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David M. Baasch
Executive Director's Office for the Platte River Recovery Implementation Program, baaschd@headwaterscorp.com

Patrick D. Farrell
Executive Director's Office for the Platte River Recovery Implementation Program, farrellp@headwaterscorp.com

Aaron T. Pearse
U.S. Geological Survey Northern Prairie Wildlife Research Center, apearse@usgs.gov

David A. Brandt
USGS Northern Prairie Wildlife Research Center, dbrandt@usgs.gov

Andrew J. Caven
Platte River Whooping Crane Maintenance Trust, acaven@cranetrust.org

See next page for additional authors

Authors
David M. Baasch, Patrick D. Farrell, Aaron T. Pearse, David A. Brandt, Andrew J. Caven, Mary J. Harner, Greg D. Wright, and Kristine L. Metzger

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Research Paper

Diurnal habitat selection of migrating Whooping Crane in the Great Plains

David M. Baasch[1], *Patrick D. Farrell*[1], *Aaron T. Pearse*[2], *David A. Brandt*[2], *Andrew J. Caven*[3], *Mary J. Harner*[3,4], *Greg D. Wright*[3,5] *and Kristine L. Metzger*[6]
[1]Executive Director's Office for the Platte River Recovery Implementation Program, [2]U.S. Geological Survey Northern Prairie Wildlife Research Center, [3]The Crane Trust, [4]University of Nebraska at Kearney, [5]United States Forest Service, [6]U.S. Fish and Wildlife Service

ABSTRACT. Available stopover habitats with quality foraging opportunities are essential for migrating waterbirds, including Whooping Crane (*Grus americana*). Several studies have evaluated habitats used by Whooping Crane for roosting throughout its migration corridor; however, habitats associated with foraging and other diurnal activities have received less attention. We used data collected from 42 Whooping Crane individuals that included 2169 diurnal use locations within 395 stopover sites evaluated during spring 2013 to fall 2015 to assess diurnal habitat selection throughout the U.S. portion of the migration corridor. We found that Whooping Crane selected wetland land-cover types (i.e., open water, riverine, and semipermanent wetlands) and lowland grasslands for diurnal activities over all other land-cover types that we evaluated, including croplands. Whooping Crane generally avoided roads, and avoidance varied based on land-cover class. There has been considerable alteration and destruction of natural wetlands and rivers that serve as roosting and foraging sites for migrating Whooping Crane. Given recent droughts and the likelihood of future landscape changes within the migration corridor, directing conservation efforts toward protecting and enhancing wetland stopover areas may prove critical for continued growth of the last remaining wild population of Whooping Crane. Future studies of this Whooping Crane population should focus on specific wetland complexes and riverine sites throughout the migration corridor to identify precise management actions that could be taken to enhance and protect these imperilled land-cover types.

Sélection de l'habitat diurne de la Grue blanche en migration dans les Grandes Plaines

RÉSUMÉ. Les habitats d'escale disponibles offrant des possibilités d'alimentation de qualité sont essentiels pour les oiseaux d'eau migrateurs, y compris la Grue blanche (*Grus americana*). Plusieurs études ont évalué les habitats utilisés par la Grue blanche pour se percher tout au long de son corridor de migration; cependant, les habitats associés à la recherche de nourriture et à d'autres activités diurnes ont reçu moins d'attention. Nous avons utilisé les données recueillies auprès de 42 individus de Grues blanches comprenant 2169 sites d'utilisation diurnes sur 395 sites d'escale entre le printemps 2013 et l'automne 2015 pour évaluer la sélection d'habitat diurne dans la partie américaine du corridor de migration. Nous avons constaté que la Grue blanche sélectionnait certains types de couvertures du sol dans les zones humides (c.-à-d. zones humides ouvertes, fluviales et semi-permanentes) et les prairies de basse altitude pour les activités diurnes par rapport à tout autres types de couverture terrestre que nous avons évalués, y compris les terres cultivées. La Grue blanche évitait généralement les routes et l'évitement variait selon le type de couverture terrestre. Les zones humides et les rivières naturelles qui servent de sites de repos et d'alimentation à la Grue blanche en migration ont été considérablement altérées et détruites. Compte tenu des récentes sécheresses et de la probabilité de futurs changements du paysage dans le corridor de migration, l'orientation des efforts de conservation vers la protection et l'amélioration des habitats d'escale dans les milieux humides pourrait s'avérer essentielle à la croissance continue de la dernière population sauvage de la Grue blanche. Les futures études de cette population de Grues blanches devraient se concentrer sur les complexes de zones humides et les sites fluviaux tout au long du corridor de migration afin d'identifier des mesures précises de gestion pouvant être prises pour améliorer et protéger ces types de couverture terrestre en péril.

Key Words: *diurnal; Grus americana; habitat management; habitat selection; Whooping Crane*

INTRODUCTION

Numerous bird species worldwide migrate biannually as a key part of their annual life cycle (Moore et al. 1995, National Research Council 2004, Zink 2011). The last remaining wild flock of Whooping Crane (*Grus americana*) makes an approximately 4000 km biannual migration between the coastal plain of Texas, USA, at and near Aransas National Wildlife Refuge, and Wood Buffalo National Park in Alberta and the Northwest Territories, Canada (Kuyt 1992, Pearse et al. 2018). During migration, stopover sites are essential because they provide places for resting and energy intake (Haig et al. 1998, Webb et al. 2010). The quality of available stopover sites likely influences the probability of survival during migration and body condition going into the breeding season (Myers 1983, Moore et al. 1995, Farmer and Parent 1997, Carey 2012). The quality of available stopover sites may be especially important for critically endangered, long-

Address of Correspondent: David M Baasch, 4111 4th Avenue, Suite 6, Kearney, NE USA 68845, baaschd@headwaterscorp.com

distance migrants such as the Whooping Crane because the survival of individuals maintains important genetic diversity and has disproportionate influence on the long-term population growth rate (Meine and Archibald 1996, CWS and USFWS 2007).

