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Migrating whooping cranes avoid wind-energy infrastructure when selecting stopover habitat

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Abstract

Electricity generation from renewable-energy sources has increased dramatically worldwide in recent decades. Risks associated with wind-energy infrastructure are not well understood for endangered whooping cranes (*Grus americana*) or other vulnerable crane populations. From 2010 to 2016, we monitored 57 whooping cranes with remote-telemetry devices in the United States Great Plains to determine potential changes in migration distribution (i.e., avoidance) caused by presence of wind-energy infrastructure. During our study, the number of wind towers tripled in the whooping crane migration corridor and quadrupled in the corridor's center. Median distance of whooping crane locations from nearest wind tower was 52.1 km, and 99% of locations were >4.3 km from wind towers. A habitat selection analysis revealed that whooping cranes used areas ≤5.0 km (95% Confidence Interval = 4.8–5.4) from towers less than expected (i.e., zone of influence) and that whooping cranes were 20 times (95% CI: 14–64) more likely to use areas outside compared to adjacent to towers. Eighty percent of whooping crane locations and 20% of wind towers were located in areas with the highest relative probability of whooping crane use based on our model, which comprised 20% of the study area. Whooping cranes selected for these places, whereas developers constructed wind infrastructure at random relative to desirable whooping crane habitat. As of early 2020, 4.6% of the study area and 5.0% of the highest-selected whooping crane habitat were within the collective zone of influence. The affected area equates to habitat loss ascribed to wind-energy infrastructure; losses from other disturbances have not been quantified. Continued growth of the whooping crane population during this period of wind infrastructure construction suggests no immediate population-level consequences. Chronic or lag effects of habitat loss are unknown but possible for long-lived species. Preferentially constructing future wind infrastructure outside of the migration corridor or inside of the corridor at sites with low probability of whooping crane use would allow for continued wind-energy development in the Great Plains with minimal additional risk to highly selected habitat that supports recovery of this endangered species.

Key words: avoidance, displacement, endangered species, *Grus americana*, habitat selection, migration, renewable energy, wind energy, whooping crane, zone of influence.

Introduction

Wind-energy infrastructure has expanded greatly in recent decades, and this trend is expected to continue as nations seek to generate electricity from sources that produce lower greenhouse gas emissions (Dincer 2011, Gibson et al. 2017). Concurrent with this expansion, interactions between wind infrastructure and wildlife have received international attention (Smith and Dwyer 2016, Allison et al. 2019). Presence of wind infrastructure can cause negative outcomes for wildlife; identifying short- and long-term risks to numerous wildlife species are of interest to wildlife professionals and necessary for managing species of conservation concern.

Documented negative effects of wind infrastructure include mortality of birds and bats from collisions, and avoidance of wind infrastructure (i.e., displacement) by birds and mammals (Drewitt and Langston 2006, Allison et al. 2019). Behavioral displacement is typically identified as a decrease in density measured over distance from a disturbance source (Drewitt and Langston 2006). Herein, we consider displacement and avoidance as synonymous, although we acknowledge that others have described the terms as different behavioral responses to disturbance, which may be more informative when animals establish home ranges (Winder et al. 2014b). Wildlife are expected to select habitats where they will realize increased fitness based on tradeoffs of resource availability and risks from predators or other factors (Cody 1981). Anthropogenic disturbances like wind infrastructure may be perceived as risk factors, causing a reduction in use within a proximity of structures (May 2015). Displacement from areas wildlife would otherwise use has been identified as a form of habitat loss (Sawyer et al. 2009, Polfus et al. 2011). Habitat loss and fragmentation can lead to declines in wildlife populations and increased risk of extinction (Brooks et al. 2002).

Displacement surrounding wind-energy infrastructure has been observed internationally for several taxa of birds (Smith and Dwyer 2016, Shaffer and Buhl 2016). During breeding and non-breeding periods, birds have been displaced from otherwise available habitat (Larsen and Madsen 2000, Madsen and Boertmann 2008, Pearce-Higgins et al. 2009, Shaffer and Buhl 2016, Lange et al. 2018), yet displacement is not a universal phenomenon (Devereux et al. 2008, Pearce-Higgins et al. 2012). The magnitude of displacement can change with time (e.g., habituation; Madsen and Boertmann 2008) and can vary depending on resource or habitat availability (Fijn et al. 2012, Lange et al. 2018), where displacement is most pronounced in situations where resources are available away from towers. Evaluated interactions between wind infrastructure and birds in migration have generally revealed avoidance by birds flying but not roosting or foraging (Cabrera-Cruz and Villegas-Patraca 2016, Marques et al. 2020). Migratory birds making directional movements generally require places to stop, rest, and gather resources (Hutto 1998). Displacement of birds selecting migratory stopover habitat has received less attention, yet the ability of birds to find and select quality stopover sites can influence survival, breeding success, and population trajectory (Webster et al. 2002, Norris 2005). Therefore, it is important to understand how anthropogenic development may influence migratory birds during this energetically stressful and critical portion of their annual cycle.

The whooping crane (*Grus americana*) is a federally listed endangered species in Canada and the United States (U.S.). The sole naturally occurring population, the Aransas-Wood Buffalo population, migrates biannually within a migratory corridor through the Great Plains of the U.S., the Canadian Prairies, and the southern Boreal region in Canada between wintering areas in coastal Texas, U.S. and summering areas in and around Wood Buffalo National Park in Alberta and the Northwest Territories, Canada (Allen 1952). During migration, whooping cranes generally use wetland and upland sites characterized by unobstructed visibility and a remoteness from anthropogenic developments (Howe 1989, Pearse et al. 2017, Baasch et al. 2019b). The wind-energy industry has capitalized on the high wind potential of the Great Plains by constructing an increasing amount of wind infrastructure in this region (U.S. Department of Energy 2008, Kiesecker et al. 2011). Whooping cranes may be displaced by wind infrastructure because of the species' predisposition for avoiding anthropogenic developments (Armbruster 1990, Johns et al. 1997, Baasch et al. 2019b), which would result in degradation or loss of otherwise available migration stopover habitat. The population has grown steadily for decades, and managers express concerns that novel stressors like wind infrastructure could result in additional mortality and loss of habitat, risking prospects of recovery for this endangered species (Canadian Wildlife Service and U.S. Fish and Wildlife Service 2007).

