0.331
YEAR = 2013	-0.677	0.525						
YEAR = 2012	-1.313	0.428					-1.677	0.635
YEAR = 2011							-1.390	0.651
WEEK			-0.456	0.158	1.480	0.741		
(WEEK) ²	-0.005	0.004	0.035	0.011	-0.076	0.041		
SLOPE $\geq 20^\circ$	-0.951	0.406	0.646	0.355			-1.259	0.586
VCOV $\geq 50\%$	1.715	1.128	0.932	0.399				
TYPE = temporary	1.365	0.506	1.190	0.327			2.841	0.640

Abundance Estimates

Duck abundance was positively associated with permanent habitat type, whereas a $>50\%$ vegetation cover influenced duck numbers negatively for all models that included these variables. Effects of year, week, and slope varied by season (Table 2). Furthermore, all models predicted increased duck abundance with increased available habitat area for all seasons except during winter (Tables 2 and 3). Excluding winter, no model predicted >97.2 ducks/ha for permanent habitat or 4.6 ducks/ha for temporary habitat within the range of areas surveyed for any season (Table 4). The

maximal predicted duck abundance for the entire Drummond Flats under conditions equivalent to a 2-year flood event was greatest during spring (end of Mar beginning of Apr) and summer (mid to late Sep), thus coinciding with spring and early autumn migration (Tables 3 and 4). Predicted peak abundances were of similar magnitudes for both spring and summer, but almost 4 times greater than for autumn.

Reported Strikes

In total, there were 59 bird strikes registered within 10 km of Vance AFB below 1,000 m AGL during our study (Oct

Table 3. Parameter values for final zero-inflated Poisson models (see Table 1) of duck abundance at Drummond Flats Wildlife Management Area, Oklahoma, USA, during October 2010–March 2013, for each astronomical season and habitat type (permanent and temporary) when each model was maximized with respect to abundance. Possible parameter values were restricted to within the range of observed values for each parameter. AAH = area of available habitat (0–4,000 ha for temporary habitat and 0–6.459 ha for permanent habitat), YEAR = year (2010–2013), WEEK = time within season in weeks (1–14), SLOPE = slope at the edge surrounding wetted habitat ($<20^\circ$ or $\geq 20^\circ$), VCOV = vegetation cover in wetted habitat ($<50\%$ or $\geq 50\%$). For temporary habitat, SLOPE was always set to $<20^\circ$ because it was the only realistic value for this parameter for this habitat type at flood stage.

Season	Habitat type	AAH	YEAR	WEEK	SLOPE	VCOV
Winter	Permanent	0.109	2013	10	$\geq 20^\circ$	$<50\%$
	Temporary	0.251	2012	11	$<20^\circ$	$<50\%$
Spring	Permanent	6.459	2011	1	$<20^\circ$	$<50\%$
	Temporary	4.000	2011	1	$<20^\circ$	$<50\%$
Summer ^a	Permanent	6.459	2012	14	^b	^b
Autumn	Permanent	6.459	2012	9	$\geq 20^\circ$	^b
	Temporary	4.000	2012	9	$<20^\circ$	^b

^a Abundance was modeled for permanent habitat only because of lack of nonzero data for temporary habitat during the summer period.

^b Variable not included in the final model.

Table 4. Model predictions (mean and 95% confidence intervals [CI]) for duck abundance at Drummond Flats Wildlife Management Area, Oklahoma, USA, based on data collected during October 2010–March 2013, under conditions equivalent to a 2-year flood event (i.e., all 39.1 ha of permanent wetland habitat and 800 ha of temporary wetland habitat flooded; Heitmeyer 2012) for spring, summer, and autumn. No predictions were possible for winter (see Methods section for details). All predictions were rounded to the nearest integer.

Season	Temporary habitat		Permanent habitat		Drummond Flats total	
	\bar{x}	95% CI ^a	\bar{x}	95% CI ^a	\bar{x}	95% CI ^a
Spring	3,700	1,323–6,077	362	160–563	4,061	1,483–6,640
Summer	^b	^b	3,802	0–10,523	3,802 ^c	0–10,523 ^c
Autumn	431	0–1,298	701	0–1,853	1,132	0–3,151

^a Confidence intervals were based on standard errors approximated by the Delta Method (Cox 2005, SAS Institute Inc. 2013) and truncated at 0.

^b No estimates for temporary habitat in summer due to lack of nonzero data.

^c Total based on estimate for permanent habitat only.

