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CHARACTERISTICS OF WHOOPING CRANE HOME RANGES DURING THE NONBREEDING SEASON IN THE EASTERN MIGRATORY POPULATION

A Thesis
Presented to
the Graduate School of
Clemson University

In Partial Fulfillment
of the Requirements for the Degree
Master of Science
Wildlife and Fisheries Biology

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by
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May 2018

Accepted by:
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Ms. Anne E. Lacy

ABSTRACT

In 2001, a reintroduced population of Whooping Cranes, known as the Eastern Migratory Population (EMP), was established in the eastern United States. The breeding range for the EMP was in central Wisconsin and the populated originally migrated to the Florida Gulf coast during the nonbreeding season. Beginning in approximately 2004-05, the wintering range for cranes shifted from the Florida Gulf coast to inland marshes in Florida. Between 2007-08 and 2017-18 the winter distribution of this population expanded north to include areas as distant as southern Indiana. To date, there has been no assessment of habitat use of the EMP across the current winter distribution. The objectives of this study were to identify factors influencing daily home range sizes of wintering Whooping Cranes in the EMP, describe habitat characteristics of areas used by cranes within their daily home range, identify the water depths and vegetation heights of used areas, and assess behavior associations with habitat. During two winters (2014-15 and 2015-16), we used radio-telemetry to track 20 and 23 groups of wintering Whooping Cranes, respectively, each for one full day. We recorded their location, behavior, and the habitat characteristics of their locations. Based on natural clustering of winter areas of Whooping Cranes, we grouped winter sites into three regions: North (Illinois, Indiana, Kentucky), Central (Tennessee, Alabama), and South (Georgia, Florida, Louisiana). We calculated home range sizes using a 95% kernel density estimate, and home ranges decreased in size from north (4.9 ± 2.8 km^2) to central (3.1 ± 1.0 km^2) to south (2.3 ± 0.5 km^2). Home ranges in the south were also comprised of the greatest proportion of wetlands compared to other regions (south = 37%, central = 7%, north = 1%). To identify habitat characteristics of winter sites, we compared used locations to randomly generated locations within a crane's home range separately by region. In the north region, cranes used agricultural areas more often than forests, and used areas with hydric soil that were potentially seasonally inundated during winter. In the central region, cranes selected for both agriculture and wetlands compared to forests. Cranes wintering in the south did not select habitat characteristics out of proportion to their availability within their home ranges. We also measured water depths and vegetation heights of used areas, respective to a crane. In all regions, cranes used areas with water or vegetation below the tibiotarsal joint more often than areas with deep water or tall vegetation. Lastly, we compared foraging and loafing behavior in three habitat types (agriculture, grasslands, and wetlands), both pooled and separately by region. Whooping Cranes in the north foraged more often in agriculture than in grasslands or wetlands. However, in the central region, cranes foraged equally in all three habitats, and cranes in the south foraged in either grasslands or wetlands. Loafing behavior was associated with wetlands compared to agriculture or grasslands in all three regions. The findings of this study are the first description of habitat characteristics of areas used by cranes wintering throughout the current and entire winter range of the EMP. Results from this study will inform land managers of wintering habitat use and can benefit conservation planning with respect to future reintroduction efforts of this endangered species.

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BACKGROUND: WHOOPING CRANE CONSERVATION

Whooping Cranes (*Grus americana*) are a migratory bird, native to North America. In 1941 the entire species included only 16 individuals occurring in one population. This small population wintered at the Aransas National Wildlife Refuge on the Texas Gulf Coast, USA, and its breeding site was at the Wood Buffalo National Park, in northern Alberta, Canada (the Aransas-Wood Buffalo Population, hereafter AWBP, CWS - USFWS 2007). Conversion of wetland habitats to agriculture and over-hunting likely led to the decline of Whooping Cranes (Allen 1952, Meine and Archibald 1996). In 1973, Whooping Cranes were listed as endangered by the Endangered Species Act, and as a result of this designation, the Whooping Crane Recovery Team (WCRT) was formed. The WCRT is a partnership between the governments of the USA and Canada, and is responsible for developing a recovery plan for the species throughout its entire historical range.

