INLAND HABITAT SELECTION MODEL FOR WINTERING WHOOPING CRANES

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Abstract: Inland habitat use by wintering Aransas-Wood Buffalo whooping cranes (*Grus americana*) is expected to increase given projected population growth and observations of some whooping cranes using inland winter habitat in addition to coastal marshes. We developed resource utilization functions using 'random forests' to model whooping crane use as a function of environmental covariates considered important for whooping crane use. Covariates associated with distance to cropland, distance to development, and wetness or standing water were the most influential in model prediction. The model estimated that the 50% predicted use contour encompassed 34,925 hectares (ha) and the 95% predicted use contour encompassed 328,928 ha within the study area. While presently limited by the small sample size of inland wintering areas observations (n = 7 cranes with \geq 50 locations), this model provides an initial tool for identifying potential effects to whooping crane inland habitat use in proximity to anthropogenic development. The model can be expanded to incorporate future data to reduce uncertainty.

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The Aransas-Wood Buffalo population (AWBP) of the whooping crane (Grus americana) winters primarily near wetlands on the Texas coast at the Aransas National Wildlife Refuge and surrounding areas (Allen 1952, Stehn and Prieto 2010, Metzger et al. 2020). The AWBP has increased from <20 birds in 1941 (Allen 1952) to an estimated 536 in the winter of 2022-23 (95% confidence interval = 443.5-644.1) within the primary survey area (Butler et al. 2023). Although overwintering habitat use is heavily concentrated in coastal areas (Stehn and Prieto 2010, Metzger et al. 2020), the wintering range along coastal marshes has been expanding and inland habitat use away from the primary survey area on wintering grounds has been documented (Wright et al. 2014, Jung et al. 2022, Butler et al. 2023, Crouch et al. 2024). Across 2011-2021 winters, 6 cranes were documented spending 3.1-99.3% of their winter in inland habitat (i.e., latitudes \geq 29.0 and longitudes \leq -95.5) within Colorado and Wharton counties and Granger Lake (Crouch et al. 2024). The use of these inland habitats does not represent shortstopping (shortening their total migration distance; Elmberg et al. 2014) as cranes were documented using both traditional coastal areas and inland habitat (Crouch et al. 2024).

Increased inland habitat use may place whooping cranes closer to anthropogenic land use, increasing the potential for disturbance and collision risk. In addition, new development may increase the potential for cranes to experience or be affected by habitat loss and fragmentation. Given projections of continued population growth (Traylor-Holzer 2019) and observations that inland habitat use away from the primary wintering grounds is increasing (Butler et al. 2022, 2023; Crouch et al. 2024), it is hypothesized that inland habitat use will continue to increase in the future. However, it is unknown to what extent individuals will expand their coastal or inland wintering ranges. Therefore, a model describing inland habitat use outside the primary wintering grounds can be helpful to identify potential use areas that can serve as expanded wintering habitat for whooping cranes. Although inland habitat use by wintering whooping cranes has been documented in Granger Lake (Crouch et al. 2024), Granger Lake is within the 50% core area of the whooping crane migration corridor (Pearse et al. 2018) approximately 235 km from the U.S. Fish and Wildlife Service (USFWS) defined wintering range, and thus, not included in our study. The primary objectives of this research were to develop a demonstration of concept model that generated landscape-level predictions of relative probability of use of inland habitat near coastal Texas by wintering whooping cranes, and to provide preliminary information about the development of this model. We used resource utilization functions (RUF) to model habitat

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relationships and predict space use of wintering whooping cranes (Millspaugh et al. 2006, Winder et al. 2014, Eckrich et al. 2020). We expect this model to provide preliminary insight into areas where potential effects from anthropogenic development could occur.

