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RESEARCH ARTICLE

Opportunistically collected data reveal habitat selection by migrating Whooping Cranes in the U.S. Northern Plains

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ABSTRACT

The Whooping Crane (*Grus americana*) is a federally endangered species in the United States and Canada that relies on wetland, grassland, and cropland habitat during its long migration between wintering grounds in coastal Texas, USA, and breeding sites in Alberta and Northwest Territories, Canada. We combined opportunistic Whooping Crane sightings with landscape data to identify correlates of Whooping Crane occurrence along the migration corridor in North Dakota and South Dakota, USA. Whooping Cranes selected landscapes characterized by diverse wetland communities and upland foraging opportunities. Model performance substantially improved when variables related to detection were included, emphasizing the importance of accounting for biases associated with detection and reporting of birds in opportunistic datasets. We created a predictive map showing relative probability of occurrence across the study region by applying our model to GIS data layers; validation using independent, unbiased locations from birds equipped with platform transmitting terminals indicated that our final model adequately predicted habitat use by migrant Whooping Cranes. The probability map demonstrated that existing conservation efforts have protected much top-tier Whooping Crane habitat, especially in the portions of North Dakota and South Dakota that lie east of the Missouri River. Our results can support species recovery by informing prioritization for acquisition and restoration of landscapes that provide safe roosting and foraging habitats. Our results can also guide the siting of structures such as wind towers and electrical transmission and distribution lines, which pose a strike and mortality risk to migrating Whooping Cranes.

Keywords: migration, observation bias, spatial model, species conservation

Datos observacionales colectados de modo oportunista revelan selección de hábitat por parte de individuos migratorios de *Grus americana* en las Planicies del Norte de EEUU

RESUMEN

Grus americana es una especie en peligro a nivel federal en los Estados Unidos y Canadá que depende de hábitat migratorio en su largo pasaje entre los sitios de invernada en la costa de Texas, EEUU y los sitios reproductivos en Alberta y los Territorios del Noroeste, Canadá. Combinamos observaciones oportunistas de *Grus americana* con datos del paisaje para identificar correlaciones de la ocurrencia de *G. americana* a lo largo del corredor migratorio de Dakota del Norte y Dakota del Sur, EEUU. Los individuos de *G. americana* seleccionaron paisajes caracterizados por diversas comunidades de humedales y oportunidades de forrajeo en las tierras altas. El desempeño del modelo mejoró sustancialmente cuando se incluyeron variables relacionadas con la detección, enfatizando la importancia de contabilizar los sesgos asociados con la detección y los informes de aves en bases de datos oportunistas. Creamos un mapa predictivo que muestra la probabilidad relativa de ocurrencia a través de la región de estudio, mediante la aplicación de nuestro modelo a las capas de datos de SIG; la validación usando ubicaciones independientes no sesgadas a partir de aves equipadas con terminales de transmisión de plataforma indicó que nuestro modelo final predijo adecuadamente el uso por parte de los individuos migratorios de *G. americana*. El mapa de probabilidad demuestra que los esfuerzos actuales de conservación han protegido mucho hábitat de primer nivel para *G. americana*, especialmente en las porciones de Dakota del Norte y Dakota del Sur al este del Río Missouri. Nuestros resultados pueden apoyar la recuperación de especies al permitir priorizar la compra y la restauración de paisajes que brindan hábitats seguros para dormidero y forrajeo. Nuestros resultados también pueden guiar la instalación de estructuras tales como torres eólicas y líneas de transmisión y distribución eléctrica que pueden poner en riesgo a los individuos migratorios de *G. americana*.

Palabras clave: conservación de especies, migración, modelo espacial, sesgo de observación

INTRODUCTION

The Whooping Crane (*Grus americana*) is a federally endangered species in the United States and Canada whose only self-sustaining wild population breeds in and near Wood Buffalo National Park in Alberta and Northwest Territories, Canada, and winters 4,000 km to the south along the Texas Gulf Coast, USA, in the vicinity of Aransas National Wildlife Refuge (Kuyt 1992). The Aransas–Wood Buffalo population has increased in number from a low of <20 adults in 1941 (CWS & USFWS 2007) to an estimated 431 birds on the wintering grounds in the winter of 2016–2017 (Butler and Harrell 2017).

The 4,000-km-long corridor along which Whooping Cranes migrate is critical to the species' annual life cycle and long-term viability. Migrants roost in palustrine, lacustrine, and riverine wetlands and use a variety of croplands, grasslands, and wetlands for foraging (Johns et al. 1997, Austin and Richert 2005, Urbanek and Lewis 2015), which occupies ~40% of their daily time budget (Howe 1989). Little is known about the nutritional and energetic needs of migrating Whooping Cranes (CWS & USFWS 2007). However, active foraging by Whooping Cranes during migration (Howe 1989), weight gain and fat deposition by the congeneric Sandhill Crane (*Antigone canadensis*) along a similar migration corridor (Krapu et al. 1985, Pearse et al. 2010), and the importance of nutritional condition to avian reproductive success (Sandberg and Moore 1996) all reinforce the importance of habitat along the migration corridor to meet the energetic requirements of migration and eventual reproduction (Calvert et al. 2009, Butler et al. 2014a). Causes of mortality during migration include predation, shooting, and collisions with fences and power lines (Howe 1989, Kuyt 1992, CWS & USFWS 2007, Stehn and Haralson-Strobel 2014). For these reasons, identifying and protecting migration and stopover habitat is a priority action for Whooping Crane conservation (Lingle 1987, Beyersbergen et al. 2004, CWS & USFWS 2007, Butler et al. 2014a).

Potential habitat in the Whooping Crane migration corridor is being lost and degraded at increasing rates in the Northern Plains. Conversion of grassland, particularly native prairie, to cropland in the region is extensive and ongoing (Stephens et al. 2008, Rashford et al. 2011, Lark et al. 2015), which reduces upland foraging opportunities in a landscape where grass is increasingly scarce. Waste grain in crop fields provides food for Whooping Cranes (Howe 1989), and the area of cropland and associated foraging opportunities in the region are increasing. However, the increase in cropland is causing a reduction in the ecological functioning of wetlands in crop fields relative to those in grasslands (Euliss and Mushet 1999). In addition, wetlands in crop fields continue to be drained, especially during times of high commodity prices (Dahl 2011, Johnston 2013, Lark et al. 2015). Large numbers of wind turbines are planned or have been erected in the Northern Plains to take advantage of high wind potential in the area (U.S. Department of Energy 2008, Kiesecker et al. 2011). Oil and gas development can lead to degradation of wetlands in which Whooping Cranes roost and feed (Lingle 1987, Gleason et al. 2011, Preston et al. 2014) and may cause direct disturbance from activity and traffic associated with drilling. Oil and gas drilling in northwestern North Dakota, USA, has increased dramatically in recent years as hydraulic fracturing has made petroleum extraction from the Bakken Formation economically viable; an estimated 40,000 to 70,000 additional wells are expected to be drilled in the next 20 yr (North Dakota Department of Mineral Resources 2014). Wind energy development and oil and gas extraction often require the erection of electricity transmission and distribution lines, which increases the potential for Whooping Crane collisions with power lines, a known source of mortality in the Aransas–Wood Buffalo population (Stehn and Haralson-Strobel 2014, Smith and Dwyer 2016).