Since the mid-1900s, management of the federally endangered Whooping Crane has included research on major aspects of its annual cycle, including wintering and breeding grounds and, more recently, stopover sites during migration (Allen 1952, Hefley et al. 2015, Pearse et al. 2017*a,* 2018). Past research has identified major riverine systems and palustrine wetlands as important roosting habitats for migrating Whooping Crane (Faanes and Bowman 1992, Weddle 1996, Van Schmidt et al. 2014, Hefley et al. 2015). The Big Bend reach of the central Platte River in Nebraska, USA, has been the focus of several Whooping Crane studies, and recent management efforts have been directed at increasing the quantity and quality of riverine roosting sites for Whooping Crane after decades of degradation (Faanes and Bowman 1992, Stahlecker 1997, Davis 2003, Pfeiffer and Currier 2005, PRRIP 2017). Other studies have found wetlands throughout the migration corridor to be important habitats for Whooping Crane (Howe 1989, Armbruster 1990, Kuyt 1992, Austin and Richert 2001, 2005). However, in the classical sense of hierarchical habitat selection (Johnson 1980), Whooping Crane individuals make choices about: (1) where to stop, i.e., stopover site in general; (2) which locations to use within the stopover site; and (3) which resources to use after choosing the site. Whereas all of these decisions can have fitness consequences, the actual locations the Whooping Crane preferentially uses within a stopover site directly determine how local managers along the flyway need to think about stopover sites that they manage. This latter factor is our focus here.

Previous studies of stopover sites have predominantly relied on opportunistic observations of cranes during migration (e.g., Lingle et al. 1986, Faanes and Bowman 1992, Johns et al. 1997) or early tracking studies following a limited number of individuals and descriptively characterized stopover sites (Howe 1989, Kuyt 1992). Because of tracking study limitations, opportunistic observations have thus far provided the best information to evaluate stopover sites during migration because they encompass many crane observations over a long time period and large spatial extent (e.g., Austin and Richert 2001). However, opportunistic observations may lead to biases in results because of higher detection potential at more conspicuous stopover locations (Howe 1989, MacKenzie et al. 2002, Kéry and Schmidt 2008, Belaire et al. 2014, Hefley et al. 2015). For example, human population and road density have been found to increase the detectability of Whooping Crane during migration and provide strong evidence for unequal detection of individuals in the Whooping Crane population when using opportunistic information (Kéry 2011, Hefley et al. 2013, 2014, 2015, Lahoz-Monfort et al. 2014, Monk 2014). Additionally, assuming that cranes evaluate both positive (e.g., forage abundance) and negative (e.g., human disturbance) attributes when selecting use sites, individuals may only select sites near roads that are of higher relative quality to compensate for the increased disturbance level (Pearse et al. 2017*a,b*).

Because of the uncertainty in defining and identifying quality stopover habitat for the Aransas-Wood Buffalo population (AWBP) of Whooping Crane based on opportunistic sightings or limited information from past telemetry studies (Howe 1989), we initiated a field-based effort to characterize stopover sites distributed throughout a large portion of the Whooping Crane migration corridor. We sought to minimize observation bias introduced by opportunistic sighting data by using Global Positioning System (GPS) data collected at stopover sites identified through a large-scale satellite telemetry project that included a sample of 68 individuals (~20% of the AWBP) comprising all age classes (Pearse et al. 2018). We also used data collected through on-site evaluations of habitat conditions experienced by Whooping Crane during their use to define what was available. Other research efforts have used telemetry-based approaches to track Whooping Crane, which minimize observational bias (Howe 1989); however, detailed land-cover data were not collected at use locations. Our objective was to determine how land cover influences Whooping Crane diurnal habitat selection at stopover sites during migration. Our results add to the current knowledge of Whooping Crane habitat relationships and provide information about large-scale stopover habitat availability for Whooping Crane during migration based on systematically collected empirical data.