STUDY AREA

The inland winter habitat study area was defined as all portions of the Southern Subhumid Gulf Coastal Prairies and Northern Humid Gulf Coastal Prairies (Environmental Protection Agency Level IV Ecoregions) located west of Galveston Bay and north of Baffin Bay in Texas (U.S. Environmental Protection Agency [USEPA] 2012; Fig.1). Most of the coastal prairies within these ecoregions have been converted to cropland, pasture, or urban land uses (USEPA 2012). All areas ≤ 2 km from salt marsh (Texas

Ecological Mapping Systems [Elliot et al. 2009-2014]) were excluded as these areas consisted of coastal portions of the wintering range which were unlikely to inform selection of inland habitats. The study area encompassed 2,689,324 ha.

METHODS

We compiled a set of environmental spatial data layers considered to be important for whooping crane habitat use as predictor variables in the RUF modeling, including land cover, terrain, and selected satellite imagery (Hunt and Slack 1989, Chavez-Ramirez 1996, Westwood and Chavez-Ramirez 2005, Niemuth et al. 2018, Metzger et al. 2020, Urbanek and Lewis 2020; Table 1).



Figure 1. Inland winter habitat study area for the resource utilization function model in relation to the wintering range of whooping cranes as defined by the U.S. Fish and Wildlife Service and the Aransas National Wildlife Refuge, Texas, USA.

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Table 1. List of environmental covariates used to predict whooping crane winter use and the spatial scales considered in resource utilization function modeling. Covariates include, among others, Digital Elevation Model (DEM), Ecological Mapping Systems (EMS), Normalized Difference Built-up Index (NDBI), Normalized Difference Vegetation Index (NDVI), Modified Normalized Difference Water Index (MNDWI), Topographic Position Index (TPI), and U.S. Fish and Wildlife Service (USFWS), along with different National Land Cover Database (NLCD) classes from the Multi-Resolution Land Characteristics Consortium (MRLC). The spatial scale is presented in meters. Sources for the data include NLCD, U.S. Census Bureau (USCB), USFWS National Wetlands Inventory (NWI), U.S. Geological Survey (USGS), and others.

Covariate	Description	Spatial scales	Source	
NLCD cropland	Cropland (NLCD class cultivated 270 m, 1200 m crops), taken as a proportion of land cover		Yang et al. 2018, MRLC 2019	
NLCD forest	Forest (NLCD class deciduous forest, evergreen forest, or mixed forest), taken as a proportion of land cover	270m, 1200 m	Yang et al. 2018, MRLC 2019	
NLCD grassland	Grassland (NLCD class 270 m, 1200 m herbaceous, hay/pasture, and developed: open space), taken as a proportion of land cover		Yang et al. 2018, MRLC 2019	
NLCD shrubland	Shrubland (NLCD class shrub/ scrub), taken as a proportion of land cover	270 m, 1200 m	Yang et al. 2018, MRLC 2019	
NLCD developed	Developed (NLCD class developed 270 m, 1200 m low, medium, high intensity), taken as a proportion of land cover		Yang et al. 2018, MRLC 2019	
EMS salt marsh	Proportion of salt marsh land cover	270 m, 1200 m	Elliott et al. 2009-2014	
Wetlands proportion	Proportion of wetland cover	270m, 1200 m	USFWS NWI 2020	
Wetlands count	Count of individual wetlands	270 m, 1200 m	USFWS NWI 2020	
Wetlands distance	Distance to nearest wetland	NAª	USFWS NWI 2020	
Cropland distance	nce Distance to nearest cropland		Yang et al. 2018, MRLC 2019	
Road distance	Distance to primary/secondary NA ^a roads from 2017 TIGER/Line		USCB 2017	
Road density	Density of primary/secondary roads from 2017 TIGER/Line	1200-m	USCB 2017	
DEM roughness	Standard deviation of elevation	1200-m	USGS 2011	
TPI	Elevation value minus average elevation within 1200-m square	1200-m	Weiss 2001, Wilson et al. 2007	
MNDWI	MNDWI	270-m, 1200-m	USGS 2016	
NDBI	NDBI	270-m, 1200-m	USGS 2016	
NDVI	NDVI	270-m, 1200-m	USGS 2016	

^aNot applicable.