2010–Mar 2013), 49 of which were identified to taxonomic group. Passerines were the most frequently struck avian group, making up 57% ($n = 28$) of all bird–aircraft strikes where group identity was known, compared with 12% ($n = 6$) for all wetland avifauna combined. Among wetland avifauna, shorebirds were the most commonly struck with 8% ($n = 4$) of all identified strikes, followed by blackbirds and double-crested cormorant (*Phalacrocorax auritus*) with 1 (2%) recorded strike each. Total flight-hours for all aircraft at Vance AFB during the study were 184,211.5 hr and total number of sorties were 126,949, which makes for an overall strike probability of 1 collision/2,152 sorties for this time period. For wetland avifauna, the overall strike probability was 1 collision/30,702 flight-hours or 21,158 sorties, on average. Moreover, if we restrict wetland avifauna to include only obligate wetland species (i.e., exclude killdeer [*Charadrius vociferus*] and upland sandpiper [*Bartramia longicauda*; Helmers 1992]) that occur with any regularity at Drummond Flats (i.e., exclude black-bellied plover [*Pluvialis squatarola*] and double-crested cormorant), the average strike probability drops to 1/184,212 flight-hours or 126,949 sorties.

Although the apparent strike probability for shorebirds was 1/31,737 sorties, all of the shorebird species struck were either species that are not truly wetland dependent (i.e., killdeer and upland sandpiper [Helmers 1992]) or that do not occur with any regularity at Drummond Flats (i.e., black-bellied plover). The strike probability for blackbirds was 1 strike/126,949 sorties, but this single strike could not be tied specifically to Drummond Flats because we lacked concurrent survey data from Vance AFB, where blackbirds are known to regularly occur. However, the greatest estimated abundances for blackbirds indicated that Drummond Flats did not attract the large flocks (>10,000 birds) of blackbirds that are regularly observed in the general area surrounding the site during the nonbreeding season (K. Andersson and J. R. Heinen, personal observations).

DISCUSSION

The only wetland-associated avian guilds that used Drummond Flats in significant numbers and a consistent manner were ducks, shorebirds, wading birds, and blackbirds. Among these guilds, ducks pose the greatest hazard to aircraft given their abundance, large size, and tendency

to assemble in larger flocks, increasing the possibility of extensive damage in the event of a collision (DeVault et al. 2011). Despite their consistent use of Drummond Flats, our estimates of duck numbers based on proportional area surveyed in each habitat class were modest for most of the year, with the greatest numbers encountered during spring migration (late Feb through early May). Model-predicted duck abundances presented a somewhat different scenario, with peak abundances predicted for mid- to late-September (i.e., during early autumn migration) and at the end of March and early April (i.e., during spring migration). However, the uncertainty in the predictions was substantial, especially for the peak in mid- to late-September. Thus, both raw counts and model predictions point to a peak in duck numbers during spring migration. Model predictions indicate a peak during early autumn migration as well. Without the modeling approach, the potential peak in duck abundance and possible contribution to strike risk in mid- to late-September would go undetected. This finding underscores the importance of a modeling approach when estimating avian abundances in relation to possible contributions to strike risk.

During wetland surveys, and as evidenced by our modeling results, ducks selected permanent wetland habitat over temporary wetland habitat. Thus, the largest increase in duck abundance, and therefore increase in potential risk, would result from an increase in the amount of permanent wetland habitat at Drummond Flats. From a biological standpoint, it is difficult to predict when habitat will transition from temporary to permanent. However, in its current state, flood water drains very quickly at Drummond Flats once water levels in nearby creeks have receded to the point where they are no longer overflowing. For example, during each of the 3 significant flooding events experienced at Drummond Flats during the study, the area flooded with water had decreased to <7% of the estimated maximal flooded area only 2 weeks later. Thus, these observations suggest that flooding events at Drummond Flats in its current state do not increase the amount of permanent habitat.