The potential risk that wind infrastructure poses to whooping cranes and other vulnerable crane species is an identified knowledge gap (Harris and Mirande 2013). Our objective was to determine if presence of wind infrastructure influenced the probability of whooping cranes using sites to stop, rest, and forage during migration (i.e., stopover sites). To identify potential displacement behavior, we estimated a threshold distance at which wind infrastructure affected habitat selection (i.e., zone of influence [ZOI]; Boulanger et al. 2012), the magnitude of the effect within the ZOI, and potential amount of habitat loss within the migration corridor that could be associated with presence of wind infrastructure.

Methods

Study area

Whooping cranes of the Aransas-Wood Buffalo population migrate within a migratory corridor that spans from coastal Texas, U.S. to Wood Buffalo National Park in Alberta and the

Northwest Territories, Canada. In the U.S., whooping cranes primarily use areas in Texas, Oklahoma, Kansas, Nebraska, South Dakota, North Dakota, and northeastern Montana (Kuyt 1992). Pearse et al. (2018) established migration corridors for this population that included 50% and 95% of locations of migrating birds, 1942–2016 (Fig. 1A). We used a 50-km buffer surrounding the 95% migration corridor in the U.S. to define our study area (Fig. 1A). We included only the U.S. (60% of the migration corridor; Pearse et al. 2018) because this is the portion of the migration corridor that has a longer history and greater density of wind-energy infrastructure development compared to Canada during our study period (IEA Wind 2017). The study area is primarily within the Great Plains, which is an extensive grassland ecoregion in North America. Most land is in private ownership, forming a mosaic of lands in agricultural production as cultivated lands and grasslands (Samson et al. 2004). Certain landscapes within the region have a high abundance of wetland features, such as the Playa Lakes Region, Rainwater Basin Area, Nebraska Sandhills, and Prairie Pothole Region (Laubhan and Fredrickson 1997). Major river systems across the Great Plains include the Missouri River, Platte River, Arkansas River, and Red River drainages (Matthews 1988). Diverse aquatic plant and animal communities, including millions of migratory waterfowl and waterbirds, are supported by these wetlands and rivers. During migration, whooping cranes roost and forage in wetlands, rivers, upland grasslands, and agricultural fields (Austin and Richert 2005, Pearse et al. 2017).

Wind infrastructure presence and distance

We calculated wind-energy infrastructure presence and growth during 2010–2016 using a dataset of wind-tower locations from Hoen et al. (2018). We included three areas of interest for comparison: the 50% whooping migration corridor, the center-most portion of the migration corridor where approximately half of migrating whooping crane locations exist (Pearse et al.

2018); the 95% whooping crane migration corridor; and the conterminous U.S. We calculated annual and overall rate of wind-infrastructure construction in each of these three areas of interest by subtracting the natural logarithm of constructed towers present in the previous year from the natural logarithm of towers present in the current year. Annual growth rates were the exponential of yearly differences, and the overall growth rate was the exponential of mean yearly differences.

To summarize distance from wind infrastructure to whooping crane locations, we created spatial data rasters expressing distance from the nearest tower within the study area for each year of the study. We overlaid these rasters with non-flight whooping crane locations (methods described below) and calculated percentiles of distance from nearest tower.

Avoidance analysis

General approach – We investigated potential changes in whooping crane stopover site distribution during migration in response to presence of wind infrastructure using multiple analytical steps. Our goal was to estimate the maximum distance at which wind infrastructure affected whooping crane space use (i.e., ZOI, Boulanger et al. 2012) after accounting for whooping crane stopover site selection of landscape features. We developed a model to explain variation in nonrandom space use in relation to land cover and landscape features during migration by comparing locations used by whooping cranes paired with a set of 19 available locations (Forester et al. 2009, Duchesne et al. 2015, Avgar et al. 2016). We constrained this analysis to used and available locations >20 km from existing wind infrastructure, based on an assumption that presence of wind infrastructure would not influence behavioral responses of whooping cranes at distances >20 km. After determining which set of predictor variables influenced habitat selection in the presumed absence of wind infrastructure, we included all data to iteratively fit an asymptotic ZOI at different critical distances using piecewise regression

(Toms and Lesperance 2003, Ficetola and Denoel 2009), which allowed for estimation of a threshold distance and the relative magnitude of effect that distance from wind infrastructure would have on whooping crane habitat selection.

Whooping crane location data - We captured 68 whooping cranes between 2009–2014 and attached platform transmitting terminals with global position system (GPS) capabilities (North Star Science and Technology LLC, Baltimore, Maryland, USA and Geotrak, Inc., Apex, North Carolina, USA) at sites along coastal Texas and in and around Wood Buffalo National Park. Only 57 of 68 marked whooping cranes provided locations during migration for use in these analyses. Pearse et al. (2015) further described capture and marking details. In brief, birds were captured by hand at breeding grounds and by use of modified leg snares at wintering grounds (Kuyt 1979, Folk et al. 2005). Transmitters were programmed to collect 4–5 GPS locations daily at equal time intervals. We initially inspected GPS locations for errors occurring during collection or transmission on the Argos satellite system (Service Argos 2001) and performed multiple assessments to determine plausibility of locations (see Pearse et al. 2015 for details). We classified locations as occurring in flight when instantaneous velocity reading was >2.6 m/s (Byrne et al. 2017).

We used a step selection function to investigate habitat selection of migrating whooping cranes. Step selection functions provide a framework in which habitat selection can be inferred by pairing and comparing each location used by an individually marked animal with a matched set of available locations that would be accessible from the previously observed location, thereby incorporating the animal's movement (Fortin et al. 2005). We collated all locations associated with each migration made by whooping cranes, which included the starting location (i.e., last point before migration initiation), all subsequent points in flight and on ground, and the final location (i.e., first location after completion of migration). Migration initiation was defined by consistent movements away from wintering or summering areas, and completion of migration was determined by settling behavior, generally at known or traditional terminal locations (Pearse et al. 2020b).

We identified two types of movements during migration that required different methods for randomly selecting paired available locations–migration movements and stopover movements. Migration movements were defined as movements between previously identified stopover sites (Pearse et al. 2020b). We selected available locations to pair with migration movement locations by first calculating the distance and bearing between successive stopover sites. We selected available locations to pair with each used migration movement location (i.e., the first ground location at a stopover site) by selecting 19 random locations that were <2 times the migration distance (constrained to distances to between 5 and 1,500 km) and at a bearing ±22.5˚ from the migration movement bearing (Fig. 1B). We used this value because when we compared consecutive movement bearings, approximately 90% were <45˚. When migration movements were <6 km, we selected locations between 1 km and 2 times the movement distance and removed the bearing constraint.