These environmental covariates were acquired at a 30-m spatial resolution. The focal statistic for each covariate was then processed using moving windows at 2 spatial scales: 9×9 m (270 m) and 40×40 m (1,200 m). Metzger et al. (2020) used 250 m in their analyses, but because our covariates were at 30-m resolution, we used 270 m. In Niemuth et al. (2018), relative probability of occurrence models were best supported using data from a moving window with a 1,200-m radius relative to 800- and 1,600-m windows. The 30-m grid cells were then aggregated up to a 250-m scale for RUF predictions.

Whooping crane location data between December 2009 and November 2018 were acquired from Pearse et al. (2020). These cranes were monitored with legmounted transmitters that obtained locations via the global positioning system (GPS) network and transmitted 4-6 locations daily for each crane via the Argos satellite system. Pearse et al. (2020) provided detailed descriptions of capture and marking procedures, transmitter design and function, and permits authorizing whooping crane capture and marking. We also used data from inland winter whooping cranes between 2017 and 2023 (Pearse et al. 2024). These cranes were fitted with Global System for Mobile Communications (GSM) transmitters using third and fourth generation cellular networks which provided locations every 15 minutes (Ornitela, Vilnius, Lithuania). To exclude migrating birds, locations were filtered to include only locations of wintering cranes, when cranes were on the ground (instantaneous speeds ≤ 5 km per hour). Wintering birds were those that occurred within the ANWR or counties near the Texas coast or, if telemetered, those remaining at a southern terminus for >3 weeks. We restricted our data to cranes with \geq 50 locations within the study area. Fifty was chosen as a threshold to minimize including locations of incidental habitat use within the study area, produce a biologically defensible utilization distribution, and allow for incorporation of future data into the model.

For each individual whooping crane included in modeling, we computed a utilization distribution (UD) to quantify space use intensity using kernel density estimation and the plug-in bandwidth estimation method (Wand and Jones 1995, Millspaugh et al 2006). All individual whooping crane UDs were generated at a 250-m spatial resolution and scaled to sum to 1.0. To avoid spatial-autocorrelation and overfitting in RUF modeling, we subsampled response (UD height) and predictor (environmental covariate) values from the 250-m resolution rasters using a 1-km point grid. For model training, the resulting datasets consisted of a 1-km point grid with 19,458 points.

Random forests were used to predict whooping crane spatial use as a function of the environmental covariates. Random forests are a machine learning technique that inherently accounts for non-linear habitat relationships and covariate interactions (Breiman 2001). This predictive model indicates which covariates are most influential in allowing accurate prediction of spatial use but does not describe the direction of relationships between covariates and spatial use. To facilitate model interpretation and reduce computation time, we limited the number of covariates considered in the random forests by including only a single spatial scale for each covariate in the model. For each covariate we calculated a Pearson's correlation between the covariate and the response (UD height) and excluded the spatial scale with the lowest correlation.

A random forest regression model was fit with 1,000 trees using the *randomForest* package (4.6-14; Liaw and Wiener 2002) in R Version 4.1.0 (R Core Team 2021). The regression value of p/3 was used for *mtry* (number of candidate variables considered in each split), where p is the number of predictor variables, resulting in an *mtry* value of 6. The variable importance of each predictor covariate was assessed by quantifying the percent increase in model error (mean square error) that occurred when the values of a given covariate were randomly permuted (Breiman 2001). Variables resulting in the largest increase in mean square error after random permutation were interpreted as more important for predictive power in the model.