These threats reinforce the importance of habitat conservation along the Whooping Crane migration corridor. However, identifying and protecting Whooping Crane migration habitat is not a simple matter. Some stopover and staging sites, which have been identified as critical habitat, are regularly used by Whooping Cranes (Urbanek and Lewis 2015), but habitat throughout much of the migration corridor is widespread, dispersed, and irregularly used (Lingle 1987, Howe 1989, Pearse et al. 2015). Consequently, there are few regularly used and easily identified sites for Whooping Crane conservation across much of the migration corridor.

Whooping Crane use of habitat along the migration corridor is poorly understood, as early studies of telemetered birds (e.g., Howe 1989) predated the widespread availability of digital land cover data and geographic information systems (GIS), and therefore lacked quantitative data on habitat use relative to availability. Recent attempts to identify Whooping Crane habitat within the migration corridor have used opportunistic data (Tacha et al. 2010) to identify sites that have been previously used, either by recording the occurrence of sightings in counties (e.g., USFWS 2014b), identifying spatial corridors defined by the distribution of crane sightings (e.g., Tacha et al. 2010), or buffering repeated stopover sites (e.g., Fargione et al. 2012). Using opportunistic sightings imposes limitations, though, as it is estimated that as few as 4% of Whooping Crane stopovers are confirmed annually (T. Stehn cited in Tacha et al. 2010). In addition, such analyses have limited capacity to guide management because they suffer from extremely coarse spatial resolution and do not identify relationships between Whooping Cranes and their habitat (Niemuth et al. 2009). Finally, opportunistic data

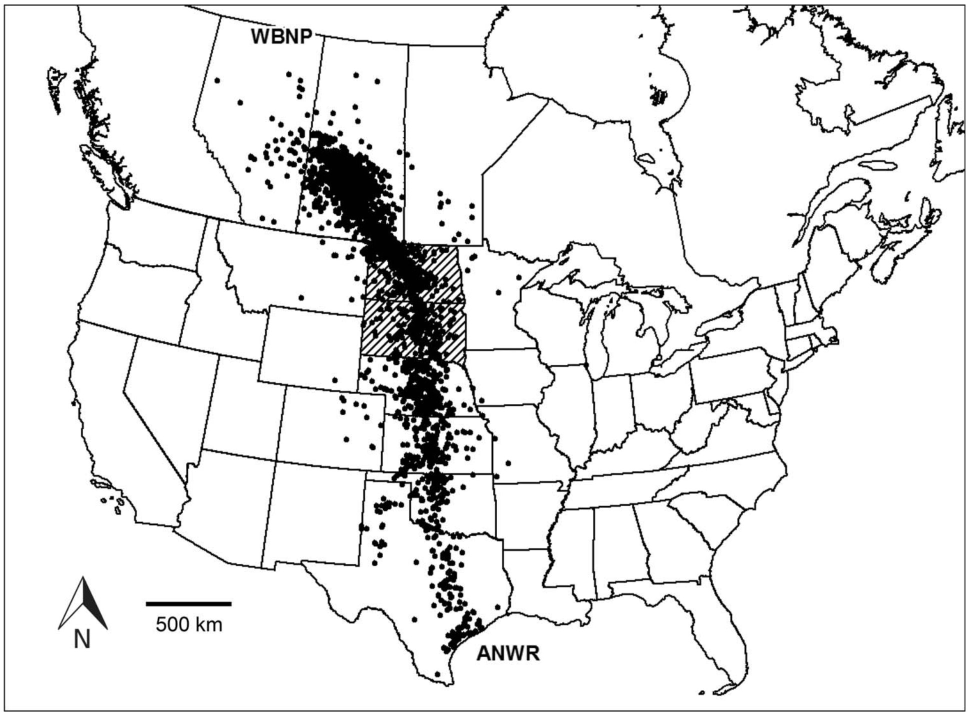

FIGURE 1. Whooping Crane sightings (black dots) in the Cooperative Whooping Crane Tracking Project database (Tacha et al. 2010) showing the migration corridor between Wood Buffalo National Park (WBNP) in west-central Canada and the Texas coast around Aransas National Wildlife Refuge (ANWR) in the southern United States. Diagonal hatching shows our North Dakota and South Dakota, USA, study region.

likely contain bias based on the presence of observers and other factors influencing detection (Anderson 2001, Niemuth et al. 2009, Hefley et al. 2013). However, some of the shortcomings of opportunistic data can be resolved by using model-based approaches that explicitly address biases in the data (Barry and Elith 2006, Mateo et al. 2010, Warton et al. 2013, Hefley and Hooten 2016).

We used Whooping Crane sightings, landscape data, and statistical models to provide insights into Whooping Crane habitat use along the migration corridor in North Dakota and South Dakota, USA. Our primary goal was to develop and evaluate habitat models characterizing the selection of stopover sites by Whooping Cranes in North Dakota and South Dakota. We used a model-based approach to account for biases that likely were present in the opportunistic dataset, particularly factors related to the detection of Whooping Cranes through space and time that could influence estimates of habitat relationships. These models were developed at a scale of hundreds of hectares, which is consistent with the scale of extensive and ongoing conservation programs in the region. We then implemented the best-supported model in a GIS framework to create predictive maps that can be used to guide conservation actions such as the acquisition of perpetual easements and restoration of wetlands, as well as to provide guidance for the siting of wind turbines and electrical transmission and distribution lines.

METHODS

Study Area

We modeled Whooping Crane sightings reported across the entire states of North Dakota and South Dakota, approximately midway between Wood Buffalo National Park and Aransas National Wildlife Refuge (Figure 1). Our study region is part of the Great Plains, which, prior to settlement by Europeans, was dominated by native grasslands (Samson et al. 2004, Licht 1997). Conversion of grassland, particularly native prairie, to cropland is stimulated by agricultural subsidies, new crop varieties, and altered climate that enable the planting of lands that were previously considered unsuitable for crop production (Stephens et al. 2008, Rashford et al. 2011, Lark et al. 2015). The portions of North Dakota and South Dakota that are east and north of the Missouri River are part of the Prairie Pothole Region, which is noted for high densities of wetlands that are also greatly diminished from historical levels due to agricultural intensification (Dahl 2011, Johnston 2013, Lark et al. 2015). The climate in the study region is continental, with high interannual variation in precipitation (Woodhouse and Overpeck 1998).