Stopover movements were defined as movements occurring while whooping cranes resided at a stopover for one to multiple days, and available locations were selected using a different procedure than was used for migration movements. We first removed redundant nighttime locations, as whooping cranes generally do not move from nighttime roosts (Pearse et al. 2017). We identified nighttime periods (0.5 hour after sunset to 0.5 hour before sunrise) where multiple locations were acquired and randomly selected one to represent the nighttime location. For selected nighttime locations and remaining diurnal locations at stopover sites, we selected 19 available locations within a 5-km radius surrounding the used location (Fig. 1C). We chose 5 km as defining available locations because 95% of movements within stopover sites were <5 km.

Predictor variables – We derived landscape variables to explain space use of migrating whooping cranes based on a habitat selection model completed in North Dakota and South Dakota (Niemuth et al. 2018). This work described space use of migrating whooping cranes with multiple predictor variables that described geographic, wetland, and land use features. We derived predictor variables across the study area at a 30-m resolution. We used the recognized nature of whooping crane migration within a corridor (Howe 1989, Kuyt 1992) to identify a geographic predictor variable for analysis. We calculated a distance raster from the center of the 95% whooping crane migration corridor (Pearse et al. 2018), which served as a variable defining geographic position in relation to the migration corridor.

We assessed landscape composition using a 1,200-m moving window, which was identified by Niemuth et al. (2018) as the best-fitting spatial scale for landscape variables. Because wetland use has been described as a key determinant of whooping crane habitat selection (Howe 1989, Austin and Richert 2005, Niemuth et al. 2018, Baasch et al. 2019b), we calculated the percentage of area defined as wetland basin based on National Wetlands Inventory data (U.S. Fish and Wildlife Service 2020). We omitted intermittent riverine features because we assumed this basin type would not be consistently available to whooping cranes. Otherwise, as with Niemuth et al. (2018), we did not discriminate among wetland basin types, because our data were collected during years with varying wetland conditions.

Agriculture production dominates the Great Plains, and cropland is a ubiquitous land cover type. Whooping cranes use croplands during migration as foraging sites and roost in wetlands within croplands (Howe 1989, Baasch et al. 2019b). We used National Land Cover Databases (NLCD) from 2011, 2013, and 2016 (Yang et al. 2018) to identify areas categorized as cropland. We used a 1,200-m moving window to calculate percentage of cropland throughout the study area. We used NLDC 2011 for locations collected during 2010–2012, NLCD 2013 for data during 2013–2014, and NLCD 2016 for data collected during 2015–2016.

Disturbances from anthropogenic activity, specifically vehicle and human activity on roads, can affect habitat selection of migrating whooping cranes (Armbruster 1990, Baasch et al. 2019b). We included a road density metric, which we assumed was correlated with human activity (Venter et al. 2016), by summing the length of roads within 1,200-m moving windows throughout the study area. We used the USGS national map to identify the road network for this predictor variable (U.S. Geological Survey 2014).

We calculated distance from nearest wind infrastructure across the study area to serve as a predictor variable describing the potential influence of wind infrastructure to whooping crane space use. We calculated a distance raster for each year of our study, because the number of wind towers across the region increased with time. Wind tower locations and year of initial service were included in Hoen et al. (2018).

All predictor variables were scaled by subtracting the mean and dividing by the standard deviation (Bring 1994). For percentage cropland and distance from wind infrastructure, we used mean and standard deviations for 2016 to scale other years. This standardization allowed for easier computation and interpretation of effect sizes (Muff et al. 2020).

Model development, fitting, and validation – We estimated a step selection function for a subset of data where used and available whooping crane locations were >20 km from existing wind towers to serve as a base habitat model. This base model was used to predict relative probability of space use by migrating whooping cranes in the absence of influences by wind infrastructure. When developing competing base models of whooping crane habitat selection, we initially checked for correlations between predictor variables, and we did not include predictor variables in the same model when $|r| > 0.5$. Our most complex model included all predictor variables (i.e., distance to corridor center, percentage wetland basin, percentage cropland, and road density), a quadratic effect of percentage cropland, and an interaction effect between percentage wetland and percentage cropland. We compared this model with seven additional competing models. One model emulated the best model from Niemuth et al. (2018), which included all linear main effects, an interaction between percentage cropland and wetland basins, and a three-way interaction among percentage cropland, percentage wetland basins, and distance to corridor center. We included a simplified version of the Niemuth model, in which we removed the three-way interaction. We also included a model with all main effects (with and without quadratic cropland effect), one that did not include road density, one that considered geography only, and one that considered wetland basin and land use only (Table 1).

We fit models using generalized linear mixed models within the glmmTMB package (Brooks et al. 2017) as implemented in Program R (R Core Team 2019). We fit a mixed Poisson model, including a random intercept term for individual steps, where the intercept variance was fixed to a large value using procedures detailed by Muff et al. (2020) to avoid bias in the analysis due to shrinkage of estimated values. We used Akaike's Information Criterion (AIC) to rank competing models based on differences in AIC values and to calculate model weights (Burnham and Anderson 2003).

For model validation and additional analyses described below, we created a surface describing the relative probability of use across the study area by incorporating spatial predictor variables and parameter estimates from the base habitat model. A relative probability of use was estimated from the linear equation of the best-approximating base habitat model at a 30-m resolution. After estimating relative probability of use, we categorized values into 10 equal-area ordinal categories using quantiles that identified low to high (i.e., 1–10) relative probability of use (Holbrock et al. 2017). Categorized values allowed us to validate the base model using k-fold cross validation to assess the predictive ability of our best-approximating model. We used three folds and derived the rank correlation between bin ranks and frequency of test locations across equal-area bins, allowing for a comparison of expected and observed locations among bins (Boyce et al. 2002).