The Whooping Crane Recovery Plan, developed in 1986 by the WCRT, lists two objectives to reach the goal of recovery of the species; (1) establish and maintain self-sustaining populations of Whooping Cranes in the wild that are genetically stable and resilient to stochastic environmental events, and (2) maintain a genetically stable captive population to ensure against extinction of the species (CWS - USFWS 2007). There are multiple criteria, or scenarios in which the first objective can be reached. In one recovery scenario, the AWBP would reach 1000 individuals with 250 productive breeding pairs (productive defined as a pair that nests regularly and has fledged offspring). The other two scenarios of recovery require the establishment of one or two additional reintroduced population(s) of Whooping Cranes, in addition to self-sustainability in the AWBP. Beginning in 1967, biologists began removing eggs from nests of breeding Whooping Cranes at Wood Buffalo National Park, Canada, to begin a captive breeding population, which would eventually produce crane chicks for release into reintroduced populations.

Since 1975, there have been four attempts to reintroduce populations of Whooping Cranes in the USA. The first attempt was the Grays Lake Population, where from 1975 - 1989, Sandhill Cranes breeding at Grays Lake National Wildlife Refuge, Idaho, were used to cross-foster Whooping Crane chicks and teach them to migrate to wintering areas in New Mexico. The second attempted Whooping Crane reintroduction, from 1993 - 2004, was the Florida Non-migratory Population (FNMP), in central Florida, USA. The Grays Lake Population and the Florida Non-migratory Population both were unsuccessful reintroductions, and no longer are being augmented by captive-raised cranes. In 2001, another attempt at a reintroduced migratory population of Whooping Cranes began in the eastern USA (the Eastern Migratory Population, or EMP). In 2011, a second attempt at establishing a non-migratory population began in Louisiana, USA (the Louisiana Non-Migratory Population). Currently, captive-bred cranes are continuing to be released into the EMP and the LNMP. More detail on the history of reintroduced Whooping Crane populations can be found in Ellis et al.
(1992), Nesbitt et al. (2001), Folk et al. (2008), Urbanek et al. (2008), and Olsen and Chandler (2016).

The EMP, the focus of this study, was reared in captivity by people in Whooping Crane costumes to avoid imprinting on humans. Between 2001 - 2015, juvenile Whooping Cranes were taught to migrate by following costumed pilots in ultralight aircraft (UL) from breeding areas in Wisconsin to wintering areas in Gulf coastal Florida (either Chassahowitzka or St. Mark's National Wildlife Refuges). In 2005, the Direct Autumn Release (DAR) technique was implemented, in which juvenile Whooping Cranes were costume-reared in captivity, but were then released in breeding areas in Wisconsin, near adult Whooping Cranes from who they would presumably learn the migration path to wintering areas in the southern USA. Most recently, from 2013 - present, Whooping Crane chicks have been reared in captivity by adult cranes, instead of by costumed caretakers, and released in Wisconsin in the fall, similar to the DAR method. Specific rearing and release methods used in the EMP can be found in Maguire (2008), Urbanek et al. (2010a), Fondow (2013), and Urbanek et al. (2014).

Whooping Cranes from the wild AWB population winter in Gulf coastal Texas on or near the Aransas National Wildlife Refuge (ANWR), show strong winter site fidelity, and exhibit natal philopatry to winter territories (Stehn and Prieto 2010). In Texas, the AWBP spends the winter defending territories in saltmarsh habitat where they forage, primarily on blue crabs (*Callinectes sapidus*) and Carolina wolfberries (*Lycium carlinianum*, Stehn and Johnson 1987, Chavez-Ramirez 1996, Stehn and Prieto 2010). When wintering areas were originally chosen for ultralight aircraft to lead juvenile Whooping Cranes in the EMP, the WCRT selected areas with habitat similar to ANWR. The habitat most similar to coastal Texas in the eastern USA, was determined to be the Gulf coastal marshes of Florida (Urbanek et al. 2010a).