Whooping Crane Data

We used sightings from the Cooperative Whooping Crane Tracking Project that were entered into a GIS to facilitate spatial analysis of migration data (Tacha et al. 2010). The Cooperative Whooping Crane Tracking Project is coordinated by the U.S. Fish and Wildlife Service and relies on principal contacts within state and federal agencies to evaluate and submit reported sightings of migrant Whooping Cranes in each state in the Central Flyway (Tacha et al. 2010). The resulting database contains sightings from as early as 1942 and is updated annually; we used 478 confirmed sightings of Whooping Cranes using wetlands and uplands in North Dakota and South Dakota collected from spring of 1990 through spring of 2014. We chose this time period because its 2002 midpoint approximately coincided with 2001 land cover data derived from satellite imagery that we used to characterize upland habitat composition. Locations were variously reported using global positioning system (GPS) coordinates, cadastral descriptions, latitude and longitude, and distances from landmarks such as towns. The accuracy of locations varied, and in many cases points were assigned to the center of a legal section of 1.6 km × 1.6 km. Consequently, the data were only appropriate for coarse-grained analysis and were not suitable for measures such as distance to the nearest road (Tacha et al. 2010). Sightings in the Whooping Crane database show biases toward urban centers and national wildlife refuges (Howe 1989, Tacha et al. 2010). However, collection of Whooping Crane location data without detection biases has been limited, highlighting the need to address biases in analyses. Extensive field surveys are infeasible due to the rarity of Whooping Cranes over a large migration area, and telemetry-based research has been scant and difficult to conduct due to technological limitations (Howe 1989, Kuyt 1992) and perceived risks of capturing and marking birds.

Following the guidelines of Nielson et al. (2004), Pearce and Boyce (2006), and Northrup et al. (2013), we generated 10,000 random points throughout the entire study region to describe available habitat. We used points with known Whooping Crane use in conjunction with available (pseudoabsence) points to develop a resource selection function, which estimated relative probability of occurrence following a used–available design (Manly et al. 2002, Johnson et al. 2006). Although resource selection functions developed with a used–available design are generally robust to contamination where available points were in fact used (Johnson et al. 2006), we only used random points >1,600 m from reported crane sightings to reduce contamination. All random points were assigned a year value from a uniform distribution of years 1990–2014.

Predictor Variables

Predictor variables in our modeling effort fit into 3 general categories related to geographic location, landscape-level habitat characteristics, and detection (Table 1). The fundamental determinant of Whooping Crane presence in North Dakota and South Dakota is a migration path between Aransas National Wildlife Refuge and Wood Buffalo National Park (Howe 1989, Kuyt 1992). Therefore, we included distance to the centerline of the migration corridor to describe spatial positon within the migration corridor, similar to the directional bearing variable used by Belaire et al. (2014) and analogous to the first-order selection of Johnson (1980). We calculated the migration centerline following the methodology of Tacha et al. (2010), using 478 ground sightings for our selected time period in the Dakotas, as well as 339 sightings from Nebraska, USA, and 1,660 sightings from Alberta, Saskatchewan, and Manitoba, Canada, to more precisely estimate the southern and northern ends of the migration corridor in the Dakotas. In addition to increasing the predictive power of the model, incorporating covariates that account for spatial patterns of distribution helps to reduce biases in parameter estimates and nonindependence of errors caused by positive spatial autocorrelation (Lennon 2000, Beale et al. 2010).

We assessed the composition and configuration of landscapes around data points (used and available) within circular moving windows with radii of 800, 1,200, and 1,600 m, which coincided with distances commonly used for land protection and management in the region. The 1,200- and 1,600-m radii included the majority of observed distances between roosting and feeding sites (Howe 1989, Austin and Richert 2005), which accommodated the "landscape" that birds were using, rather than the point at which they roosted or fed, analogous to the second-order selection of Johnson (1980). In addition, using large sampling windows helped to reduce any effects of location error resulting from inexact geographic locations of many of the Whooping Crane sightings (Tacha et al. 2010, Hefley et al. 2014).

Landscape attributes were selected for their potential importance to Whooping Crane ecology (Howe 1989, Johns et al. 1997, Austin and Richert 2005; Table 1). Because wetlands are thought to be the primary prerequisite for stopover sites (Howe 1989), we used the National Wetlands Inventory (NWI) digital database processed to basins to identify area, variety, and number of wetlands across our study area. The NWI is based on the Cowardin et al. (1979) wetland classification system and provides water regimes (e.g., temporary, seasonal, semipermanent, permanent) identified for wetlands at the time of mapping. Even though most of the NWI data in our region were collected in the 1980s, we chose to use the NWI because its completeness, fine spatial resolution, and determination

TABLE 1. Predictor variables considered in the development of models relating sightings of Whooping Cranes in North Dakota and South Dakota, USA, to geographic location, landscape-level habitat characteristics, and factors influencing detection. Characteristics within buffers were calculated using circular moving windows with radii of 800, 1,200, and 1,600 m.