What effects an increase in permanent habitat would have on the duck abundance at Drummond Flats is difficult to predict. However, 20 years (1988–2008) of waterfowl survey data from the Salt Plains National Wildlife Refuge (located ~45 km north–northwest of Drummond Flats), which

includes the 3,500 ha Great Salt Plains Lake, never yielded duck densities >27 ducks/ha, and had an average density of <4 ducks/ha for all months (K. Andersson et al., unpublished data). Thus, it appears that our highest model-based estimate for permanent habitat (max. density = 97.2 ducks/ha during summer) is, if anything, biased high. This is not unexpected considering that this estimate was overwhelmingly based on survey data collected when standing water was scarce because of extended drought conditions and duck numbers therefore likely were inflated due to lack of available habitat for the birds to disperse over. Estimates and model results for the autumn season, on the other hand, were likely influenced negatively by waterfowl hunting activity. All surveys conducted where the survey unit was actively being hunted yielded zero ducks. Although these surveys were excluded from the data set prior to analysis, it is likely that the hunting activity at some survey units influenced duck numbers negatively on other units in close proximity. It is also likely that the effects lingered so that surveys conducted later the same day also yielded lower numbers than if no hunting had taken place. In fact, it is well-documented that waterfowl often disperse from hunted to nonhunted areas if such areas are available (Madsen 1998, Casazza et al. 2012). This might be a contributing factor to why the confidence interval for the autumn model prediction was so wide, because otherwise quality habitat remained unoccupied.

Importantly, species use of a particular habitat does not immediately indicate a high strike risk. As alluded to earlier, estimates of strike risk improve as our understanding of avian behavior relative to aircraft movements improves. Specifically, only birds that occupy the same segment of air space and time as an aircraft can be involved in a strike. Therefore, we contend that, when possible, abundance data should be paired with movement patterns and flight altitudes of birds relative to aircraft movements associated with the airfield. However, we also recognize that such data are difficult to obtain because of the challenges of 3-dimensional tracking of individual birds in real time (see Gerringer et al. 2016).

Overall strike frequency (all species included) at Vance AFB during the course of this study was 1 recorded bird strike/2,152 sorties. For comparison, Sodhi (2002) reported that the average strike probability (all species included) for all civilian aircraft ranged from 1/1,700 to 1/2,500 aircraft movements (departures or landings). From 1990 to 2014, on average <15 strikes/100,000 movements were reported to the FAA (Dolbeer et al. 2015). Given that military aircraft are generally considered more susceptible to bird-aircraft collisions compared with civilian aircraft (Tedrow 1998, Sodhi 2002) and that sorties at Vance AFB generally include ≥ 2 movements, strike probability at Vance AFB did not appear greater than the norm during this study. For wetland-associated avifauna that occurred at Drummond Flats in relevant numbers and in a consistent manner during the study (i.e., ducks, wading birds, shorebirds, and blackbirds), strike probabilities approximated zero during our study.

MANAGEMENT IMPLICATIONS

The majority of bird strikes occur on, or in close proximity to, airfields at altitudes <150 m AGL (Tedrow 1998, Dolbeer et al. 2015); therefore, it is necessary to evaluate bird abundances on the airfield, but also on near-airport habitats to understand how habitats and particular species contribute to strike risk (Blackwell et al. 2009). Specifically, effective management of avian abundances also requires knowledge of what habitat characteristics drive observed abundances. We recommend a model-based approach to abundance estimates that includes relevant habitat characteristics as explanatory variables. Relevant habitat characteristics will depend on the local avifauna and the specific site; therefore, we recommend developing species-specific or guild-specific models. For example, area of available habitat, wetland class or hydro-period, emergent vegetation cover, and slope at the habitat edge are important characteristics that should be considered for ducks. Flight patterns and altitudes of aircraft, which are specific to individual airfields, are important considerations when determining the effective radius surrounding an airfield for monitoring potential bird-strike hazards. However, for civilian and joint-use airports (i.e., military and civilian air traffic), the FAA recommends an 8-km zone be managed to reduce attractants to species (primarily birds) recognized as hazardous to aviation (FAA 2007). Within this radius, we recommend all habitats likely to attract bird species hazardous to aircraft be considered, and specific sites to be monitored be selected based on documented use by hazardous avifauna. To capture fluctuations within seasons, we recommend monitoring of abundances and habitat characteristics on a weekly or bi-weekly basis, at least during peak migration or use periods.

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LITERATURE CITED

- Albanese, G., and C. A. Davis. 2015. Characteristics within and around stopover wetlands used by migratory shorebirds: is the neighborhood important? *Condor* 117:328–340.
- Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. *Journal of Wildlife Management* 74:1175–1178.
- Barclay, J. E. 1952. Origin of the Drummond Flat, Garfield County, Oklahoma. *Proceedings of the Oklahoma Academy of Science* 33:197–199.