METHODS

Study area

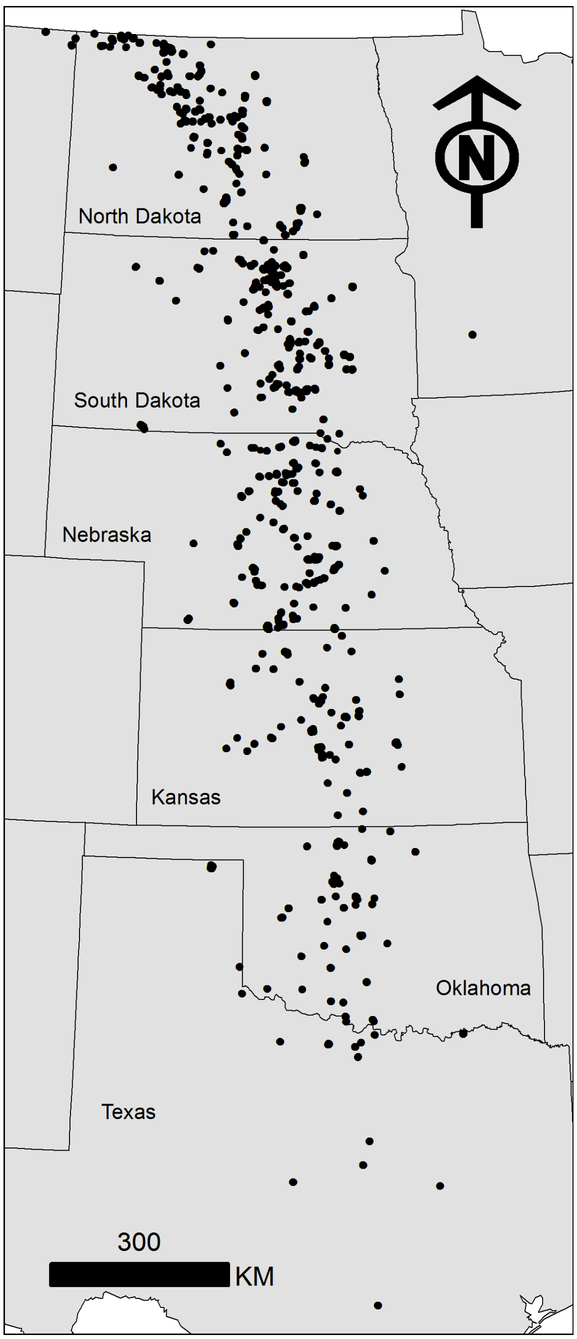
The Great Plains is an extensive grassland bioregion covering the central portions of the United States and Canada (Anderson 2006). Since European settlement in the 1800s, the region has experienced dramatic changes in land cover and use as it was transformed from primarily tall-, mixed-, and short-grass prairies to a mosaic of agricultural lands ranging from dryland farming, irrigated row crops, rangeland, and hay lands (Samson et al. 2010). Palustrine, lacustrine, and riverine wetlands exist throughout the region, most notably in the Prairie Pothole Region, Nebraska Sandhills, Rainwater Basin, and Playa Lakes Region (Tiner 1984). The AWBP migration corridor crosses the Great Plains south to north, and the center of the migration corridor generally bisects Texas, Oklahoma, Kansas, Nebraska, South Dakota, North Dakota, and Saskatchewan (Pearse et al. 2018). We focused field efforts on the U.S. portion of the migration corridor, primarily from northern North Dakota to central Texas (Fig. 1). We chose this area because it represents a diversity of landscapes encountered by the birds and is centered on the central Platte River, which is the only river segment designated as critical habitat for Whooping Crane. The central Platte River is the location of a large-scale species recovery program called the Platte River Recovery Implementation Program and was of primary interest in characterizing migration habitat for management and conservation.

Model development

We used location data from 42 Whooping Crane of all age classes that had been fitted with platform transmitting terminals with GPS capabilities (hereafter transmitters; North Star Science and Technology, Baltimore, Maryland, USA, and Geotrak, Apex, North Carolina, USA) between 2009 and 2014 (Pearse et al. 2015). Most locations from transmitters had a reported locational precision of < 26 m. In a separate test of locational accuracy, we found the median distance between a known location and the location retrieved from transmitters was 9 m (Pearse et al. 2017*a*).

Each transmitter was programmed to record four or five GPS locations daily at equal time intervals, which provided daytime and nighttime locations. This time interval was chosen to limit autocorrelation between successive locations. Location data were available from varying numbers of cranes fitted with telemetry equipment each migration season from 2013–2015. We used these data to identify stopover sites within the study area (Fig. 1).

Fig. 1. Map of the study area. Black dots indicate the evaluated stopover sites used by Whooping Crane, 2013–2015. Multiple use locations were evaluated within each stopover site.



We defined a stopover site as a collection of aggregated GPS locations in time and space that reflected that birds spent at least one night at the location before continuing migration. Spatially, we defined a stopover site as an area within a 1-km buffer surrounding clusters of stopover locations that included at least one nighttime location. If multiple transmitter-marked birds were present within a crane group at a stopover location, we only considered the bird with the most GPS locations within the stopover. If no one bird had more GPS locations, one location was randomly chosen, and others were discarded. We classified stopover sites as unique if birds moved > 15 km between consecutive nights, although we occasionally deviated from this rule based on whether a bird returned to a previous roost location during its stopover (Pearse et al. 2017*a*). We attempted to visit stopover sites within seven days after cranes were known to have left the area; however, we were unable to visit all stopover sites within this time frame for various reasons, including inability to contact landowners, denial of property access, logistical constraints, or other feasibility issues. The number of days between cranes departing stopover sites and field-based data collection efforts averaged 11 days (median = 10 days; Pearse et al. 2017*a*). Once on site, technicians collected data related to land use, land cover, and other physical and hydrological metrics (Pearse et al. 2017*a*).

We used field-based classifications of land cover potentially used by Whooping Crane and merged rare classes, as described below, which resulted in eight categories: corn field, wheat field, other agricultural field, open water lake or pond, riverine, semipermanent wetland, upland grassland, and lowland grassland. Other agricultural fields included alfalfa, canola, fallow ground, sorghum, milo, peas, sunflower, soybean, and unknown crops. Nonflowing water features and the surrounding shorelines were classified as open water lake or pond. Sites with flowing water and their associated features (e.g., sandbars) were included as riverine. Features with wetland characteristics (wetland plant community, saturated soils, etc.) that were without standing water were classified as semipermanent wetlands. Grasslands that were not periodically inundated or subirrigated were classified as upland grassland, and those that had features and plant communities indicative of periodic inundation or subirrigation were classified as lowland grassland (Tiner 2016).

For this study, we focused attention on diurnal (between 30 min before sunrise to 30 min after sunset) use locations and land-cover data that were classified within each 1-km stopover site. We used Hawth's Tools and ESRI ArcMap 9.3.1 to generate 20 random (available) locations within 1 km of each diurnal use location and classified all use and available locations by land-cover class. Because some features (e.g., wetlands) were not observable from roads, a detailed quality check of the data was performed using ESRI world imagery in ArcMap 10.4.1. Use ($N = 62$) and available ($N = 1471$) locations positioned within areas we were not able to access or otherwise did not identify the land-cover class were removed from the data set. We also removed locations that were within a wooded area, housing development, livestock feedlot, or on a road. Additionally, to reduce the influence of individual stopover sites on results, we randomly selected choice sets so that no stopover site contributed > 15% of use locations within any land-cover type. We used topologically integrated geographic encoding and referencing system (TIGER) road files to identify

Table 1. List of a priori models to explain variation in Whooping Crane diurnal habitat selection throughout the Great Plains. The hypotheses assume an a priori direction (positive or negative) in the relationship between Whooping Crane habitat use and the variables, but actual model fit, based on data, could have been in the opposite direction.