Predictor variable	Definition	Justification
Distance to centerline	Distance (km) from centerline of Whooping Crane migration corridor calculated from data	Whooping Cranes generally follow a narrow migration corridor (Howe 1989, Tacha et al. 2010)
Wetland area	Proportion of area within the buffer comprised of all temporary, seasonal, semipermanent, permanent, and lacustrine wetlands as identified by the National Wetlands Inventory (Wilen and Bates 1995)	Whooping Cranes use wetlands for roosting and foraging (Howe 1989, Johns et al. 1997, Austin and Richert 2005)
Wetland variety	Number of different wetland water regimes (temporary, seasonal, semipermanent, permanent or lake, riverine) as identified by the National Wetlands Inventory (Wilen and Bates 1995) processed to basins (Cowardin et al. 1995) within buffer	Seasonal shifts in wetland use and presence of multiple wetlands in the vicinity of Whooping Crane stopover sites (Howe 1989, Johns et al. 1997, Austin and Richert 2005) suggest that wetland complexes might be important to Whooping Cranes
Wetland number	Number of wetland basins as identified by the National Wetlands Inventory (Wilen and Bates 1995) processed to basins (Cowardin et al. 1995) within buffer	Wetlands used for roosting are generally large (Johns et al. 1997), but most prairie potholes and stock ponds are small (Kantrud et al. 1989); this variable evaluated whether multiple small wetlands of a given area were as attractive to Whooping Cranes as fewer large wetlands of the same area
Perennial cover	Proportion of buffer comprised of grassland, hay fields, and shrubs as identified by the 2001 National Land Cover Database (NLCD; Homer et al. 2007) cover classes 71, 81, and 52	Perennial cover is common at or adjacent to roosting and feeding sites (Howe 1989, Johns et al. 1997, Austin and Richert 2005)
Cropland	Proportion of buffer comprised of cultivated crops as identified by the 2001 NLCD (Homer et al. 2007) cover class 82	Whooping Cranes use agricultural fields for foraging (Howe 1989, Johns et al. 1997, Austin and Richert 2005)
Forest	Proportion of buffer comprised of forest cover as identified by the 2001 NLCD (Homer et al. 2007) cover classes 41, 42, and 43	Whooping Cranes use sites with few trees (Johns et al 1997, Austin and Richert 2005)
Distance to increased survey effort	Distance (km) from 24 areas of known intensive Whooping Crane observation effort, including district offices of wildlife management agencies and wildlife refuges and fish hatcheries with permanent staff	Disproportionate numbers of Whooping Crane sightings are in proximity to refuges or other sites with knowledgeable observers (Howe 1989, Tacha et al. 2010)
Human population density	Number of people per 2.6 km^2, derived from U.S. Census Bureau data (Seirup and Yetman 2006)	Human observers are necessary to detect and report Whooping Cranes; sightings are biased toward urban centers (Howe 1989)
Roads	Length (km) of roads (maintained gravel or better) identified by topologically integrated geographic encoding and referencing (TIGER) data (U.S. Census Bureau 2011) within each buffer	Whooping Cranes avoid roads (Johns et al. 1997, Belaire et al. 2014), but roads may enable increased detection of Whooping Cranes
Terrain roughness	Standard deviation of cells within buffer of digital elevation model with 30-m spatial resolution	Whooping Cranes use wetlands with shallow shoreline slopes (Johns et al. 1997, Austin and Richert 2005); detection of Whooping Cranes may be influenced by topographic variation
Whooping Crane population size	Number of birds estimated to be in the Aransas–Wood Buffalo flock each year	Number of Whooping Cranes detected annually increased as population size increased during the analysis period

of water regimes provided better insight into wetland community composition than datasets with coarser spatial and thematic resolution. We integrated digital polygons, some of which represented complex wetlands with more than one wetland zone identified by the NWI, into individual depressional wetland basins classified by the most permanent water regime associated with each basin (Cowardin et al. 1995). We did not discriminate among water regimes in our models for 2 reasons. First, water conditions in our study area varied greatly among years and basins could function under different water regimes depending on the year of observation (Niemuth et al. 2010). Second, our analysis included sightings from spring, when Whooping Cranes heavily use shallow, temporary, and seasonal wetlands, as well as from fall, when temporary and seasonal wetlands are generally dry and Whooping Cranes shift to semipermanent and permanent wetlands (Howe 1989, Johns et al. 1997). Finally, Whooping Cranes may use shallow perimeters of semipermanent and permanent wetland basins.

The seasonal shift in wetland use along with the presence of multiple wetlands in the vicinity of Whooping Crane stopover sites (Howe 1989, Johns et al. 1997, Austin and Richert 2005) suggest that wetland complexes may be important to Whooping Cranes. Therefore, we included a variable describing wetland variety and derived it by summing the number of different wetland water regimes in the windows surrounding use and pseudoabsence points. In addition, we included a variable that reported the number of wetland basins within windows surrounding use and pseudoabsence points to evaluate the response of Whooping Cranes to many small wetlands as opposed to few large wetlands (Howe 1989, Johns et al. 1997).

Crop fields and upland perennial cover such as pasture, wet meadows, and hay meadows are common components of Whooping Crane stopover habitat, and Whooping Cranes appear to avoid trees (Howe 1989, Johns et al. 1997, Austin and Richert 2005). We used the 2001 National Land Cover Database (NLCD; Homer et al. 2007), which was roughly centered in our analysis period, to estimate the amount of perennial cover, cropland, and forest in windows surrounding use and pseudoabsence points. Formal accuracy assessment of the 2001 NLCD is lacking, but average classification accuracy of the NLCD was 84% in 10-fold cross validation used during NLCD development (Homer et al. 2007). Estimated change in land cover composition from 1991 to 2001 varied throughout our study area, but ranged from <1% to 9% (Fry et al. 2009); changes in land cover composition from 2001 to 2014 have not been quantified. Because the amounts of cropland and perennial cover were strongly negatively correlated with each other in our study area, we did not include both variables in the same model, even though previous research has indicated that Whooping Cranes use both cover types (Table 1). Therefore, we evaluated models with each of the 2 cover variables individually and chose the combination that best explained Whooping Crane presence. In each case, we included a quadratic term to determine whether Whooping Cranes selected areas with moderate levels of one variable, which would suggest a preference for >1 cover class and is generally consistent with the "ecotone" variable of Belaire et al. (2014).

Data describing locations of Whooping Cranes were opportunistic with known biases; thus, we considered variables that might have influenced detection, assuming that variables related to detection were independent of habitat variables that influenced Whooping Crane use (Warton et al. 2013). First, we included distance to 24 sites likely to have increased observation effort, including district offices of wildlife management agencies and wildlife refuges and fish hatcheries with permanent staff. Second, we included human population density to account for increased detections reported by the general public. Finally, we included road density and digital elevation data to determine whether the probability of observing Whooping Cranes was positively related to ease of vehicular access, which could facilitate sightings, or negatively related to topographic variation, which could reduce the ability to see birds.

Sample size (i.e. the number of Whooping Crane observations) varied among years, likely influenced by weather and human activity during migration and possibly by interannual variation in water conditions (Howe 1989, Kuyt 1992). Therefore, we included the year of observation as a random intercept in a mixed effects model, as random effects can correct for unbalanced designs (Gillies et al. 2006). All other variables were treated as fixed effects.