- Bart, J., and S. Earnst. 2002. Double sampling to estimate density and population trends in birds. *Auk* 119:36–45.
- Blackwell, B. F., T. L. DeVault, E. Fernández-Juricic, and R. A. Dolbeer. 2009. Wildlife collisions with aircraft: a missing component of land-use planning for airports. *Landscape and Urban Planning* 93:1–9.
- Blackwell, B. F., P. Schmidt, and J. A. Martin. 2013. Avian survey methods for use at airports. Pages 153–165 in T. L. DeVault, B. F. Blackwell, and J. L. Belant, editors. *Wildlife in airport environments: preventing animal-aircraft collisions through science-based management*. The Wildlife Society and Johns Hopkins University Press, Baltimore, Maryland, USA.
- Blumstein, D. T., L. L. Anthony, R. Harcourt, and G. Ross. 2003. Testing a key assumption of wildlife buffer zones: is flight initiation distance a species-specific trait? *Biological Conservation* 110:97–100.
- Buler, J. J., F. R. Moore, and S. Woltmann. 2007. A multi-scale examination of stopover habitat use by birds. *Ecology* 88:1789–1802.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer, New York, New York, USA.
- Casazza, M. L., P. S. Coates, M. R. Miller, C. T. Overton, and D. R. Yparaguire. 2012. Hunting influences the diel patterns in habitat selection by northern pintails *Anas acuta*. *Wildlife Biology* 18:1–13.
- Coccon, F., M. Zuchetta, G. Bossi, M. Borrotti, P. Torricelli, and P. Franzoi. 2015. A land-use perspective for birdstrike risk assessment: the attraction risk index. *PLoS ONE* 10:e0128363.
- Cochran, W. G. 1977. Sampling techniques. Third edition. John Wiley & Sons, New York, New York, USA.
- Cowardin, L. M., V. Carter, F. C. Golet, and E. T. LaRoe. 1979. Classification of wetlands and deepwater habitats of the United States. U.S. Department of the Interior, Fish and Wildlife Service, Washington, D.C., USA.
- Cox, C. 2005. Delta Method. Pages 1409–1411 in P. Armitage and T. Colton, editors. *Encyclopedia of biostatistics*. Second edition. John Wiley & Sons, New York, New York, USA.
- Daubenmire, R. 1959. A canopy-coverage method of vegetational analysis. *Northwest Science* 33:43–64.
- DeVault, T. L., J. L. Belant, B. F. Blackwell, and T. W. Seamans. 2011. Interspecific variation in wildlife hazards to aircraft: implications for airport wildlife management. *Wildlife Society Bulletin* 35:394–402.
- DeVault, T. L., B. F. Blackwell, T. W. Seamans, and J. L. Belant. 2016. Identification of off airport interspecific avian hazards to aircraft. *Journal of Wildlife Management* 80:746–752.
- DeVault, T. L., B. F. Blackwell, T. W. Seamans, S. L. Lima, and E. Fernández-Juricic. 2015. Speed kills: ineffective escape responses to virtual oncoming vehicles by a passerine bird. *Proceedings of the Royal Society B-Biological Sciences* 282:2014–2188.
- Dolbeer, R. A. 2011. Increasing trend of damaging bird strikes with aircraft outside the airport boundary: implications for mitigation measures. *Human-Wildlife Interactions* 5:235–248.
- Dolbeer, R. A., S. E. Wright, J. Weller, A. L. Anderson, and M. J. Begier. 2015. Wildlife strikes to civil aircraft in the United States 1990–2014. U.S. Department of Transportation, Federal Aviation Administration, Office of Airport Safety and Standards, Serial Report 21, Washington, D.C., USA.
- Eberhardt, L. L., D. G. Chapman, and J. R. Gilbert. 1979. A review of marine mammal census methods. *Wildlife Monographs* 63.
- Farmer A., and F. Durbian. 2006. Estimating shorebird numbers at migration stopover sites. *Condor* 108:792–807.
- Federal Aviation Administration [FAA]. 2007. Advisory circular 150/5200-33B-Hazardous wildlife attractants on or near airports. https://www.faa.gov/documentLibrary/media/advisory_circular/150-5200-33B/150_5200_33b.pdf. Accessed 04 May 2007.
- Gerringer, M. B., S. L. Lima, and T. L. DeVault. 2016. Evaluation of an avian radar system in a midwestern landscape. *Wildlife Society Bulletin* 40:150–159.
- Hart, J. D., A. Colyer, and J. R. Allan. 2009. Developing bird-strike risk assessment models for open-water restorations. *Human-Wildlife Conflicts* 3:186–198.