In the beginning of the reintroduction of the EMP, Whooping Cranes showed site fidelity and philopatry of winter sites near the release areas at Chassahowitzka or St. Mark's National Wildlife Refuges (Fondow 2013). As early as winter 2004 - 2005, Whooping Cranes in the EMP began wintering further from their coastal release areas, and instead selecting areas in inland Florida (Fondow 2013). By winter 2006 - 2007, the winter distribution of the EMP was expanding outside of the state of Florida, but the majority of cranes in the population were wintering in Florida (Fondow 2013). Between 2007 - 2018, the number of cranes wintering north of the original release areas in Florida increased (Urbanek et al. 2014). This expansion of the winter distribution has been attributed to warmer winter weather (Urbanek et al. 2014), and social learning of northern wintering areas by young cranes from older cranes (Teitelbaum et al 2016). However, the only study of winter habitat use of this population was done between 2004 – 2006, when the majority of the EMP wintered in Florida (Fondow 2013). There has not been another study of winter habitat use in this population after cranes began using wintering areas across the southeastern USA. Additionally, shifts in winter habitat use may contribute to reduced breeding success of cranes (Burnham et al. 2017), and the EMP must be successfully reproducing and self-sustaining to down-list the species according to the Endangered Species Act.

The objectives of this study were to address the knowledge gap of winter ecology of Whooping Cranes in the EMP, across the current distribution by assessing (1) factors influencing daily home range sizes, (2) habitat use, (3) water depths and vegetation heights of used areas, and (4) crane behaviors associated with habitat types. Here we focus on habitat use within an individual’s home range, which may guide management decisions at crane wintering areas.

INTRODUCTION

Migratory birds encounter a wide variety of conditions throughout the year that potentially affect their reproduction and survival. For example, quality of winter habitat can influence body condition and spring migration dates, which subsequently affect arrival time on the breeding areas as well as breeding success (Gill et al. 2001, Gunnarsson et al. 2005, Studds and Marra 2005). Habitat quality and use can be assessed at multiple scales, from landscape-level to specific foraging sites, and each level can provide insight to limiting factors or requirements during various life history stages. The various scales of habitat use can also inform conservation planning and land management, both of which require an understanding of habitat needs and space use (i.e. home range sizes and distribution) of a population, as well as the scale at which an individual interacts with the environment (Levin 1992, Guisan et al. 2006, Thornton and Fletcher 2014).

Whooping Cranes (*Grus americana*), a migratory species of bird, are endangered in North America (ESA 1973, as amended). The only extant population of wild Whooping Cranes, the Aransas Wood Buffalo Population (AWBP), breeds in Wood Buffalo National Park, Canada, and winters at Aransas National Wildlife Refuge, USA (Fig. 1). Multiple reintroduction efforts have attempted to establish additional populations of Whooping Cranes, including one migratory population in the eastern USA (Fig. 1). This Eastern Migratory Population (EMP) was established in 2001 with captive-bred cranes taught to summer in Wisconsin and winter in Florida, USA. Beginning in 2007, Whooping Cranes in the EMP expanded their winter range naturally to include more northern areas in the southeastern USA (Urbanek et al. 2014, Teitelbaum et al. 2016). As of 2016, the EMP consisted of approximately 100 individuals and 27 breeding pairs, although the population was not self-sustaining (Whooping Crane Eastern Partnership 2016).