Model Development and Validation

We used logistic regression (Hosmer and Lemeshow 2000, Agresti 2007) to estimate a resource selection function based on characteristics of predictor variables at locations used by and available to Whooping Cranes (Manly et al. 2002, Johnson et al. 2006). We treated each sighting of Whooping Cranes as one occurrence, regardless of stopover length or the number of individuals present, as the latter are likely influenced by weather and behavior rather than habitat (Howe 1989, Kuyt 1992). Prior to developing models, we used scatter plots and Pearson's correlations to assess collinearity among predictor variables to ensure that highly correlated ($|r| > 0.7$) predictors were not considered simultaneously. In an attempt to develop a parsimonious model and avoid spurious correlations with Whooping Crane observations, we initially evaluated main effects of linear relationships except for the previously mentioned quadratic relationship with the amount of cropland or perennial cover in the landscape. After assessing main effects, we evaluated several interaction terms, specifically wetland area*wetland number, distance to centerline of the migration corridor* distance to area of increased survey effort, and wetland area*cropland area*distance to centerline of the migration corridor. We used model selection to balance bias and variance, discriminating among reduced versions of the full model using Akaike's information criterion (AIC), beginning with the full model and holding out one parameter or set of parameters at a time and assessing improvements in AIC values (Burnham and Anderson

2002, Crawley 2007, Beale et al. 2010). We also calculated Akaike weights (w_i) for each model within 4 AIC units of the model with the lowest AIC value, which is a useful rule of thumb for identifying the set of models plausibly supported by the data (Burnham and Anderson 2002). Akaike weights provide an indication of the relative likelihood of competing models best fitting the data, which enabled us to evaluate the relative strength of evidence for models relating Whooping Crane sightings to predictor variables. We conducted statistical analyses in the R environment (R Core Team 2013), specifically the generalized linear mixed models capacity of the lme4 package (Bates et al. 2014, 2015), using a binomial error distribution with a logit link.

We created a map showing the predicted probability of occurrence across the 2 states by incorporating corresponding GIS data layers into the logistic response equation for the final model, using a constant for fixed effects that were associated with detection across space (i.e. road density and distance to areas of increased survey effort) or time (i.e. Whooping Crane population size). By using a constant, predictions across the study area were set to the same value for each variable that may cause bias, thereby correcting for effects of bias across the study area (Warton et al. 2013). The random year effect accounted for interannual variation in detection; the probability map therefore reflected predicted habitat use across all years of the analysis period. Because we followed a used–available design and the proportion of Whooping Crane stopovers that was confirmed is unknown, mapped values represent relative probabilities of use (Manly et al. 2002, Johnson et al. 2006). To aid interpretation of the mapped output for conservation planning, we used an equal-area slice to divide the probability map for the 2 states into 10 equal-area bins, or deciles, with decile values of 1 indicating the highest probability of occurrence by Whooping Cranes and decile values of 10 indicating the lowest probability of occurrence. Deciles provide a simple structure with clear thresholds that field personnel can use to identify and rank land parcels for conservation, particularly acquisition of perpetual easements. In addition, dividing the region into deciles provided the foundation for validation of the final model using independent data, which we performed by calculating the rank correlation between frequencies of occurrence from the validation data in each of the 10 equal-area slices of the final model (Boyce et al. 2002).

We validated the final model using unbiased location data collected from 46 Whooping Cranes outfitted with platform transmitting terminals (PTTs) that collected GPS coordinates during 2010–2013 (see Pearse et al. (2015) for capture, marking, and data handling procedures). Validation data included one randomly selected daytime location from multiple locations collected at each stopover site to simulate situations in which cranes may be observed.

Assessing Effectiveness of Conservation Programs

We assessed the predicted value of existing land conservation efforts for migrating Whooping Cranes by quantifying the area of protected lands by habitat decile. We used GIS data layers to summarize 4 categories of protected lands: (1) federal fee-title lands, which included national forests, national grasslands, national parks, national wildlife refuges, and waterfowl production areas; (2) state fee-title lands, which included wildlife management areas and school trust lands; (3) wetland easements held by the U.S. Fish and Wildlife Service, wherein land remains in private ownership but specified wetlands are protected from draining, filling, leveling, or burning; and (4) grassland easements held by the U.S. Fish and Wildlife Service, wherein land remains in private ownership and grassland may not be cultivated at any time or mowed prior to July 15 each year. We did not include tribal lands because of the large, varying, and unknown amounts of private inholdings on reservations. The area of wetlands protected under easements may differ from that observed in databases such as the NWI or NLCD due to annual variation or differences in data acquisition. Not all fee-title public lands that we considered are dedicated to conservation, but we included them as they are subject to public policy that generally requires that conservation or wildlife management at least be considered in management decisions. Because the portions of the 2 states east of the Missouri River have a long history of wetland and waterfowl conservation that is largely absent west of the Missouri River, we divided our assessments by areas east and west of the river as well as by land protection categories to evaluate patterns of land protection relative to potential use by Whooping Cranes. We used Spearman's rank correlation to evaluate relationships between area of protected land, by land protection category and location (east vs. west of the Missouri River), and habitat decile.

RESULTS

Models of Landscape-level Habitat Selection

The number of confirmed Whooping Crane sightings varied among years ($\bar{x} = 19.1$, range $= 8$–37) and tracked the size of the Aransas–Wood Buffalo flock, which increased during our analysis timeframe; however, reported sightings showed substantial interannual variation (Figure 2). Areas of cropland and perennial cover within moving windows were negatively correlated ($r = -0.87$ at all 3 scales), so we evaluated models separately, one with cropland and the other with perennial cover. The model with cropland and other covariates had an AIC value 7.4 points lower than the same model with perennial cover replacing cropland, so we no longer considered perennial cover during model selection. No other pairs of continuous variables were strongly ($|r| > 0.6$) correlated.

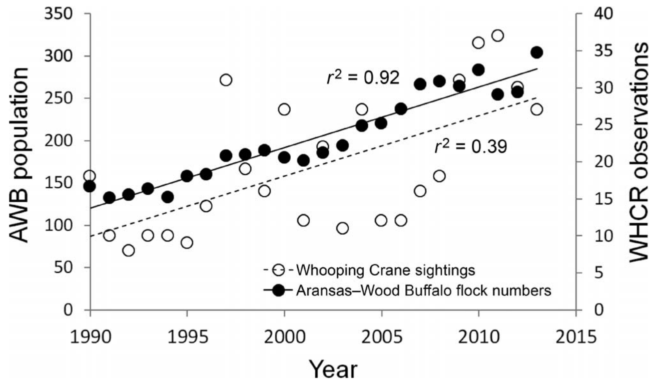

FIGURE 2. The number of Whooping Crane (WHCR) sightings available for analysis each year (open circles, dashed trend line) tracked the increasing population size of the Aransas–Wood Buffalo (AWB) flock (solid circles, solid trend line) in 1990–2013, but showed greater interannual variation. Aransas–Wood Buffalo flock numbers are from Butler et al. (2014b), USFWS (2014a), and W. Harrell (personal communication).