- Heitmeyer, M. E. 2012. Hydrogeomorphic evaluation of ecosystem restoration options for Drummond Flats, Oklahoma. Unpublished report. Greenbrier Wetland Services, Advance, Missouri, USA.
- Helmers, D. L. 1992. Shorebird management manual. Western Hemisphere Shorebird Reserve Network, Manomet, Massachusetts, USA.
- Lima, S. L. 1998. Nonlethal effects in the ecology of predator-prey interactions. *Bioscience* 48:25–34.
- Madsen, J. 1998. Experimental refuges for migratory waterfowl in Danish wetlands. II. Tests of hunting disturbance effects. *Journal of Applied Ecology* 35:398–417.
- Martin, J. A., J. L. Belant, T. L. DeVault, B. F. Blackwell, L. W. Burger, Jr., S. K. Riffell, and G. Wang. 2011. Wildlife risk to aviation: a multi-scale issue requires a multi-scale solution. *Human-Wildlife Interactions* 5:198–203.
- Metcalfe, N. B. 1984. The effects of habitat on vigilance of shorebirds: is visibility important? *Animal Behavior* 32:981–985.
- Oklahoma Mesonet. 2014. Daily rainfall, maximum, minimum, and average air temperatures for Oklahoma Mesonet weather station in Lahoma, Oklahoma. http://www.mesonet.org/index.php/weather/daily_data_retrieval. Retrieved 31 Jan 2014.
- Potts, J. M., and J. Elith. 2006. Comparing species abundance models. *Ecological Modeling* 199:153–163.
- Rodgers, J. A., Jr., and H. T. Smith. 1995. Set-back distances to protect nesting bird colonies from human disturbance in Florida. *Conservation Biology* 9:89–99.
- SAS Institute Inc. 2013. SAS/STAT® 13.1 User's Guide. Cary, North Carolina, USA.
- Sodhi, N. 2002. Competition in the air: birds versus aircraft. *Auk* 119:587–595.
- Suter, W. 1994. Overwintering waterfowl on Swiss lakes: how are abundance and species richness influenced by trophic status and lake morphology? *Hydrobiologia* 279/280:1–14.
- Tedrow, C. A. 1998. Bird strike risk assessment for United States Air Force airfields and aircraft. Thesis, Virginia Polytechnic Institute and State University, Blacksburg, USA.
- Tuite, C. H., P. R. Hanson, and M. Owen. 1984. Some ecological factors affecting winter wildfowl distribution on inland waters in England and Wales, and the influence of water-based recreation. *Journal of Applied Ecology* 21:41–61.
- U.S. Air Force Safety Center. 2014. Strikes by Fiscal Year 1985–2013. <http://www.afsec.af.mil/shared/media/document/AFD-140124-024.pdf>. Accessed 07 Mar 2014.
- U.S. Department of Agriculture. 1983. Watershed plan—environmental impact statement for Turkey Creek Watershed. U.S. Department of Agriculture, Soil Conservation Service, Stillwater, Oklahoma, USA.
- U.S. Department of the Air Force. 2001. Air Force Instruction 11-401. Headquarters, U.S. Air Force Director of Operations and Training, Pentagon, Washington, D.C., USA.
- Webb, E. B., L. M. Smith, M. P. Vrtiska, and T. G. LaGrange. 2010. Effects of local and landscape variables on wetland bird habitat use during migration through the Rainwater Basin. *Journal of Wildlife Management* 74:109–119.
- Whittingham, M. J., and K. L. Evans. 2004. The effects of habitat structure on predation risk of birds in agricultural landscapes. *Ibis* 146:210–220.
- Zakrajsek, E., and J. A. Bissonette. 2005. Ranking the risk of wildlife species hazardous to military aircraft. *Wildlife Society Bulletin* 33:258–264.
- Zuur, F. A., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. *Mixed effects models and extensions with R*. Springer, New York, New York, USA.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site

Table S1. Greatest estimated seasonal abundances for the entire Drummond Flats Wildlife Management Area, Oklahoma, USA, for wetland-associated avian guilds across all years (2010–2013; see Wetland Avifauna above for definitions of avian guilds).

Table S2. The 12 nonnested models generated *a priori* within each season by the consideration of 4 model types

(negative binomial, quasi-Poisson, zero-inflated Poisson, and zero-inflated negative binomial models) and 2 functional relationships with area of available habitat (untransformed and square-root transformed).

Table S3. All wetland bird species (see Wetland Avifauna above for definition) observed during wetland surveys at Drummond Flats Wildlife Management Area, Oklahoma, USA, during October 2010–March 2013.