Zone of influence estimation - We conducted ZOI analyses using the same generalized linear mixed model approach as was used for the base habitat model. The additional predictor variable included in this analysis was distance from the nearest wind tower. Distance from the nearest wind tower was calculated for used and available locations each year. The variable was developed by year because new wind towers were constructed each year as the study progressed. To estimate a threshold effect of distance from wind infrastructure, we used a piecewise or segmented regression methodology (Toms and Lesperance 2003), wherein we constructed multiple predictor variables to define varying ZOI distances. To test a specific ZOI, we constructed a new predictor variable where all values above the tested ZOI distance were set to the test ZOI value. For example, to set up a model testing a ZOI of 3 km, all distance values >3 km were set to 3 km and values <3 km retained their original value. We compared models with potential ZOI distances at 0.5 km increments from 1–6 km and at 1-km increments up to 20 km. For each competing ZOI model, we included random slopes of the ZOI effect for each individual and year to allow for influence of this predictor variable to differ by areas available to individual whooping cranes (Duchesne et al. 2010) and to test whether effect size changed with time.

We compared log-likelihood values of ZOI models and interpreted the model with the maximum log-likelihood value as the best-fitting model. We also interpreted the shape of the log-likelihood curve and calculated 95% confidence intervals for the best ZOI distance as log-likelihood values <1.92 of the maximum value as was described in Boulanger et al. (2012). We estimated a magnitude of effect for how wind infrastructure influenced whooping crane habitat selection by estimating the odds ratio of the effect at the estimated ZOI. We estimated 95% confidence intervals by bootstrapping the analysis and using the 2.5 and 97.5 percentiles of odds ratios as the lower and upper confidence limits. After estimating a ZOI for wind infrastructure, we created a buffer with the ZOI radius surrounding all known wind infrastructure constructed as of early 2020 within the study area. We calculated the percentage of the total area and areas identified by ordinal classes of relative probabilities of whooping crane use. Data used in analyses are available in the public domain from the U.S. Geological Survey ScienceBase data repository (Pearse et al. 2020a).

Results

Wind towers increased 3.4 times in the 95% whooping crane migration corridor from 2010 (2,215) to 2016 (7,622; Fig. 2). Within the 50% migration corridor, wind tower numbers increased 4.3 times from 2010 (298) to 2016 (1,284; Fig. 2). Wind towers were constructed at an average annual rate of 23% in the 95% migration corridor, 28% annually in the 50% migration corridor, and 9% annually across the conterminous U.S. As of early 2020, there were 1,486 towers in the 50% migration corridor and 9,347 within the 95% migration corridor.

We collected 13,529 whooping crane locations in the U.S. during migrations, 2010–2016. After removing locations in flight, those outside of the study area, and redundant night locations, we had 9,347 ground locations available for analysis. Our sample included more locations during 2011–2015 (90%) than the beginning or end of the study (517 locations in 2010; 431 locations in 2016). Half of whooping crane locations from 2010–2016 were >52.1 km from wind towers. The 5th percentile distance was 9.9 km, 1st percentile distance was 4.3 km, and minimum distance was 0.7 km. During 2016, when the greatest number of towers existed within the study area, median distance from wind towers to all positions (30-m cell size) within the study area was 44.0 km, 5th percentile was 6.8 km, and the 1st percentile was 1.2 km (Table 2).

Correlations among predictor variables were low ($r < |0.292|$). The best-approximating base model of whooping crane habitat selection at stopover sites >20 km from wind infrastructure included percentage of wetland basin area, percentage of cropland area (quadratic effect), road density, distance to migration corridor center, and an interaction between wetland area and cropland density ($w_i = 1.0$, Table 1). All inferences were made using this model, wherein whooping cranes selected for locations with greater percentage of wetland basins, closer to the migration corridor centerline, and with lower road density (Table 3). There was support for a quadratic effect of cropland area, where relative probability of use was greatest for moderate values. The interaction between wetland basin and cropland area suggested a synergistic relationship such that relative probability of use was predicted at increasing intensities for moderate values of cropland area when wetland area percentage was high. The k-fold cross validation analysis suggested that the model fit the data well (average rank correlation = 0.970).

We investigated various ZOI possibilities <20 km and found that 5 km (95% CI: 4.8–5.4 km) was best supported by the data (Fig. 3A). Relative probability of use increased with increasing distance from wind towers <5 km ($\beta = 31.6$, SE = 10.7, 95% CI: 10.6–52.6); odds ratios increased with distance from wind towers from 1.9 (95% CI: 1.7–2.4) at 1 km, 3.5 (3.0–5.7) at 2 km, 6.6 (5.2–13.8) at 3 km, 10.6 (7.9–26.5) at 4 km and 19.9 at ≥5 km (13.6–63.5), suggesting that whooping cranes were approximately 20 times more likely to use areas outside of the ZOI compared to locations next to wind towers, holding all other predictor variables constant (Fig. 3B). Odds ratios of whooping crane use ≥5 km from wind towers varied among years (included as a random slope effect) but did not follow a consistent pattern with time (Fig. 4). We also included individual bird identity as a random effect; odds ratio ≥5 km ranged from 3.3 to 100.8.

Wind towers within the study area included in the Hoen et al. (2018) dataset (version 2.3; *n* = 11,999) were constructed in locations with varying relative probabilities of whooping crane use. Six percent of wind towers were within the highest-ranked category, and 20% of towers were within the two highest-ranked categories (Fig. 5). In contrast, 80% of whooping crane locations were found within the two highest-ranked categories and 95% within the top five categories (Fig. 5). When applying a 5-km buffer around wind towers built before early 2020, 4.2 million ha or 4.6% of the study area was within this cumulative ZOI (Fig. 1D). The ZOI included 3.8% of the highest-ranked category and 5.0% of the two highest-ranked probability of use categories.

Discussion

Avoidance behavior

The presence of wind infrastructure had an identifiable influence on the distribution of stopover sites selected by migrating whooping cranes in the Great Plains. Areas ≤5 km from constructed wind towers had relative probability of use by whooping cranes reduced compared to what would be expected based on other landscape features. The 5-km ZOI we estimated was larger than has been determined for many bird species, which typically has been ≤800 m (Larsen and Madsen 2000, Pearce-Higgins et al. 2009, Shaffer and Buhl 2016). Notable exceptions include findings that distances ≤4.5 km from onshore wind infrastructure influenced Dupont's lark (*Chersophilus duponti*) distribution (Gómez-Catasús et al. 2018), distances ≤8 km from onshore wind infrastructure influenced distribution of sandhill cranes (Navarrete 2011), and distances ≤16 km from offshore infrastructure influenced distribution of loon species (*Gavia* spp.) in the German North Sea (Mendel et al. 2019). Displacement from wind infrastructure for upland birds in Ireland occurred at greater distances in open compared to forested areas (Fernández-Bellon et al. 2018). Whooping cranes seek out stopover sites with open areas and high visibility, likely as a means of detecting predators and other dangers (Armbruster 1990, Austin and Richert 2005, Baasch et al. 2019b, 2019a). These preferences and behaviors may explain the large ZOI associated with wind infrastructure. Variation in how birds with different habitat associations respond to wind infrastructure suggests that the ZOI for whooping cranes in the Great Plains may be inappropriate to be generalized widely, especially beyond cranes, as other species likely perceive and respond to wind infrastructure differently.