Models were best supported using data from the moving window with a 1,200-m radius; AIC values increased ≥5.0 points when full models were developed using data from the 800- and 1,600-m windows relative to the full model developed using data from the 1,200-m window. The best-supported model indicated that Whooping Crane occurrence was positively associated with wetland area, wetland variety, cropland area, road density, and Whooping Crane population size; negatively associated with distance to centerline of the migration corridor, wetland number, distance to area of increased survey effort, and terrain roughness; and also positively influenced by the interactions of wetland area*wetland number, distance to centerline of the migration corridor*distance to area of increased survey effort, and wetland area*cropland area* distance to centerline of the migration corridor (Tables 2 and 3). The best-supported model had an Akaike weight of 0.45; the 3 models within 4 units of the best-supported model had Akaike weights of 0.27 to 0.11 and differed from the best-supported model due to the inclusion or exclusion of one variable and/or one interaction term (Table 3). A model including forest cover was not treated as competitive even though its AIC value was just 2 points higher than that of the best-supported model, as the forest cover parameter was uninformative and did not improve the model (Arnold 2010).

We considered 2 variables in the final model (road density and distance to increased survey effort) to be related to detection of Whooping Cranes. Removing these 2 variables from the best model resulted in a $\Delta AIC = 97.1$, indicating that detection was an important component of the best-approximating model. Removing the terrain roughness variable, which could be associated with selection of flat, open landscapes by Whooping Cranes

TABLE 2. Parameter estimates ± standard error (SE) for variables included in the best-supported model relating sightings of migrant Whooping Cranes in North Dakota and South Dakota, USA, to geographic location, landscape characteristics within 1,200 m of analysis points, and factors influencing detection, 1990–2014. 95% confidence intervals for all parameter estimates exclude 0, except for the wetland area*cropland area*distance to centerline interaction term.

Variable	Parameter estimate ± SE
Intercept	−2.93 ± 0.52
Distance to centerline	$-3.1 \times 10^{-2} \pm 2.4 \times 10^{-3}$
Wetland area	1.72 ± 0.45
Wetland variety	0.44 ± 0.08
Wetland number	−0.019 ± 0.003
Wetland area*Wetland number	0.09 ± 0.02
Cropland area	1.69 ± 0.24
Distance to increased survey effort	$-2.3 \times 10^{-2} \pm 2.9 \times 10^{-3}$
Road density	0.12 ± 0.05
Terrain roughness	−0.07 ± 0.02
Whooping Crane population size	0.006 ± 0.001
Distance to increased survey effort*Distance to centerline	$1.1 \times 10^{-4} \pm 3.6 \times 10^{-5}$
Wetland area*Cropland area*Distance to centerline	0.032 ± 0.017

or reduced detection of Whooping Cranes in hilly terrain, caused a further increase of 10.1 AIC points.

The relative probability map created by applying the final model to data layers suggested habitat selection within a north–south corridor bisecting the 2 states (Figure 3). The top 3 deciles of the relative probability map contained 89% of the Whooping Crane sightings used to develop the model and 79% of the independent validation observations (Table 4). The number of independent validation locations derived from telemetered Whooping Cranes in each decile was strongly correlated with decile rank (Spearman's rho = 1.0), with a strong differential between high and low deciles, indicating that the model performed well (Boyce et al. 2002).

Distribution of Protected Lands

Protected lands in the study region totaled 3.8 million ha, or ∼10% of the 38.5-million-ha study area (Figure 4). The area of protected land was ∼1.9 million ha on each side of the Missouri River; however, the distribution of protected lands among deciles differed greatly between those portions of the study area east and west of the Missouri River (Figure 4). Protected lands east of the Missouri River were more evenly distributed among ownership classes than lands west of the Missouri River, which were dominated by national forests and national grasslands (Figure 4) and where U.S. Fish and Wildlife Service

TABLE 3. Constituent variables (with sign indicating direction of relationship), Akaike's information criterion (AIC) values, AIC differences (Δ_i), and Akaike weights (w_i) for candidate models with $\Delta_i < 4$ relating sightings of migrant Whooping Cranes in North Dakota and South Dakota, USA, to geographic location, landscape-level habitat characteristics, and factors influencing detection, 1990–2014.

	Model 1	Model 2	Model 3	Model 4
Variable				
Distance to centerline	−	−	−	−
Wetland area	+	+	+	+
Wetland variety	+	+	+	+
Wetland number	−	−	−	−
Cropland area	+	+	+	+
Cropland area^2			−	−
Distance to increased survey effort	−	−	−	−
Road density	+	+	+	+
Terrain roughness	−	−	−	−
Whooping Crane population size	+	+	+	+
Distance to centerline*Distance to increased survey effort	+	+		+
Wetland area*Wetland number	+	+	+	+
Wetland area*Cropland area*Distance to centerline	+		+	
Log-likelihood	−1300.7	−1302.2	−1300.7	−1302.2
AIC value	2629.4	2630.4	2631.3	2632.3
Δ_i	0.0	1.0	1.9	2.9
w_i	0.45	0.27	0.17	0.11