To generate a prediction of whooping crane habitat use throughout the study area, we created a combined UD by summing the scaled UDs for each crane and fit the random forest model across all cranes. To assess the predictive accuracy and fit of the RUF model, we divided the UD predictions into 20 equal-area bins to compare to the combined location data from birds with <50 locations (n = 22) for use as validation locations. We calculated the observed and predicted proportion of these validation locations occurring in each bin and computed the Spearman rank correlation between the observed and prediction proportions.

Predicted use contours were then calculated by converting the raw RUF predictions into volume UD rasters that delineate the area expected to contain a given percentage of habitat use (e.g., a 95% use area). To assess the fit of the RUF model across volume contours, we calculated the observed proportion of validation locations that occurred within the 25, 50, 75, 95, and 99 predicted percent use contours.

RESULTS

Twenty-two wintering whooping cranes had at least 1 collected location within our study area (Table 2). Of these, 7 had \geq 50 locations and were observed between 7 and 407 unique days in the study area. Variables resulting in the largest increase in mean square error after random permutation were identified as having the greatest predictive power to the model. The covariates with the largest increase in mean square error after permutation included distance to cropland, distance to development, measures of urban development (Normalized Difference Built-up Index) within 1,200 m, and measures of wetness or standing water (Modified Normalized Difference Water Index) within 270 m (Fig. 2).



Figure 2. Final covariates used in the resource utilization function model fit showing variable importance (percent increase in mean squared error [MSE] when variable is permuted).

BirdID	First date observed	Last date observed	Number of locations	Number of unique days	Number of unique weeks
15E	27 Oct 2019	2 Jan 2023	39,120	407	69
D24	22 Nov 2012	29 Dec 2013	426	123	21
5A	7 Feb 2018	8 Mar 2018	964	23	5
14E	20 Nov 2021	22 Dec 2022	659	22	6
11G	24 Nov 2022	14 Dec 2022	1,582	20	4
4H	20 Oct 2022	12 Nov 2022	593	12	4
1J	26 Nov 2022	22 Dec 2022	99	7	3
12G	17 Mar 2022	18 Mar 2022	4	2	1
2Н	17 Mar 2022	18 Mar 2022	3	2	1
A01	5 Feb 2010	31 Oct 2010	3	2	2
B04	16 Nov 2011	20 Nov 2011	2	2	2
11E	29 Oct 2020	29 Oct 2020	14	1	1
A02	16 Mar 2011	16 Mar 2011	1	1	1
B01	18 Feb 2011	18 Feb 2011	1	1	1
C04	8 Jan 2012	8 Jan 2012	1	1	1
C12	2 Apr 2014	2 Apr 2014	1	1	1
C15	28 Dec 2013	28 Dec 2013	1	1	1
C16	8 Dec 2011	8 Dec 2011	1	1	1
C99	1 Mar 2012	1 Mar 2012	1	1	1
D26	18 Oct 2013	18 Oct 2013	1	1	1
D42	22 Feb 2013	22 Feb 2013	1	1	1
E52	5 Jan 2015	5 Jan 2015	1	1	1

Table 2. Summary of w	ooping crane	Global Positio	ning System	s locations for each bir	l (BirdID	D) that occurred	ed within the study	y area
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Table 3. Comparison of resource utilization function-predicted use volume contours and observed percentages of whooping crane validation locations occurring in each contour.

Predicted contour	Observed percent of validation locations		
25	10.8		
50	31.8		
75	64.1		
95	93.9		
99	96.1		

Within the 20 equal area bins, the predicted RUF model fit the observed validation locations well with a Spearman's rank correlation of 0.858. Within the predicted percent use counters, the RUF model underpredicted use in the area of greatest predicted occurrence (25% predicted use contour) and over-predicted use in areas of lowest predicted occurrence (95% and 99% predicted use contours; Table 3). These results indicate use in the validation dataset was more concentrated in the 25% predicted use contour than expected by the model. The model predicted spatial use concentrated in Wharton and Colorado counties and to a lesser degree portions of eastern Brazoria and southern Galveston counties (Fig. 3). The model further estimated 50% of use was within approximately 34,925 ha (50% use contour), whereas the 75% and 95% contours encompassed 92,625 and 328,928 ha, respectively.