Model number	Variable combination[†]	Hypothesis
1	Land cover	Select specific land-cover classes
2	Distance to Major Road	Avoid major roads
3	Distance to Any Road	Avoid all roads
4	Land cover + Distance to Major Road	Select specific land-cover classes and avoid major roads
5	Land cover + Distance to Any Road	Select specific land-cover classes and avoid all roads
6	Land cover + Distance to Major Road + (Distance to Major Road)²	Select specific land-cover classes and avoid major roads; the avoidance of major roads is nonlinear
7	Land cover + Distance to Any Road + (Distance to Any Road)²	Select specific land-cover classes and avoid all roads; the avoidance of roads is nonlinear
8	Land cover : Distance to Major Road + (Distance to Major Road)²	Select specific land-cover classes and the avoidance of major roads varies by land cover and is nonlinear
9	Land cover : Distance to Any Road + (Distance to Any Road)²	Select specific land-cover classes and the avoidance of all roads varies by land cover and is nonlinear
10	Land cover : (Distance to Major Road)² + Distance to Major Road	Select specific land-cover classes and the avoidance of major roads varies by land cover and the nonlinear effect is land-cover specific
11	Land cover : Distance to Major Road + Landcover : (Distance to Major Road)²	
12	Land cover : (Distance to Any Road)² + Distance to Any Road	Select specific land-cover classes and the avoidance of all roads varies by land cover and the nonlinear effect is land-cover specific
13	Land cover : Distance to Any Road + Landcover : (Distance to Any Road)²	

[†]The ":" indicates an interaction between variables.

all roads within the study area. We used the spatial join tool in ArcGIS to calculate distance between each use and available location and the nearest major road (primary or secondary road within the TIGER system) as well as to the nearest road of any type. As defined by the TIGER system, primary roads are generally divided, limited-access highways within the interstate highway system or are under state management and are distinguished by the presence of interchanges; secondary roads are main arteries, usually in the U.S. Highway, State Highway, or County Highway system. Distances to nearest major road and any road were capped at 1600 m when no major road or any road, respectively, was located within 1600 m of the use or available location.

We developed a list of 13 candidate models with a priori habitat selection hypotheses, each containing combinations of and interactions between land cover, distance to any road, distance to major road, a quadratic effect of distance to any road, and a quadratic effect of distance to major road (Table 1). Resource selection functions were then developed to test hypotheses of Whooping Crane habitat selection by identifying nonrandom associations of individuals or groups of cranes to land-cover features at stopover sites (Cooper and Millspaugh 1999, Keating and Cherry 2004, Wiltermuth et al. 2015, PRRIP 2017). We contrasted characteristics at use locations with characteristics at randomly selected "available" locations within a 1-km buffer of the use location. We limited available locations to ≤ 1 km specifically to evaluate small-scale habitat selection within stopover sites throughout the migration corridor. To model habitat selection, a conditional logistic regression (i.e., discrete choice) model of resource selection was fit to the data, where use locations = 1 and associated available locations = 0 (Appendix 1). Conditional logistic regression or discrete-choice models enabled us to model habitat selection when the habitat availability changed both temporally and spatially (Ben-Akiva and Lerman 1985, Cooper and Millspaugh 1999, McDonald et al. 2006, Baasch et al. 2010). Conditional logistic regression models, with exact conditional likelihood, were developed using R statistical software (R Core Development Team 2016) and RStudio (RStudio Team 2015) using clogit models from the survival package in Program R (Gail et al. 1981, Logan 1983). This modeling technique provides population-average selection of land-cover characteristics available at Whooping Crane stopover sites, which are appropriate for making management decisions (Duchesne et al. 2010).

We used the Akaike Information Criterion (AIC) statistic to determine which a priori model was most useful in understanding diurnal habitat selection. The most parsimonious discrete choice model in the a priori list with ΔAIC ≤ 2.0 was used to infer

Table 2. Akaike Information Criterion (AIC) model selection results for diurnal habitat selection by Whooping Crane.

Model number	Model†	df	AIC	Δ AIC	W_i
9	Land cover : Distance to Any Road + (Distance to Any Road)²	16	10,356.36	0	0.83
12	Land cover : Distance to Any Road + Land cover : (Distance to Any Road)²	23	10,360.13	3.76	0.13
13	Land cover : (Distance to Any Road)² + Distance to Any Road	16	10,362.16	5.79	0.05
7	Land cover + Distance to Any Road + (Distance to Any Road)²	9	10,396.14	39.78	0
10	Land cover : (Distance to Major Road)² + Distance to Major Road	16	10,446.05	89.69	0
11	Land cover : Distance to Major Road + Land cover : (Distance to Major Road)²	23	10,448.05	91.68	0
8	Land cover : Distance to Major Road + (Distance to Major Road)²	16	10,452.20	95.84	0
5	Land cover + Distance to Any Road	8	10,456.80	100.44	0
6	Land cover + Distance to Major Road + (Distance to Major Road)²	9	10,481.52	125.16	0
1	Land cover	7	10,485.30	128.93	0
4	Land cover + Distance to Major Road	8	10,485.53	129.16	0
3	Distance to Any Road	1	12,198.17	1,841.81	0
2	Distance to Major Road	1	12,281.17	1,924.81	0

†The ":" indicates an interaction between variables.

conclusions about habitat selection (Burnham and Anderson 2002). We also calculated AIC weights to assist in the interpretation of AIC rankings. The AIC weights were calculated for each model as the proportion of the relative likelihood of the model to the sum of the relative likelihoods over the complete model set. After identifying the best model, we estimated the predicted relative selection ratios across the range of values observed in the data set. We provided a graphical display of the modeled relationships between the predictor variables (use-site characteristics) and the response (selection by Whooping Crane) in which relative selection ratios were constrained between 0 and 1.