The magnitude of aversion for potential stopover sites ≤5 km from wind infrastructure varied by year of study and individual. Habituation to wind infrastructure post construction (Madsen and Boertmann 2008, Pearce-Higgins et al. 2012, Farfán et al. 2017) and intensification of displacement (Shaffer and Buhl 2016, Farfán et al. 2017) have been reported. Yearly variation in the effect size for whooping cranes did not support waning or strengthening of avoidance behavior. Longer-term research may be necessary before more definitive conclusions can be drawn, as effects, especially for long-lived species, may take time to manifest (Dohm et al.

2019). Wind towers were constructed at a 23% annual rate; therefore, novel structures were continually present on the landscape. Additional study during a period with little or no construction would provide greater insight into long-term effects of wind infrastructure on migrating whooping crane distribution.

Whooping cranes exhibited displacement in all years and for all individuals, suggesting that wind infrastructure influenced stopover site distribution over a range of available resource situations. The random yearly and individual variation in displacement effect size suggests environmental conditions and available habitat may affect displacement behavior. Available surface water related to drought conditions interacted with avoidance of wind infrastructure by redheads (*Aythya americana*) such that years with more available habitat provided numerous places for individuals to avoid ponds near wind infrastructure (Lange et al. 2018). Fijn et al. (2012) determined that avoidance of wind infrastructure by Bewick's swans (*Cygnus columbianus bewickii*) decreased as food resources more distant from wind infrastructure decreased. For whooping cranes, available areas for roosting and foraging varied among years and throughout their migration corridor, especially during a drought in 2012–2013 (Livneh and Hoerling 2016) when avoidance effect sizes were lowest. Some climate change predictions throughout the Great Plains suggest warmer temperatures and more severe and frequent drought conditions (USGCRP 2018). If drought limits available stopover sites for whooping cranes as we speculate may have occurred during 2012–2013, birds may be forced to select stopover sites closer to disturbance features like wind-energy infrastructure, which would compound stressors on birds during an already energetically demanding time.

Consequences of avoidance

A direct consequence of avoiding permanent disturbance features is loss of surrounding potentially available habitat. The collective presence of wind infrastructure as of early 2020 affected 5% of areas identified most likely for migrating whooping cranes use within the study area. Habitat loss related to wind infrastructure within the ZOI was not absolute; whooping cranes did use locations ≤5 km of wind infrastructure infrequently, although the chance of using these areas was much less likely than locations with the same landscape features in the absence of wind infrastructure. Moreover, we extrapolated the ZOI estimate beyond the time of our study (2017–2020) to calculate a more current area affected, which assumes a constant long-term ZOI. Additional monitoring into effects of further construction of wind infrastructure merits consideration to test this assumption and consider how whooping crane behavior and demography might change with greater numbers of wind towers and with time. Although our study focused on whooping crane avoidance of wind infrastructure, these are not the only anthropogenic features that potentially elicit displacement behavior and resulting stopover site habitat loss. Road density was found to negatively influence relative probability of use in our study and diurnal habitat use within stopover sites (Baasch et al. 2019b). Urban, suburban, rural, and other energy (e.g., oil and gas) developments are among other features that have potential to decrease stopover site habitat for whooping cranes. Future research into cumulative impacts is warranted.

An implied collateral benefit of avoiding wind infrastructure is reduced collision risk (Chamberlain et al. 2006). Collision, especially with overhead electric power distribution lines (i.e., power lines), has been cited as a cause of mortality for migrating whooping cranes (Stehn and Haralson-Strobel 2014), which has prompted concern that wind infrastructure could pose a similar risk (Canadian Wildlife Service and U.S. Fish and Wildlife Service 2007). Whooping crane behavioral avoidance of wind infrastructure would attenuate those concerns, although if placed in high-quality habitat (Heuck et al. 2019), wind infrastructure may continue to pose collision risk during times of low visibility, such as darkness, precipitation, or fog (Navarrete and Griffis-Kyle 2014). Furthermore, understanding trade-offs of avoidance-induced habitat loss and reduced collision mortality would require more data and analysis of fine-scale movements close to wind infrastructure, allowing for better assessment of collision risk. If collision risk is high, then large-scale avoidance and associated habitat loss could be a net positive for whooping cranes. Collisions result in individual death and mortality rate increases, whereas habitat loss could influence fitness and vital rates in more subtle ways, such as cross-seasonal effects (Norris 2005). Finally, construction of wind infrastructure arrays often involves erecting distribution power lines, which may result in an assumed incremental increase in risk of mortality from this source.

Linking avoidance of disturbance features to demographic consequences has been rare and provided mixed results. Avoidance by mule deer (*Odocoileus hemionus*) of areas around oil and gas wells was linked to declines in population size (Sawyer et al. 2009, 2017), whereas avoidance of wind infrastructure by greater prairie-chickens (*Tympanuchus cupido*) realized little measurable demographic consequences (McNew et al. 2014, Winder et al. 2014a, 2015). The continued growth of the Aransas-Wood Buffalo population during times of rapid wind-energy development throughout their migration corridor in the U.S. provides circumstantial evidence that current migration habitat loss has not resulted in immediate population-level demographic consequences (Wilson et al. 2016). Habitat loss without demographic consequence may suggest that migration habitat is not currently limiting population growth. Given the slow life-history strategy of whooping cranes, however, there remains potential for a lagged response (Thompson and Ollason 2001). There is also potential for a threshold effect, where at a certain point of habitat loss from multiple anthropogenic disturbances, whooping cranes may realize negative consequences (Shaffer and Buhl 2016).