The lack of recruitment to the EMP has been attributed primarily to poor quality breeding habitat and low rates of chick survival (Urbanek et al. 2010b, Runge et al. 2011, Converse et al. 2013). However, in other species of migratory cranes, low reproductive success has also been attributed to poor quality habitat during the nonbreeding season, which may result in lower fat reserves which are needed to sustain cranes through the nesting season (Gil-Weir 2006, Burnham et al. 2017). Although habitat use patterns of the EMP on the breeding grounds are well understood as is the winter distribution, data gaps still exist with respect to habitat use during winter (Maguire 2008, Urbanek et al. 2014, Van Schmidt et al. 2014). In contrast, the winter behavior and habitat use of the AWBP has been studied more completely, although individuals within that population exhibit unique behaviors (e.g. defend territories primarily in saltmarshes; Stehn and Prieto 2010). In contrast, the EMP has increasingly wintered in groups in agricultural areas and inland freshwater wetlands (Fondow 2013, Teitelbaum et al. 2016), and to date has not displayed any territorial defense behavior (Urbanek et al. 2014). Therefore, applying habitat use data from AWBP to EMP for conservation planning purposes is not prudent.

Our goal was to assess the characteristics of home ranges of cranes in the EMP during the nonbreeding season across the entire wintering range (Fig. 2). To date previous studies have focused on winter range expansion or habitat selection of EMP Whooping

Cranes wintering in Florida, but a range-wide comparison will provide data needed to understand the impacts of the winter range expansion on habitat use of the entire population (Fondow 2013, Urbanek et al. 2014, Teitelbaum et al. 2016). Therefore, we sought to determine (1) if region, social group types, or proportion of the home range comprised of wetlands affected the daily home range size of cranes, (2) which habitat characteristics best described areas used by wintering Whooping Cranes in each region, (3) if in areas used by Whooping Cranes, individuals used areas with high, low, or no water or vegetation, and (4) if cranes use agricultural areas and grasslands for foraging and wetlands and open water for loafing.

METHODS

Study area

During this study, we collected data on groups of cranes across the entire known nonbreeding range; Illinois, Indiana, Kentucky, Tennessee, Alabama, Georgia, Louisiana, and Florida (Fig. 2). Frequently used wintering areas, with multiple groups of cranes during two winters (2015 - 2016), included protected areas at St. Mark's National Wildlife Refuge in Wakulla County, Florida; Wheeler National Wildlife Refuge in Morgan County, Alabama; and Goose Pond Fish and Wildlife Area in Greene County, Indiana. Habitats used in protected areas included brackish marshes, moist soil management units, areas in cooperative farming programs, and restored wetlands. Crane wintering areas on private properties represented a range of habitat types including livestock pastures, a crawfish farm, and harvested corn and soy fields.

Data collection

Between 29 December 2014 – 1 February 2015 (winter 1) and 2 January – 12 February 2016 (winter 2) we monitored cranes in the EMP. Individuals were previously outfitted with satellite tags (n = 27, Microwave Telemetry, Columbia, MD) and VHF telemetry tags (n = 78, 164-166 MHz, Advanced Telemetry Systems, Isanti, MN, between 2002 and 2015). Details regarding handling and tag deployment can be found in Urbanek et al. (2010a). Data streams from satellite and VHF tags were maintained by members of the Whooping Crane Eastern Partnership as part of ongoing monitoring programs for cranes in the EMP.

To address our objectives, we subsequently located cranes within the EMP range using satellite telemetry, historical records, and sighting reports from the public or partner organizations. Once we confirmed the presence of cranes at a site using the aforementioned sources, we used VHF telemetry to locate birds and initiate data collection procedures. During winter 1 and winter 2, we located 20 and 23 groups of radio-tagged Whooping Cranes respectively (representing 61 and 52 individual birds), on their wintering grounds (Fig. 2). We used apparent clustering of crane observations to create three latitudinal categories to describe the nonbreeding range: North (> 36 degrees north, including Illinois, Indiana, Kentucky), Central (32 - 36 degrees north, including Tennessee and Alabama), and South (< 32 degrees north, including Louisiana, Georgia, and Florida; Fig. 3).