Model validation

We used k-fold cross validation and partitioned the full data set into training and testing choice sets by randomly separating two-thirds, or 1384 choice sets, of the data into the training set, and one-third, or 691 choice sets, into the testing set (Boyce et al. 2002). The AIC-ranked top model based on all data was then populated with the training data choice sets to obtain model parameter estimates to predict relative resource selection for all training set locations (use and available) and testing data set use locations. Training and testing data sets were used to assess model performance using two methods as described in Appendix 2.

RESULTS

We included data collected from 42 of the 68 Whooping Crane individuals marked with telemetry equipment between 2009 and 2014. Some telemetry-marked birds were excluded for various reasons, including multiple transmitter-marked birds in a crane group, equipment failure, bird mortality prior to migration, and previously described logistical constraints that prevented access to use locations for some birds. From the 42 birds included in our study, we identified 2075 diurnal use locations with identifiable land-cover type within 395 stopover sites during spring 2013 to fall 2015 and used these locations in our analyses. Of the 42 individual cranes, no one crane contributed > 7% of locations. The first year of the study yielded the most use locations, and more locations were observed in spring than in fall each year. Whereas time spent migrating between the breeding and wintering grounds is typically longer in duration in the fall (Pearse et al. 2017*a*), the number of days telemetry-marked Whooping Crane individuals spent within the U.S. portion of the migration corridor during our study (2013–2015) was substantially fewer during fall (mean = 10.5, median = 8.5) than spring (mean = 20.5, median = 17.0; Platte River Recovery Implementation Program, *unpublished data*). There were 943 use locations collected during 2013 (686 spring and 257 fall locations), 624 during 2014 (497 spring and 127 fall locations), and 508 during 2015 (324 spring and 184 fall locations).

Diurnal habitat selection by Whooping Crane was found to be influenced by land-cover type and distance to road; however, avoidance of roads varied based on land-cover type (Tables 2 and 3, Fig. 2, Appendix 1). At 200 m from any road, all water-based land-cover types (river, open water, and semipermanent wetlands) were estimated to be at least three times as likely and lowland grassland was more than twice as likely to be selected as diurnal use sites than other nonwater-based land-cover types (upland grass, corn, wheat, and other agriculture; Fig. 3). Corn was more than three times as likely to be selected at 1 km compared to 200 m, whereas open water and river were similarly selected at 200 m and 1 km (Fig. 3). Semipermanent wetland was the only exception to the pattern of water-based land-cover types, and distance to road had the biggest influence on the relative selection ratio within semipermanent wetland features. Semipermanent wetlands were almost three times as likely to be selected at 1 km compared to 200 m, whereas lowland grasslands had similar selection at distances of 200 m and 1 km from any road (Fig. 3).

For method 1 model validation, 55% of iterations indicated acceptable or good model fit; however, model fit varied by land-cover class (Table 4). For method 2 model validation, 93% of iterations indicated adequate or good model fit.

Table 3. Variable estimates in the top discrete choice model to describe diurnal habitat selection by migrating Whooping Crane.

Variable[†]	Coefficient	Exp(B)	Standard error(B)	Lower confidence limit	Upper confidence limit	*Z*	*P*
Open water	2.5332	12.5943	0.1549	9.2974	17.0603	16.3592	< 0.0001
Riverine	2.3538	10.5255	0.2288	6.7222	16.4807	10.2890	< 0.0001
Semipermanent wetland	1.4156	4.1188	0.2247	2.6515	6.3983	6.2991	< 0.0001
Wheat field	0.1564	1.1692	0.1640	0.8478	1.6126	0.9533	0.3404
Other agriculture	-0.4536	0.6353	0.2084	0.4222	0.9559	−2.1765	0.0295
Lowland grassland	1.0740	2.9270	0.1883	2.0237	4.2335	5.7038	< 0.0001
Upland grassland	−1.0301	0.3570	0.1792	0.2512	0.5072	−5.7469	< 0.0001
Distance to any road	0.3167	1.3726	0.0311	1.2915	1.4588	10.1948	< 0.0001
Distance to any road (quadratic)	−0.0136	0.9865	0.0020	0.9827	0.9904	−6.8158	< 0.0001
Open water : Distance to any road	−0.1626	0.8499	0.0273	0.8057	0.8966	−5.9615	< 0.0001
Riverine : Distance to any road	−0.1883	0.8284	0.0380	0.7689	0.8924	−4.9560	< 0.0001
Semipermanent wetland : Distance to any road	−0.0368	0.9639	0.0332	0.9032	1.0286	−1.1088	0.2675
Wheat field : Distance to any road	−0.0574	0.9442	0.0298	0.8907	1.0010	−1.9273	0.0539
Other agriculture : Distance to any road	−0.1680	0.8454	0.0504	0.7659	0.9331	−3.3344	0.0009
Lowland grassland : Distance to any road	−0.1402	0.8692	0.0342	0.8128	0.9295	−4.0981	< 0.0001
Upland grassland : Distance to any road	−0.1218	0.8853	0.0294	0.8358	0.9378	−4.1471	< 0.0001

[†]The “:” indicates an interaction between variables.