The current carrying capacity of migration habitat for whooping cranes and amount required to sustain recovery goals are unknown. Predicted growth in population size increases the potential for future limitation (Wilson et al. 2016). Quantifying limitations must be considered in concert with other disturbances, other stressors (e.g., wetland loss), and temporally varying factors (e.g., periodic drought). Determining potential regional stopover site limitations within the migration corridor may be of greater concern, because whooping cranes require stopovers along the entire corridor. Moreover, the amount of stopover site habitat varies spatially and temporally because of differences in potential surface water across the corridor, suggesting varying sensitivities to habitat loss. For example, loss of high-quality habitat in the southern portion of the migration corridor would result in a greater percentage loss than the same amount lost in parts of the corridor with more available options such as in the Prairie Pothole Region (Caven et al. 2020).

Initial implications for siting wind infrastructure

The greater rate of wind-infrastructure construction within the whooping crane migration corridor relative to the entire U.S. provides evidence that the Great Plains is a highly desirable landscape in which to develop wind-energy capacity. Our results provide initial insight into potential considerations for placement of wind infrastructure (i.e., macro-siting) in the Great Plains while minimizing additional stopover habitat loss for migrating whooping cranes. Existing towers were constructed at random with respect to highly selected whooping crane stopover habitat, yet better outcomes are possible, as was found with wintering sandhill cranes in Texas, where only 5% of wind towers were constructed in places where 80% of sandhill crane locations occurred (Pearse et al. 2016). For whooping cranes, siting wind infrastructure outside of the migration corridor would result by far in the lowest risk of further habitat loss. Areas within the migration corridor include relatively poor habitat representing opportunity for construction at sites with lower impact; 50% of the study area (45 million ha) included site characteristics where only 5% of whooping crane locations occurred. In general, locations that might pose the least additional risk to whooping crane habitat loss would be farther from the migration corridor center, have low wetland basin density, have low or high cropland conversion, and include other potential disturbances like a high density of roads. Finally, a regional perspective to development and conservation could be beneficial, as availability of habitat varies latitudinally, cranes require periodic stops during migration events (average daily migration distance 300 km), and time spent at stopovers varies seasonally and regionally (Pearse et al. 2020b).

We limited our analysis to the U.S. because wind-energy development has been more extensive in the U.S. Great Plains than in the Canadian Prairies (IEA Wind 2017). During our study, there were only 109 wind towers in seven discrete locations within the 95% migration corridor and no towers were within the 50% corridor in Canada (Federal Aviation Administration 2020), resulting in few opportunities for interactions between whooping cranes and wind infrastructure compared to the U.S. However, wind infrastructure is expected to increase on the Canadian Prairies (IEA Wind 2017). Since 2016, there has been a 50% increase in number of wind towers within the whooping crane migration corridor in Canada (Federal Aviation Administration 2020) and two large wind energy projects are planned to be completed in the migration corridor by 2021, which will more than double the installed wind energy capacity in Saskatchewan alone (Canada Wind Energy Association 2020). Given broad similarities in available stopover habitat in the U.S. Great Plains and the Canadian Prairies (Howe 1989), patterns of habitat selection and response to wind energy infrastructure by whooping cranes are likely to be similar, suggesting knowledge gained from the U.S. can be applied to inform future development in Canada.

Considerations for minimizing additional habitat loss directly relating to migrating whooping cranes would have some relevance to other species that rely on surface water and cultivated lands for roosting and foraging during migration, such as many species of waterfowl and waterbirds. Inevitably, however, efforts to minimize loss of whooping crane habitat may not be optimal for species with different habitat requirements and could, in fact, be deleterious if siting considerations for wind infrastructure were designed solely to minimize risk to whooping cranes. For example, the lesser prairie-chicken (*Tympanuchus pallidicinctus*) requires large blocks of grassland and occurs primarily on the periphery and outside of the whooping crane migration corridor (Hagen et al. 2004), areas of marginal benefit as whooping crane stopover habitat. In addition, general guidance for developing wind energy in previously disturbed lands (Fargione et al. 2012) may not be optimal for whooping cranes specifically, as cultivated lands can be attractive at moderate levels. Ultimately, comprehensive guidelines for maximizing benefit to wildlife would be those that minimize loss of habitat for a suite of sensitive species rather than single-species directives.

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ATP conceived the original idea and performed data analyses. ATP, DAB, MTB, and WH collected data. ATP and KLM wrote the manuscript with support and review from all authors.

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Data availability: Data used in this study area available on ScienceBase (Pearse et al 2020a):

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Table 1. Model selection results for step selection functions of migrating whooping cranes at sites >20 km from wind-energy infrastructure in the United States Great Plains, 2010–2016.

Model Structure[a]	K[b]	ΔAIC[c]	w_i[d]
Wetland + Cropland + Cropland^2 + Road + Center + Wetland × Cropland + Wetland × Cropland^2	8	0.0	1.0
Wetland + Cropland + Road + Center + Wetland × Cropland	6	53.1	0
Wetland + Cropland + Road + Center + Wetland × Cropland + Wetland × Cropland × Center	7	54.1	0
Wetland + Cropland + Wetland × Cropland	4	193.7	0
Wetland + Cropland + Cropland^2 + Road + Center	6	439.8	0
Wetland + Cropland + Road + Center	5	662.3	0
Wetland + Cropland + Center	4	726.8	0
Center	2	3591.0	0

[a] Wetland = percentage of 1,200-m radius area surrounding locations identified as a National Wetlands Inventory wetland basin; Cropland = percentage of 1,200-m radius area surrounding locations identified as cropland; Road = road density within 1,200-m radius area surrounding locations (km/ha); Center = distance to center of the 95% whooping crane migration corridor (km).

[b] Number of estimated parameters.

[c] Difference between minimum Akaike's Information Criterion (AIC) value and the AIC of the current model. The AIC of the top model = 138027.1.

[d] Model weight.

Table 2. Univariate summaries of predictor variables used to model step selection functions at locations used by and available to migrating whooping cranes in the United States Great Plains, 2010–2016.

Predictor variable[a]	Mean	SD	Median	5%	95%
Wetland (%)	4	11	0	0	17
Cropland 2011 (%)	29	30	18	0	86
Cropland 2013 (%)	30	32	18	0	89
Cropland 2016 (%)	31	32	19	0	89
Road (km/ha)	0.040	0.041	0.036	0.000	0.088
Center (km)	100.1	61.8	96.5	9.6	208.9
Tower distance 2010 (km)	82.3	59.9	67.7	14.5	211.9
Tower distance 2016 (km)	59.2	52.8	44.0	6.8	164.7

[a] Wetland = percentage of 1,200-m radius area surrounding locations identified as a National Wetlands Inventory wetland basin; Cropland = percentage of 1,200-m radius area surrounding locations identified as cropland; Road = road density within 1,200-m radius area surrounding locations (km/ha); Center = distance to center of the 95% whooping crane migration corridor (km).