To assess habitat use and behavior within a site, we tracked each group of cranes from 30 min before sunrise until 30 min after sunset. At each 30 min interval (hereafter, interval), we recorded the group's location (hereafter, location) either by triangulating (hereafter, remote data) or visually observing their position, and if we were able to visually observe the cranes we also recorded behavior and habitat (described below). When using telemetry to locate cranes we triangulated their locations and estimated spatial error using the maximum likelihood estimator described by Lenth (1981) within the LOCATE III software (Nams 2006). During visual observations we recorded observer locations using a handheld GPS and recorded the azimuth and estimated distance from the observer to the crane. Distance was estimated using landmarks and aerial photos. Using this information and a Euclidean calculation, we then computed the coordinates for the focal cranes (projection: NAD 1983 UTM Zone 16N).

When we were able to observe cranes directly via visual observations, we conducted behavioral observations from a vehicle or a blind at an estimated range of 100 - 2500 m from the focal Whooping Cranes, although most birds were observed from a distance of < 500 m. We recorded the following behavioral and habitat data: number of Whooping Cranes in the group, behavior (foraging, locomotion, vigilance, and loafing; De-Jun et al. 2011), and water and vegetation levels respective to the crane. The water depth and vegetation height categories used were measured using crane anatomy as a reference point and were adapted from Fitzpatrick et al. (2015). Categories included: water or vegetation (1) absent, (2) below the crane's tibiotarsal joint (hock), or (3) above the crane's hock (Fig. 4).

Whooping Cranes in the EMP often occur in groups during the nonbreeding season. We defined a group as one or more individual(s) that remained together for an entire day, and during this study, group size ranged from 1 – 8 cranes. If a group of cranes interacted with other cranes, we defined the group as the smallest unit that moved together for the entire focal day. Social group types were defined as single (one bird), pair (two adult birds), family (two adults and one juvenile, either their own wild-hatched chick or an adopted captive-reared chick), and group (three unrelated birds, or more than three birds which may consist of multiple pairs or family units). Individual life histories, breeding stage, and pair status was known for every crane in the EMP, due to an intensive banding and monitoring program by Whooping Crane Eastern Partnership organizations. We used this information to distinguish pairs and families from groups in our analyses. To avoid pseudo-replication in behavior or habitat use data we only used data collected on one individual crane per group. If data were collected on multiple cranes in one group, we selected the individual with the maximum number of visual observations, or if all cranes were visually observed equally often, we randomly selected one individual per group. We conducted a chi-square analysis to determine if social group types of cranes were related to region. Only groups with known sizes and types were included in this analysis (Appendix 1).

Data analysis

Daily home ranges

To estimate daily home range sizes, we randomly selected 20 (remotely obtained or visually observed) locations per group, so all home ranges were comparable and not affected by the number of locations used. By using 20 locations per group we were able to optimize the number of locations used per group and the number of groups included in this analysis. We excluded remotely obtained locations with a spatial error > 5 km^2 to avoid artificially large home ranges due to triangulation inaccuracies (mean spatial error of remotely obtained locations used in home range analysis = 0.65 ± 0.08 km^2). Remotely obtained locations accounted for 162 of the 700 total locations used to calculate home range sizes (mean number of remotely obtained locations per group = 4.6 ± 0.7 locations). Groups with fewer than 20 locations per day or groups that interacted with captive cranes that had not yet been released at St. Mark's National Wildlife Refuge were excluded from subsequent home range analyses (Appendix 1).

We calculated home range sizes using 95% kernel density estimates (kdes) in Geospatial Modelling Environment and ArcGIS 10.3 (ESRI 2011, Beyer 2015, R Core Team 2017). The smoothing parameters (*h*) were calculated individually for each group of cranes using the likelihood cross-validation method (CVh), which produces estimates with better fit and less variability than least-squares cross-validation, especially for samples with <50 locations per individual (Horne and Garton 2006). We averaged smoothing parameters from all groups and used the mean value ($\overline{h}$= 264 m) to create kdes and to estimate area so all home ranges were equally sensitive to bird locations (as in Fondow 2013, Van Schmidt et al. 2014).