Table 4. Model validation results based on 1000 iterations of cross validation using the top diurnal habitat selection model.

Land-cover type	Number of sampling iterations	Number of “good” or “adequate” validation iterations	Percent “good” or “adequate” validation iterations
Open water	1000	429	43
Riverine	1000	915	92
Semipermanent wetland	1000	891	89
Corn field	1000	880	88
Wheat field	1000	47	5
Other agriculture	1000	211	21
Lowland grassland	1000	873	87
Upland grassland	1000	156	16

DISCUSSION

Out of necessity, many past Whooping Crane studies focused on small geographical scales, and Nebraska has been the focus of several habitat selection studies (USFWS 1981, Shenk and Armbruster 1986, Armbruster 1990, Biology Workgroup 1990, Lingle et al. 1991, Richert 1999, Stahlecker 1997, Hefley et al. 2013, 2014, 2015, Howlin and Nasman 2017). Although these state- or location-specific habitat selection studies have been useful, a broader understanding of habitat selection throughout the migration corridor will help Whooping Crane management efforts across a greater extent of the migratory range.

Availability of water is an inherent requirement for Whooping Crane, and several general characteristics such as palustrine and lacustrine wetlands and riverine land-cover types for roosting are common among Whooping Crane stopover sites (Howe 1989, Austin and Richert 2001, Belaire et al. 2014, Howlin and Nasman 2017, PRRIP 2017, Niemuth et al. 2018). Whooping Crane uses shallow water features as nocturnal roosting habitat during migration (Howe 1989, Austin and Richert 2001). Similarly, we found that Whooping Crane was more than three times as likely to select the types of wetland features (open water, riverine, and semipermanent wetlands) we evaluated for foraging and resting during diurnal hours over all upland land-cover types within the stopover sites during migration. As has been found in other studies, areas with intermediate to high wetland (i.e., riverine, open water, and semipermanent wetlands) coverage and a low density of roads had higher predicted relative probabilities of use for diurnal use by Whooping Crane (USFWS 1981, Belaire et al. 2014, Hefley et al. 2015, Howlin and Nasman 2017). Whooping Crane avoided areas within 400 m of disturbance features such as roads along the central Platte River (Howlin and Nasman 2017). However, water-based land-cover types appeared to be perceived by Whooping Crane as more secure compared to upland areas (USFWS 1981) because selection ratios within open water and riverine land-cover types were similar at 200 m and 1 km, whereas selection generally increased in other land-cover classes. Habitat quality or activities (foraging, roosting, resting, etc.) associated with water-based land-cover classes may decrease the aversion of roads and other disturbance features on the landscape, whereas activities within other land-cover classes may increase alertness and aversion to roads. Pearse et al. (2017*b*) demonstrated that Sandhill Crane (*Antigone canadensis*) is less sensitive to disturbance in higher quality roosting habitat that has lower bank vegetation and wider channels within the central Platte River. It is possible that North American Gruidae species perceive greater

Fig. 2. Land-cover specific relative selection ratios and 95% confidence intervals for Whooping Crane throughout the migration corridor in relation to proximity of roads. Plots are displayed between the minimum and maximum distances to roads observed at use locations within each land-cover class. Numbers of use locations within each land-cover class are indicated in parentheses.