Table 3. Parameter estimates (log scale), standard errors, and 95% confidence limits from the highest-ranked model estimating step selection functions of migrating whooping cranes at sites >20 km from wind-energy infrastructure in the United States Great Plains, 2010–2016.

Variable[a]	Estimate	SE	Lower 95% CL	Upper 95% CL
Intercept	-4.711	12.406	-29.027	19.605
Wetland	0.587	0.014	0.560	0.614
Cropland	0.503	0.034	0.436	0.570
Cropland^2	-0.202	0.027	-0.255	-0.149
Road	-0.363	0.037	-0.436	-0.290
Center	-0.791	0.119	-1.024	-0.558
Wetland × Cropland	0.292	0.014	0.265	0.319
Wetland × Cropland^2	0.033	0.016	0.002	0.064

[a] Wetland = percentage of 1,200-m radius area surrounding locations identified as a National Wetlands Inventory wetland basin; Cropland = percentage of 1,200-m radius area surrounding locations identified as cropland; Road = road density within 1,200-m radius area surrounding locations (km/ha); Center = distance to center of the 95% whooping crane migration corridor (km). Predictor variables were scaled by subtracting the mean and dividing by the standard deviation before performing analyses.

Figures

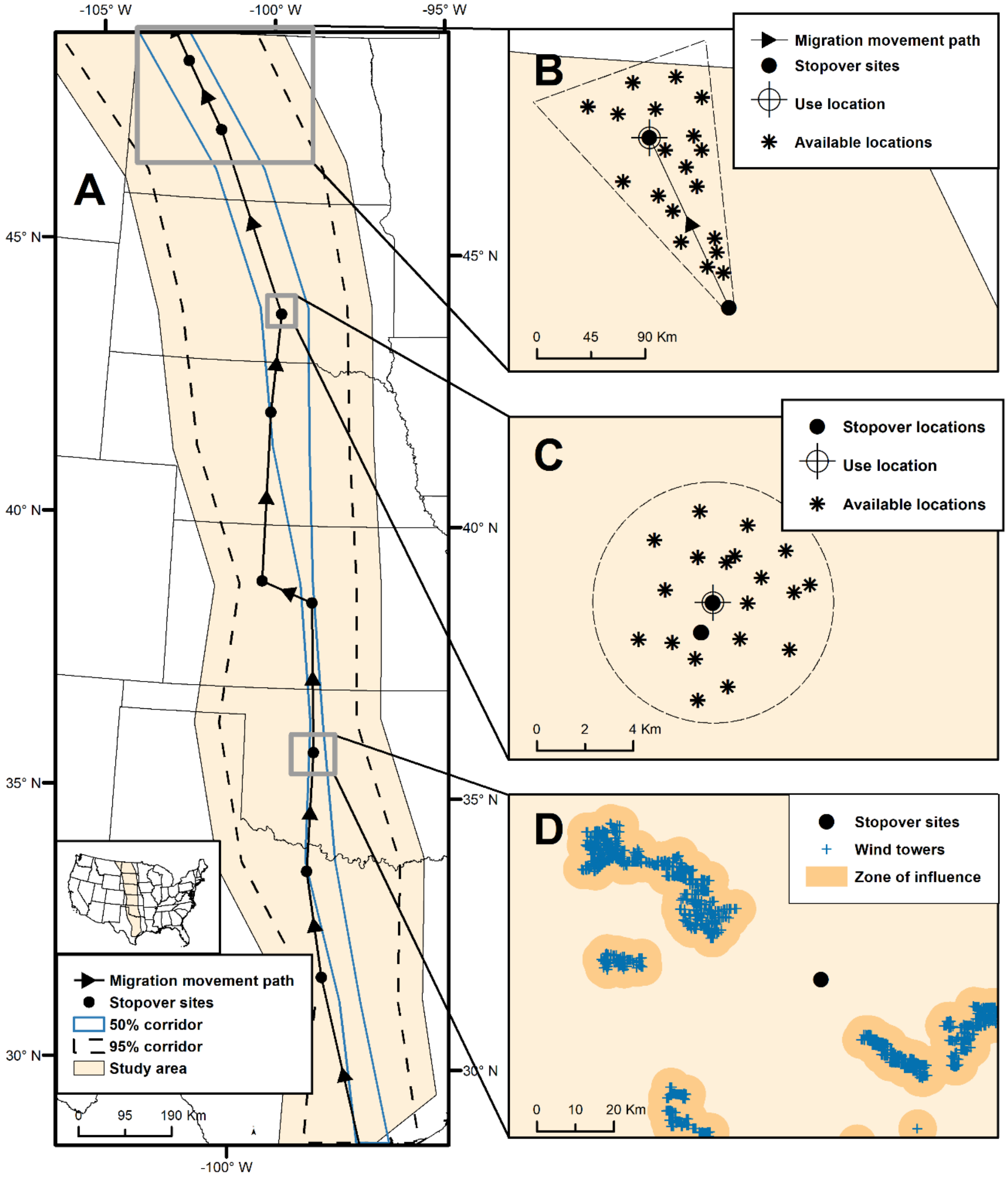

Figure 1. Whooping cranes migrate biannually through the United States Great Plains within previously defined migration corridors (50% and 95%; Pearse et al. 2018b). Our study area included a 50-km buffered area outside and including the 95% whooping crane migration corridor (A). For use in a habitat selection analysis, we selected 19 available locations to pair

with use locations for two types of movements: movements between stopover sites–migration movements (B), and movements within a stopover site–stopover movements (C). For migration movements, we selected available locations that occurred within ±22.5° of the bearing of the movement and <2 times the movement distance (B). For stopover movements, available locations within a stopover site were selected from a 5-km radius area (dashed circle) surrounding used locations (C). Selection of migration stopover sites by whooping cranes was influenced by wind-energy infrastructure at distances ≤5 km (D).