We assessed home range sizes in relation to social group type (single, pair, family, or group), region (north, central, south; Figs. 2 and 3), and proportion of home range comprised of wetlands. To calculate proportion of home range comprised of wetlands, we imported all 95% contours into ArcGIS 10.3 and overlaid them on the National Land Cover Database, a land cover data set for the USA at 30m resolution (ESRI 2011, Homer et al. 2015). With the Tabulate Area tool in ArcGIS, we identified the number of cells within each home range that were either woody wetlands or emergent herbaceous wetlands and calculated the proportion of each home range comprised of these two wetland types (ESRI 2011). The Tabulate Area tool internally converted our home range polygons into raster datasets of the same resolution as the National Land Cover Database, to identify land cover types within the home range polygons (ESRI 2011). We tested for relationships among independent variables using Chi-square, ANOVA, and t-tests in R and analyzed correlated variables separately in the models (R Core Team 2017). We assessed the influence of independent variables (social group type, region, social group type * region, proportion of home range comprised of wetlands, and social group type * proportion of home range composed of wetlands) on home range sizes using a generalized linear mixed model fit by maximum likelihood with year as a fixed effect in the 'lme4' package in R (Bates et al. 2015, R Core Team 2017). Categorical variables with >2 categories were analyzed compared to a reference category. Model fit was assessed by AICc in the 'AICcmodavg' package in R, and any model ≤ 2 AICc from the best model was considered valid (Burnham and Anderson 2002, Mazerolle 2017, R Core Team 2017).

Habitat characteristics

To assess habitat selection of wintering Whooping Cranes, we compared used and available habitat within their home range (third order habitat selection, Johnson 1980). We used a logistic regression to compare habitat characteristics of used locations to random locations. For each group's used locations, we randomly selected ten locations, to optimize the number of locations used per group and the number of groups included in analysis. To minimize spatial error, we did not use any remotely obtained locations with an estimated error greater than 2 km^2. Groups with fewer than ten locations meeting this criterion were excluded from analysis (Appendix I). We used 100% Minimum Convex Polygons (MCP) as the range within which used and random locations were plotted. MCPs are less sensitive to intensity of use of a location, and therefore better estimate all areas available to an individual than a fixed kernel home range (Gillies et al. 2006, Kauhala and Auttila 2009, Comfort et al. 2016). To generate MCP home ranges, we used all locations recorded for this study (14 - 25 locations per day per group), which represent all of the area available to each group of cranes. MCPs were generated with the Minimum Bounding Geometry tool and Convex Hull method in ArcGIS (ESRI 2011). We then generated ten random locations within the 100% MCP home range, using the Create Random Points tool (ESRI 2011).

The land cover characteristics assessed in this study were grouped into three general types: land cover categories, proximity to emergent wetlands, and likely surrogates of anthropogenic influence or disturbance. We used the distance to major roads and the presence of a protected area as surrogates of habitat disturbance. We used data from the USA Major Roads database and the U.S. Protected Areas Database to calculate the distance from major roads or the presence of a protected area at any used or random location (ESRI 2011, USGS GAP 2016, Table 1). We calculated the distance of every location to the nearest major road using the Generate Near Table tool, and to determine if a location was within a protected area, we conducted a spatial join (ESRI 2011, Table 1).

We used the National Wetlands Inventory (NWI) to identify emergent herbaceous wetlands, a habitat class we deemed similar to that used by Whooping Cranes in the EMP during the breeding season (Van Schmidt et al. 2014, USFWS 2016, Barzen et al. in press). To identify areas that were potentially seasonally inundated and appropriate crane roosting habitat (i.e. flooded agricultural fields), but not classified as wetlands during the entire year, we also used the presence of hydric soils from the database of the National Cooperative Soil Survey provided by the U.S. Department of Agriculture (USDA) and the National Resources Conservation Service (Soil Survey Staff 2015). We identified locations within wetlands or in areas with hydric soils with a spatial join in ArcGIS, and calculated the distance from every location to the nearest emergent wetland, or wetland of any type using the Generate Near Table tool (ESRI 2011, Table 1).