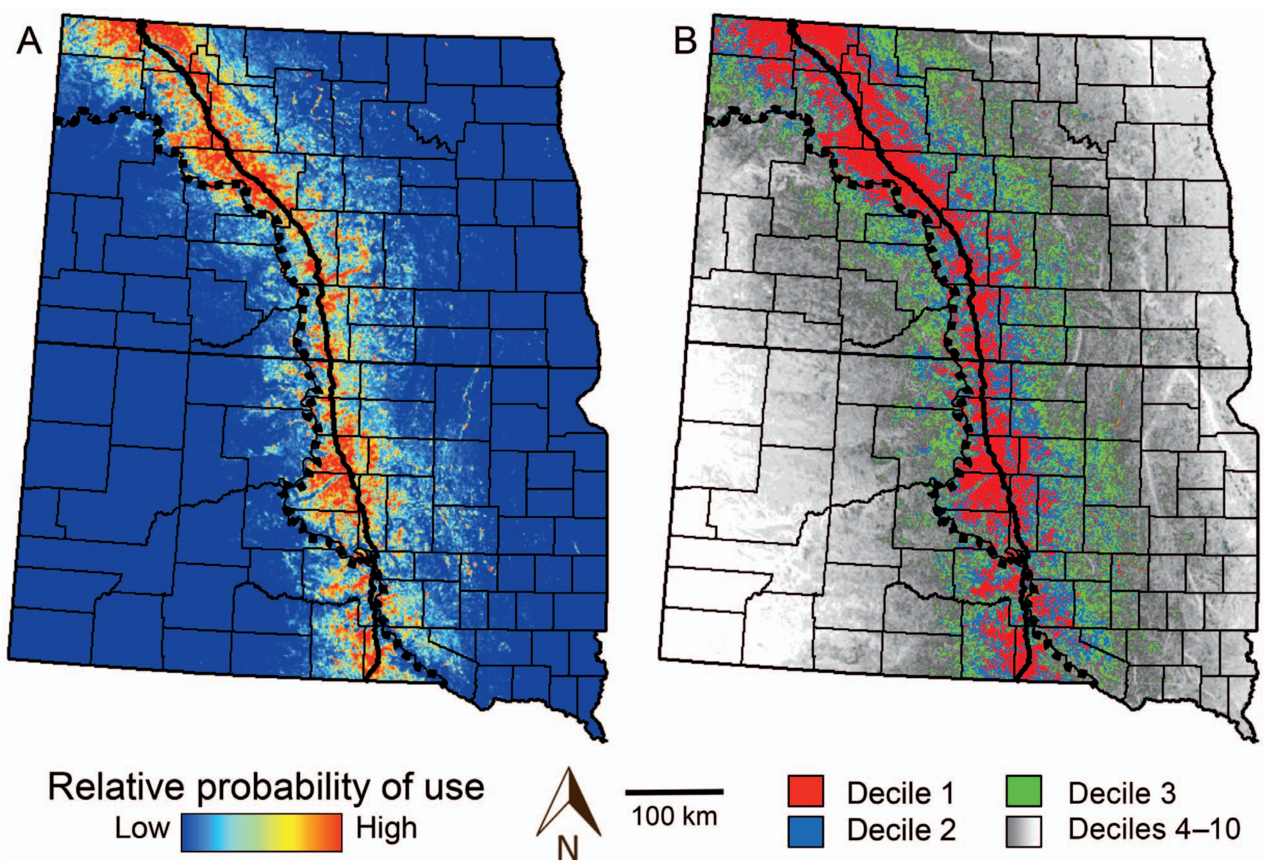

FIGURE 3. (**A**) Predicted relative probability of landscape-level habitat use by migrant Whooping Cranes in North Dakota and South Dakota, USA; and (**B**) ranked probability of landscape-level habitat use by migrant Whooping Cranes in North Dakota and South Dakota classified by equal-area deciles. The top 3 deciles (colored) contained 336 (79%) of 427 validation points. The heavy black line represents the centerline of the migration corridor for sightings used in developing the model, and the thick dotted line represents the Missouri River.

TABLE 4. Number of Whooping Crane sightings and percentage of sightings in each decile included in the probability map indicating ranked probability of use for Whooping Crane model building (MB) and validation (VAL) datasets.

	Sightings (*n*)		Percentage of sightings	
Decile	MB	VAL	MB	VAL
1	306	167	64.0	39.1
2	84	98	17.6	23.0
3	34	71	7.1	16.6
4	22	53	4.6	12.4
5	21	18	4.4	4.2
6	1	12	0.2	2.8
7	7	4	1.5	0.9
8	2	2	0.4	0.5
9	0	2	0.0	0.5
10	1	0	0.2	0.0

easements totaled <47 ha. The 2 largest ownership classes east of the Missouri River were grassland and wetland easements, each of which totaled >500,000 ha. East of the Missouri River, the area of federal fee-title lands was positively correlated with Whooping Crane habitat decile ($r = 0.95$), as was the area of state fee-title lands ($r = 1.00$), area of wetland easements ($r = 0.99$), and area of grassland easements ($r = 0.84$). West of the Missouri River, the area of state and federal fee-title lands was negatively correlated with Whooping Crane habitat decile ($r = -0.99$ and -1.00, respectively; Figure 4).

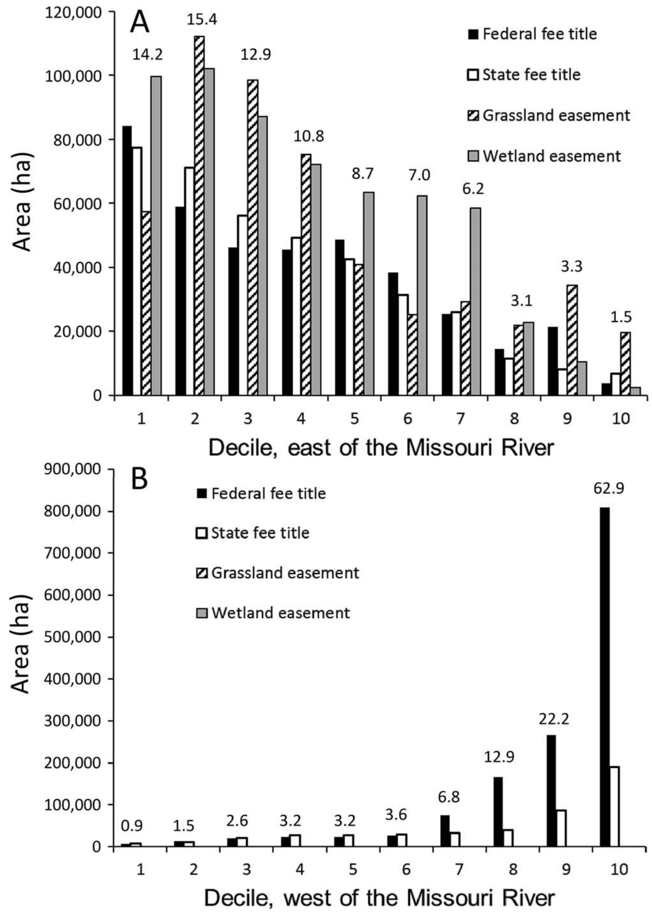

FIGURE 4. The area of land under multiple land protection categories within each Whooping Crane habitat decile differed between (**A**) the portion of the study region east of the Missouri River, USA, where ongoing waterfowl and wetland conservation efforts have protected land in upper Whooping Crane habitat deciles, and (**B**) the portion of the study region west of the Missouri River, where U.S. Fish and Wildlife Service easements totaled <47 ha. Numbers above each decile cluster of bars represent the percentage of that decile that is protected. Note the different *y*-axis scale between graphs.

DISCUSSION

Our results indicate that Whooping Cranes migrating through North Dakota and South Dakota select landscapes characterized by diverse wetland communities and upland foraging opportunities within a corridor linking breeding and wintering grounds. These findings are consistent with many observational studies (Howe 1989, Johns et al. 1997, Austin and Richert 2005, Tacha et al. 2010) as well as quantitative analyses for other portions of the migration corridor (Belaire et al. 2014, Hefley et al. 2015). The habitat model and associated predictive map that we developed are not definitive, but provide a positive step toward identifying important areas for conservation as part of an effective management strategy for Whooping Cranes (Howe 1989, Beyersbergen et al. 2004, CWS & USFWS 2007, Butler et al. 2014a).