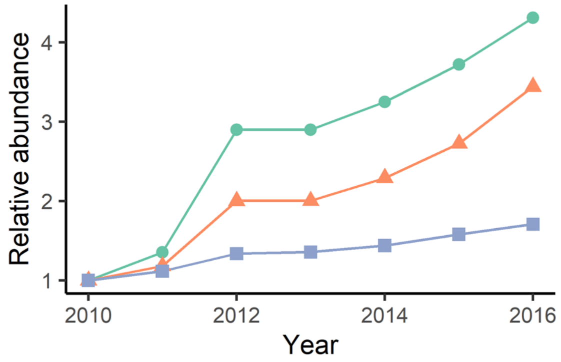

Figure 2. Wind-energy infrastructure construction growth rate 2010–2016, relative to number of towers beginning in 2010, within the 50% whooping crane migration corridor (green circle), the 95% whooping crane migration corridor (orange triangle), and the conterminous United States (blue square).

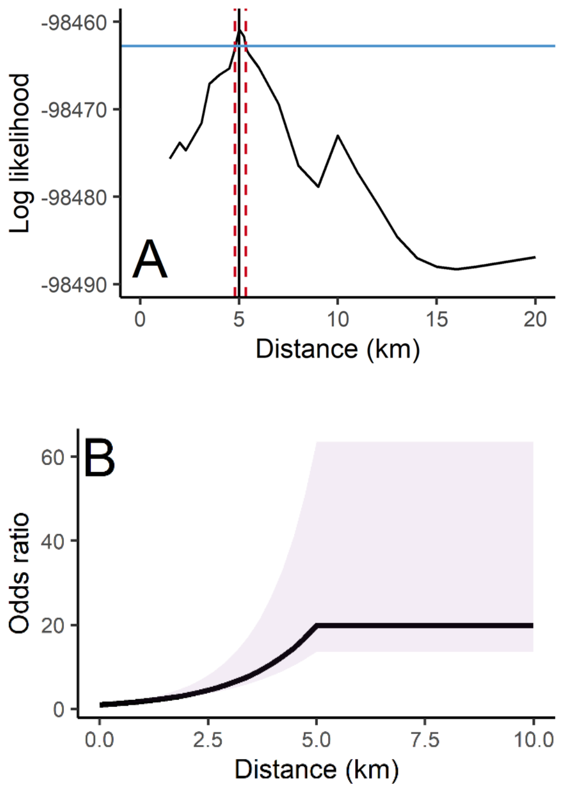

Figure 3. Likelihood curve as a function of distance from nearest wind-energy infrastructure to migrating whooping crane locations in the United States Great Plains, 2010–2016 (A). The solid black vertical line represents the zone of influence estimate for wind infrastructure, and the red dashed vertical lines identify the 95% confidence interval (maximum log likelihood - 1.92, dotted blue line). Predicted odds ratio and 95% confidence limits of relative probability of whooping crane use at increasing distances from nearest wind-energy tower (B).

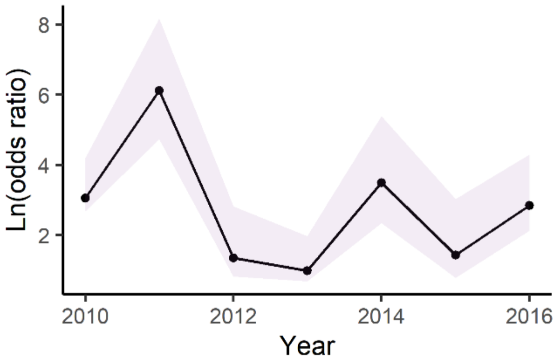

Figure 4. Predicted odds ratio (natural logarithm) and 95% confidence limits of relative probability of whooping crane use at ≥5 km from nearest wind-energy tower by year of study.

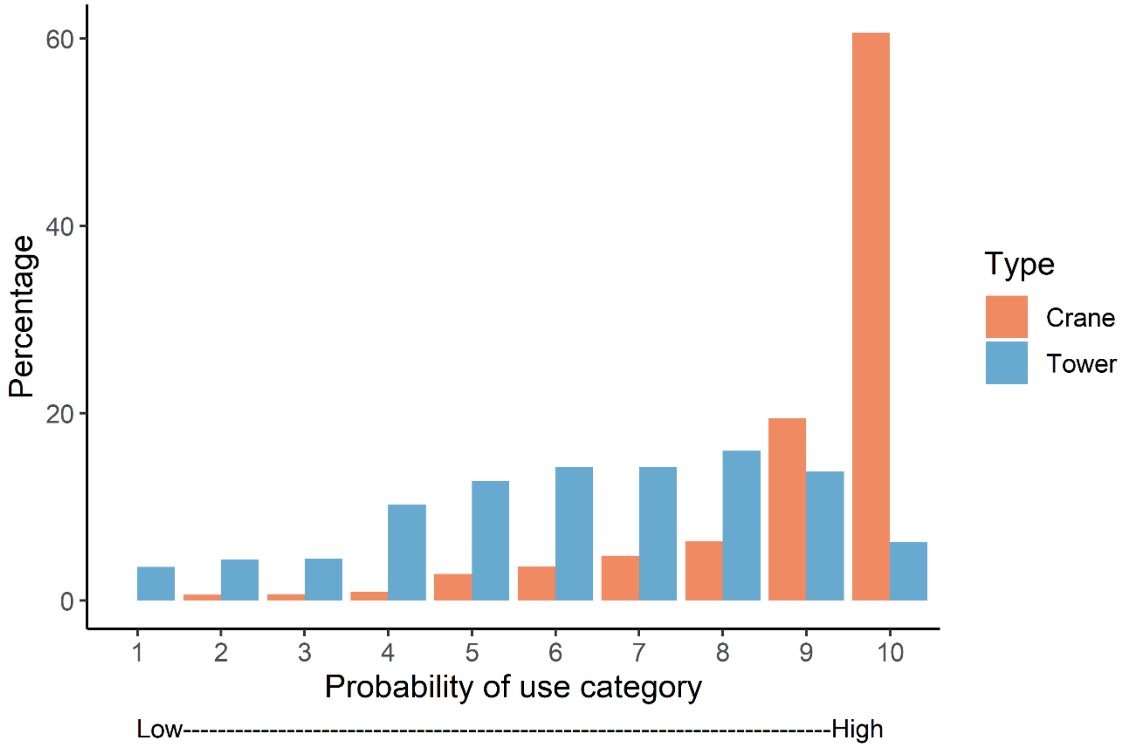

Figure 5. Percentage of wind-energy towers constructed before early 2020 and whooping crane locations at sites with characteristics indicative of low (category 1) to high (category 10) relative probability of use by whooping cranes migrating through the United States Great Plains, 2010–2016.