Due to the EMP's increased use of agricultural areas (Urbanek et al. 2014, Teitelbaum et al. 2016), we also investigated crane use of specific crops. We identified general and specific land cover types throughout the winter distribution of this population with the USDA Cropland Data Layer (CDL), an annually produced nationwide land cover database focused on agricultural areas (USDA 2014, USDA 2015). We combined the 108 CDL categories into five broader categories; agriculture, grassland, wetland, developed, and forested (Table 2). To identify both general and specific land cover categories at each location, we used the Extract Values to Points tool in ArcGIS (ESRI 2011, Table 1). Specific land cover types were not included in the analyses due to limited numbers of locations in each land cover type. However, we report the most frequently used specific land cover types for each region.

To compare habitat characteristics of used and random locations, we used a logistic generalized mixed effect model with group ID as a random effect in the 'lme4' package in R (Bates et al. 2015, Pearse et al. 2016, Eyes et al 2017, R Core Team 2017). Normality of continuous variables was tested with Shapiro-Wilk Normality Tests in R (R Core Team 2017). All continuous variables (distances to wetlands and roads) were non-normal and thus were log-transformed. We tested for correlations between independent variables using ANOVA, Pearson Correlation, and chi-square tests in R (R Core Team 2017). Post-hoc tests to determine differences in groups were done with Tukey HSD and post-hoc chi-square tests in the 'fifer' package in R (Fife 2017, R Core Team 2017). We tested for correlation of independent variables and region using only randomly generated locations within home ranges so analyses by region were not affected by selective crane use of habitats. Most independent variables were correlated to region ($P < 0.05$ for each test), therefore we conducted all subsequent analyses separately by region. Within each region, we constructed models with each independent variable separately, as well as any combinations of independent variables which were not correlated. We do not expect Whooping Cranes to select forested areas, so models with CDL categories were compared to a reference category of forested land cover. Model selection was conducted using AICc in the 'AICcmodavg' package in R. We considered any model ≤ 2 AICc from the top-ranked model valid but also report AICc weights to aid in interpretation (Burnham and Anderson 2002, Mazerolle 2017, R Core Team 2017). Measures of goodness-of-fit of top-ranked models were assessed with the Hosmer-Lemeshow goodness-of-fit tests (Hosmer et al. 2013).

Water depth and vegetation height

We recorded water depth and vegetation height data during observation intervals of cranes. We assessed the relationships between water depth and region, and between vegetation height and region using an analysis of variance in R (R Core Team 2017). To reduce the chance for pseudo-replication of data, we randomly selected eight visually-observed intervals from each group during which water depth was recorded, and ten intervals during which vegetation height was recorded. Data were not analyzed if < eight or ten intervals included visual observations of water depth or vegetation height, respectively. This step resulted in 67% (28 of 43 groups) and 79% (33 of 43 groups) of the groups for which we collected data for water depth and vegetation height analyses being included in subsequent analyses, respectively (Appendix 1). For both water depth and vegetation height analyses, we pooled data across both winters (2015 - 2016). When data from all regions were pooled, we tested for a correlation between region and water depth or vegetation height category using a chi-square test. We also analyzed water depths and vegetation heights separately by region. Both analyses (with regions pooled, and separately by region) were conducted with an ANOVA. We tested for normality of our data using a Shapiro-Wilk normality test and verified with quantile comparison plots in R (Royston 1995, R Core Team 2017). The dependent variables for these analyses were log-transformed proportions of observations within each category of water depth and each category or vegetation height. We added 0.1 to each proportion value to create non-zero values in order to log-transform proportions. When cranes used water depth or vegetation height categories differently, we used a post-hoc Tukey Honest Significant Differences test from the fifer package in R (Fife 2017, R Core Team 2017).