The retention of 9 of the 11 candidate variables in the best-supported model suggests that our data were sufficient to develop a relatively well-parameterized model and that the candidate variables that we identified were appropriate to the question and scales that we addressed. Even though the best-supported model did not include the quadratic term for area of cropland, it was included in 2 of the 3 competitive models, indicating support for its effect. Inclusion of the quadratic term supports the idea that a positive linear relationship with cropland cannot be applied across the landscape, as perennial cover and multiple upland habitat types are important to migrating Whooping Cranes (Howe 1989, Johns et al. 1997, Austin and Richert 2005, Belaire et al. 2014) and continuing loss of wetlands associated with agricultural conversion (Dahl 2011, Johnston 2013, Lark et al. 2015) will reduce opportunities for roosting and foraging. Absence of the quadratic term for cropland from the best-supported model may have resulted from more detections in cropland than perennial cover, given the intensity and number of visits required by farmers for crop production relative to other uses and a general absence of standing vegetation in crop fields during spring and fall migration, thereby increasing Whooping Crane visibility and detection. In addition, cropland was positively correlated ($r = 0.31$) with roads and negatively correlated ($r = -0.49$) with terrain roughness, both of which also could have contributed to detection. Likewise, apparent selection of cropland might reflect a diurnal detection bias, as Whooping Cranes use croplands heavily during the day, when most opportunistic sightings of Whooping Cranes are likely to occur, but telemetered Whooping Cranes were regularly found in wetlands at night (Pearse et al. 2017). Finally, availability of cropland for foraging is unlikely to be limiting, as the amount of cropland in the study area is increasing as wetlands and grasslands that are also used by Whooping Cranes are being lost (Rashford et al. 2011, Johnston 2013, Niemuth et al. 2014, Lark et al. 2015).

The strength of the positive interaction between wetland area and wetland number indicates that wetland area influenced Whooping Crane use differently depending on the number of wetland basins in the area, where one large basin of a given area was more attractive than many small basins totaling the same area. Lower use of areas with many small basins might be caused by selection of wetlands with large, unobstructed views and widths (Pearse et al. 2017) or the higher likelihood of larger wetlands containing water, especially in fall (Howe 1989, Niemuth et al. 2010). This interaction, along with the positive relationship with the variety of wetland water regimes, reinforces the importance of wetland complexes to Whooping Cranes in our study region.

Our out-of-sample validation provided stronger inference and predictive power than the within-sample validation, and indicated that, in this case, opportunistic data can be used to develop biologically sound models when appropriate adjustments are applied. Our results have implications for citizen science and monitoring activities, as opportunistic data must be used with caution and an awareness of potential biases and shortcomings (see also McKelvey et al. 2008, Hefley et al. 2013, Belaire et al. 2014). Model selection results indicated that models that did not include variables related to detectability performed poorly at describing data relative to models that contained these variables. These results show the importance of using covariates to adjust for bias rather than simply ignoring bias in opportunistic data, although interpretation of detection covariates may be difficult. For example, the negative relationship with topographic roughness could be a function of reduced detectability in hilly terrain or might suggest that Whooping Cranes selected flat landscapes with high visibility, or perhaps a combination of the 2 explanations. Similarly, it is possible that Whooping Cranes selected areas of high road density, although increased detection along roads is a more plausible explanation, especially as road density was correlated with human population density ($r = 0.53$). Detection and environmental variables are often correlated; although this reduces the effectiveness of including variables to account for detection bias, model performance is generally higher when correlated variables are included in models relative to when they are not (Warton et al. 2013). Data from birds outfitted with GPS-enabled PTTs can provide unbiased data with precise locations; these data, along with emerging analytical techniques, will likely enable the development of more readily interpreted models in the future. In addition, precise locations from marked birds enable determination of habitat relationships at much finer scales than what is possible with opportunistic data. Nonetheless, the opportunistic dataset has provided locations for decades, providing opportunities for assessing habitat use over a range of environmental conditions, whereas monitoring using telemetered birds would be limited temporally based on funding, staffing, and other logistical challenges.

The distribution of protected lands in North Dakota and South Dakota relative to predicted Whooping Crane use demonstrated substantial benefits of existing conservation lands. Patterns were strikingly different between the portions of the 2 states east of the Missouri River (i.e. the Prairie Pothole Region), where extensive waterfowl conservation efforts occur, and the portions of the states west of the Missouri River, where public lands were acquired without a specific wildlife conservation goal. However, the 1.9 million hectares of protected lands in the Prairie Pothole Region constituted only ~8% of the area of all lands east of the Missouri River, and wetland loss in the region has accelerated with intensified agricultural production in recent years (Dahl 2011, Johnston 2013, Lark et al. 2015), reinforcing the need for additional conservation. The U.S. Fish and Wildlife Service is presently spending ~$50 million annually on the acquisition of perpetual wetland and grassland easements in the eastern portions of North Dakota and South Dakota, with funding primarily coming from Migratory Bird Hunting Stamp ("Duck Stamp") sales, the Land and Water Conservation Fund, and the North American Wetlands Conservation Act, in combination with nonfederal matching funds from state wildlife management agencies or nongovernmental organizations such as Ducks Unlimited (USFWS 2015). The value of land parcels to endangered species is one of the criteria for assessing candidate land parcels for easement acquisition (USFWS 2010); the model presented here will be valuable for ensuring benefits to Whooping Cranes by protecting grassland and wetland complexes in areas of high predicted Whooping Crane use from conversion to other uses.

Unfortunately, Whooping Cranes are subject to a variety of additional threats, including disturbance from oil and gas development and related degradation of wetlands in which Whooping Cranes roost and feed (Lingle 1987, Gleason et al. 2011, Preston et al. 2014), as well as direct mortality from power lines (Stehn and Haralson-Strobel 2014). Our spatial model can help to guide the siting of new wind, oil, and electrical transmission infrastructure to minimize potential conflicts with Whooping Cranes, and also to identify threats and associated opportunities for mitigation such as transmission line marking and wetland restoration. How these threats affect Whooping Crane habitat selection, energetics, duration of stay, and survival is poorly known, but our spatial model can help to ensure that conservation and mitigation actions intended to benefit Whooping Cranes are located in areas with the greatest likelihood of use by Whooping Cranes.

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