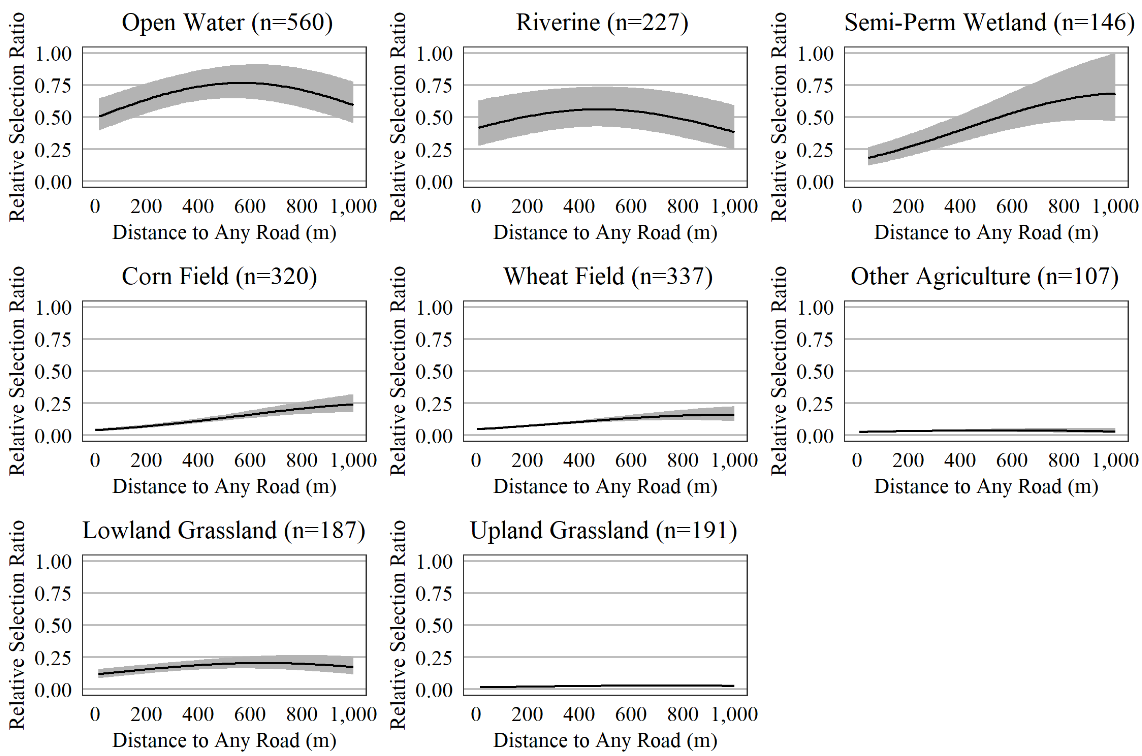
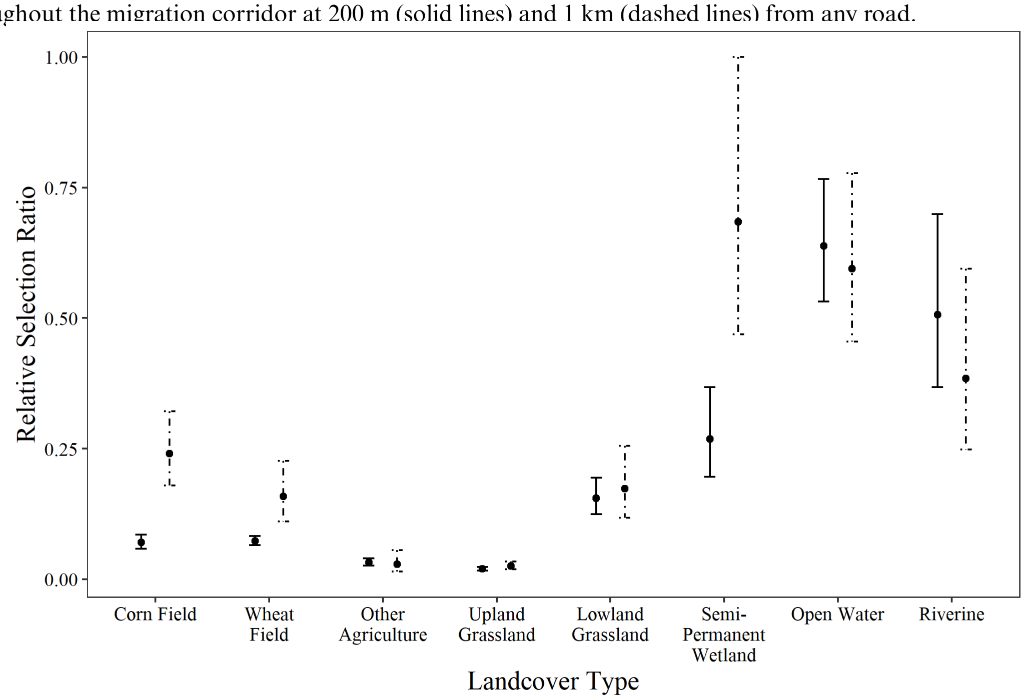


Fig. 3. Land-cover specific relative selection ratios and 95% confidence intervals for Whooping Crane throughout the migration corridor at 200 m (solid lines) and 1 km (dashed lines) from any road.



levels of security in wetland land-cover types. Although we did not directly observe or study foraging behaviors, the potential benefit of food resources or security provided by wetlands may be attractive enough to tolerate or mitigate the risk of some level of human disturbance.

Whooping Crane uses a variety of land-cover types during migration in the Great Plains. Crop fields are likely used for gathering high-energy foods in the form of grains, whereas wetland and lowland grassland use suggests a more diverse resource need: water, protein, and energy. Although Whooping Crane uses a variety of land-cover types during migration, certain land-cover types appear to be more attractive to cranes (Howe 1987, 1989, Lingle 1987, Lingle et al. 1991, Johns et al. 1997). In most Canadian provinces and U.S. states, excluding Nebraska, Whooping Crane primarily uses shallow, seasonally and semipermanently flooded, palustrine wetlands for roosting, and various emergent wetlands for feeding (Johns et al. 1997, Austin and Richert 2001). Johnson and Temple (1980) evaluated wetlands reportedly used by foraging Whooping Crane and reported that Whooping Crane is found in wetlands, ephemeral ponds, and man-made reservoirs. In Nebraska, however, sand-bed rivers are commonly used (Austin and Richert 2005). Howlin and Nasman (2017) report that Whooping Crane select in-channel riverine sites and corn fields at greater relative rates than upland grassland, soybean, and lowland grassland fields along the central Platte River in Nebraska. We found that Whooping Crane was equally likely to use wheat fields as corn fields and was less likely to use other agriculture fields and upland grasslands. When evaluated at 200 m from a road, lowland grassland was the only nonwetland land-cover type substantially more likely to be selected for use than corn fields. This result may be because wetland systems in the Great Plains often exist on an elevation gradient where lowland grasslands integrate into wetlands with saturated soils such as wet meadows and semipermanent wetlands dominated by moist soils or aquatic emergent vegetation (Tiner 1984, 2016, Henszey et al. 2004, Whiles et al. 2010). The area of interface between open water and emergent wetlands, i.e., the littoral zone, is highly biologically productive and fluctuates widely within braided river floodplains (Junk et al. 1989). Littoral zones are important foraging areas for waterbirds (Chastant and Gawlik 2018). It is possible that mesic portions of lowland grasslands, which can include littoral components on the margins of rivers and semipermanent wetlands as well as subirrigated wetlands such as wet meadows, provide important food sources for Whooping Crane during migration. Research from along the Big Bend of the Platte River suggests that Sandhill Crane spends a significantly higher proportion of its time foraging in lowland grassland land-cover types compared to their proportional availability, potentially because corn does not adequately meet its physiological needs in terms of nutrients (Sparling and Krapu 1994). However, lowland grasslands, and wetlands broadly, have experienced substantial losses and degradation because of agricultural expansion and intensive grazing strategies (WWFC 1988, Sidle et al. 1989, Noss et al. 1995, Ricketts et al. 1999, Samson and Knopf 1994, Samson et al. 2010).