DISCUSSION

Our results provide an initial demonstration of concept starting point for inland habitat predicted areas of use between the migration corridor and the traditional overwintering habitat within and near Aransas National Wildlife Refuge. The model identified portions of southern Colorado and western Wharton counties as relatively high-use inland wintering habitat. While variables associated with cropland, development, and wetness or standing water were interpreted to have the greatest importance in accurately predicting inland winter habitat use, this model predicts areas of use, rather than describing the characteristics of the habitat used. Therefore, in addition to increasing data inputs, future work could use the model's predicted areas of use to characterize and quantify availability of suitable whooping crane habitat, which can then be compared to traditional coastal wintering habitat and stopover



Figure 3. Predicted inland winter habitat use based on the combined models of 7 cranes with more than 50 locations within the study area. Predicted utilization volume contours indicate expected habitat use; for example, 75% of habitat use is expected to occur within the combined bins of 0-50 and 51-75.

locations in the southern portion of the flyway.

The validity of model predictions is dependent on the quality of the input datasets. Although the predicted RUF models fit validation locations well and predicted rates of use were reflective of past use patterns of the GPS-telemetered whooping cranes from 2009 through 2022, model predictions are limited by the small sample size of available observations at inland wintering areas. While location data for 1 bird (15E) composed approximately 90% of location data, a utilization distribution for each bird was combined and scaled so that each individual had equal weight in the random forest model regardless of the number of locations. These data currently provide the best available information on inland habitat use for this species, yet it is possible these 7 birds may not be representative of future inland wintering habitat use by whooping cranes.

Currently, whether the increased use of inland

wintering habitat represents either a temporary or permanent shift or an expansion in the AWBP wintering grounds is unknown. These changes are not likely due to AWBP coastal wintering grounds reaching the estimated carrying capacity of 4,414 cranes (Metzger et al. 2020), as current population estimates are well below this estimate (Butler et al. 2023). Current use could be indicative of exploratory movements as whooping cranes that use inland wintering habitat have larger home ranges and greater daily movements than cranes that stay in the coastal wintering habitat (Crouch et al. 2024). Additionally, in our model's predicted high-use inland wintering habitat in Colorado and Wharton counties, whooping cranes occurred primarily in dry and flooded agricultural fields (Butler et al. 2022, 2023; Crouch et al. 2024). A similar shift from natural wetlands towards agricultural areas occurred in wintering Siberian cranes (G. leucogeranus) after their predominant food source declined due to the increased frequency of both floods and drought (Hou et al. 2020, Shao et al. 2024). Continued use of Colorado and Wharton counties by an individual across different age classes (juvenile in a family group to subadult) also indicates the potential for learned use of these areas (Crouch et al. 2024).

Predicting patterns of future habitat use for a species undergoing population growth and range expansion is challenging. If whooping crane habitat selection is altered in response to population growth, climate change, or other factors, the RUF-predicted utilization rates may under- or over-estimate actual habitat use within the study area. These models predict habitat use when whooping cranes are on the ground but do not incorporate information about movement, landscape connectivity, or potential flyways. However, this model can be expanded to incorporate future habitat use data, which would reduce uncertainty and better evaluate potential impacts to whooping crane inland habitat use in proximity to anthropogenic development.

Habitat fragmentation from anthropogenic factors may affect both habitat availability and quality for whooping cranes, which in turn may increase risks associated with exposure to human disturbance to a growing crane population with an expanding wintering range. This model should be a helpful step in determining where future threats from habitat loss or degradation, regardless of the source of those impacts, to whooping cranes are likely and provides a tool for developing conservation measures. However, the intended use of these predictions is to inform landscape-level management decisions, and practitioners should avoid interpreting habitat use patterns on a per pixel basis.

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