Our results indicate that wetlands are an integral part of Whooping Crane migration habitat needs, which is supported by the notion that it selects landscapes with diverse wetland features (Niemuth et al. 2018). However, there has been considerable alteration of the natural wetlands, rivers, and streams (Myers 1983, Tiner 1984, Farmer and Parent 1997, Samson et al. 2010) that serve as potential roosting and foraging sites for migrating Whooping Crane. Given recent droughts, the uncertainty associated with climate change, and the likelihood of future land-use changes within the migration corridor, directing conservation efforts toward protecting wetland stopover habitat may prove critical (Myers 1983, Haig et al. 1998, Johnson et al. 2010). Wetland losses from development and drought associated with global climate change pose an additive risk to both wetland connectivity and wildlife migration broadly, limiting the ability of many species, potentially including Whooping Crane, to respond to environmental conditions (Opdam and Wascher 2004, McIntyre et al. 2014). As quality habitat patches are lost and accessibility declines, Whooping Crane may be constrained to settle in suboptimal habitats or migrate farther each day to locate suitable stopover sites.

Identification and protection of stopover habitat along the migratory route is an important aspect for recovering the endangered Whooping Crane (Meine and Archibald 1996, CWS and USFWS 2007). Although we examined wetland (i.e., open water, riverine, and semipermanent wetlands) use and coverage, we did not evaluate wetland quality in our assessments, which could be an important consideration in future research (Shaw and Fredine 1956). Future studies of the AWBP of Whooping Crane should focus on wetland land-cover classes throughout the migration corridor to precisely identify management actions that could be taken to protect or even enhance these imperiled land-cover types. Protection of suitable migratory stopover habitat and reduction of crane mortality are critical for the continued growth of the last remaining wild population of Whooping Crane.

Responses to this article can be read online at:
http://www.ace-eco.org/issues/responses.php/1317

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The discrete choice model was described as (McDonald et al. 2006):

$$\hat{P}(i) = \frac{\exp(\beta_1 x_{i1} + \beta_2 x_{i2} + \cdots + \beta_p x_{ip})}{\sum_{k \in \{U' \cup A\}} \exp(\beta_1 x_{k1} + \beta_2 x_{k2} + \cdots + \beta_p x_{kp})},$$

where $\hat{P}$ was an estimate of relative selection ratios for resource unit i; x_{ij} were habitat variables; $\beta_1 - \beta_p$ were coefficients of habitat variables; U' were unique location indices; and A was the set of indices for available locations in the choice set. Based on the top model results, each location (i) in our dataset had a estimated relative selection ratio $\hat{P}$ given by the above equation, where β_1 = 2.516, β_2 = 2.317, β_3 = 1.618, β_4 = 0.128, β_5 = -0.486, β_6 = 1.018, β_7 = -0.956, β_8 = 0.0033, β_9 = -0.000002, β_{10} = -0.0015, β_{11} = -0.0017, β_{12} = -0.0012, β_{13} = -0.0005, β_{14} = -0.0016, β_{15} = -0.0012, β_{16} = -0.0012. Variables x_{i1}-x_{i7} are 7 of 8 categorical landcover types, where corn field was the reference with a β-value of zero. Variable x_{i8} was the continuous distance to road measures and x_{i9}-x_{i16} was the continuous distance to road measure interaction with each landcover type as described in Table 3.

APPENDIX 2. Methods used to validate our final discrete-choice model.
Two methods were used to validate our final model. For method 1, we followed the sample validation methods outlined by Howlin et al. (2004). However, unlike Howlin et al. (2004) our final model had a categorical variable, landcover, so we performed the following methods eight times, once for each landcover class. We partitioned the data into eight landcover-specific groups to assess how well the model performed with respect to distance to road for each landcover type. For each landcover-specific set of data (use and available locations) we parsed the data into 10 bins so that 10% of the landcover-specific locations (use and available) within the training dataset fell within each bin. We then identified relative selection ratio cutoffs for each bin. In other words, bin associations were based on predicted relative selection ratios where bin one contained all landcover-specific use and available locations with the lowest 10% of predicted relative selection ratios and bin ten contained all landcover-specific use and available locations with the highest 10% of predicted relative selection ratios. We then calculated the proportion of landcover-specific use locations within the training dataset that fell within each bin. Next, we used the model developed using our training dataset to calculate relative selection ratios for landcover-specific use locations within the testing dataset. We binned the landcover-specific use locations based on the relative selection ratio cutoffs identified using the training dataset and determined the proportion of landcover-specific use locations within the testing dataset that were within each bin. Finally, we used a simple linear regression to assess model fit where the proportion of landcover-specific use locations within each bin in the testing dataset was compared to the proportion of landcover-specific use locations within each bin from the training dataset. Ideal model performance would produce a simple linear regression line with a slope of 1 and intercept of 0 (Howlin et al. 2004). When 95% confidence intervals of the regression line slope included 1 and excluded zero, the model fit was deemed "good", "acceptable" if not including 1 or 0, and "unacceptable" if including 0 (Howlin et al. 2004). This process was repeated 1,000 times to assess the percent of iterations in which model performance was deemed "good", "acceptable", and "unacceptable" for each landcover type. These methods were repeated eight times, once for each landcover class, which allowed us to assess how the model performed with respect to distance to road for each landcover type.

For method 2, we followed the sample validation methods outlined by Howlin et al. (2004) and landcover types were evaluated together to assess the overall ability of the model to predict the relative probability of use given landcover type and distance to road. For method 2, we used the same techniques as were outlined for method 1 with two exceptions. First, we did not partition data by landcover type. Secondly, given we had much more data (i.e., all data was evaluated together rather than separated by landcover type) we partitioned the datasets into 40 bins to use in our simple linear regression model to assess overall model fit.