Behavior

We assessed the relationship between behavior and habitat of wintering Whooping Cranes. By using data from groups of cranes with ≥ ten observation intervals, we were able to optimize the number of locations per group and the number of groups included in this analysis. Groups used in this analysis represented 74% (31 groups) of the groups we tracked for this study, which included 51% of all intervals during which behaviors and habitat types were observed. We had few observations of vigilance and locomotion behaviors (31 and 90 observations, respectively), as well as very few observations of cranes in developed habitat (8 observations) and none in forested areas. Therefore, we limited our analysis to foraging and loafing behaviors (281 and 202 observations, respectively) in grasslands, agriculture, and wetlands (130, 217, and 249 observations respectively). We randomly sampled ten intervals for each individual when they were exhibiting either loafing or foraging behavior in these three habitat types.

To determine if foraging behavior was most often observed in agriculture or grasslands, and if loafing was most often observed in wetlands as found in Fondow (2013), we subset our data to either all foraging observations or all loafing observations, with both years and regions pooled. We then compared the number of observations of either foraging or loafing behavior in each habitat type (agriculture, grasslands, wetlands) using an ANOVA in R (R Core Team 2017). If there were differences in the number of observations of a behavior in the three habitat types, we used a Tukey honest significant differences post-hoc test to identify which habitats were different from each other (R Core Team 2017).

We then conducted a chi-square analysis of observations of foraging and loafing behavior in agriculture, wetlands, and grasslands, to determine if in each region Whooping Cranes were exhibiting behaviors in the same proportions in each habitat type (R Core Team 2017). We analyzed data separately for each region, with years pooled. If there was a difference in behaviors observed between habitat types, we then used a chi-square post hoc test in the fifer package in R to identify which groups were different from each other (Fife 2017, R Core Team 2017). We adjusted p-values using the fdr method to account for possible inflated p-values due to multiple comparisons (Benjamini and Hochberg 1995, Fife 2017).

RESULTS

We collected data on 43 groups of Whooping Cranes throughout the winter distribution of the EMP during the winter of 2015 (n = 20 groups) and 2016 (n = 23 groups).

Whooping Cranes in this study wintered at 16 sites in eight USA states (Appendix 1). We recorded 14 - 25 locations per day per group ($\bar{x}$ = 22 ± 2 locations) for a total of 945 locations among all sites and years. Remotely collected data accounted for 262 observations (0 - 21 intervals per group, $\bar{x}$ = 6 locations per group, mean spatial error = 3.93 ± 1.34 km^2) Visually collected data accounted for 681 observations (0 - 24 intervals per day per group, $\bar{x}$ = 16 locations).

We observed Whooping Cranes spending the winter either alone (12%), in a pair (39%), as a part of a family unit (12%), or in a larger group of cranes (37%). Region was not a significant predictor of group size, however we observed the large groups most frequently in the north region (n = 9 groups), and the most pairs in the central region (n = 9 pairs, χ^2_6 = 10.61, *P* = 0.10, Fig. 5).

Daily home ranges

We identified 35 home ranges among all sites and years. Daily home ranges in the south (n=5) had a higher proportion of 95% kdes comprised of wetland habitats ($\bar{x}$ = 0.37 ± 0.30) compared to the central (n = 13, $\bar{x}$ = 0.07 ± 0.06) or north (n = 17, $\bar{x}$ = 0.01 ± 0.02) regions (*P* < 0.001 for both pairwise comparisons with southern region, Fig. 6). Therefore, proportion wetland and region were not included in models together. The average daily home range size of all wintering Whooping Cranes in this study was 3.8 ± 2.3 km^2 (n = 35, range 1.3 - 13.5 km^2). Daily home range size was best predicted by region. There was an 72% chance this was the best model given those we tested, and this model was 5.1x as likely to be the best model compared to the next highest ranked model (Table 3). Average home range sizes were 4.9 ± 2.8 km^2 in the north (n= 17 groups), 3.1 ± 1.0 km^2 in the central region (n= 13 groups), and 2.3 ± 0.5 km^2 in the south (n= 5 groups, Fig. 7). Home ranges in the north were larger than in the central and southern regions (*P* = 0.02 and 0.01, respectively, Table 3). Models of home range size that included proportion of the home range comprised of wetlands, the classification of the group type, their interaction, or a null model were poorly supported, with each having a probability < 14% for being the best model (Table 3).

Habitat characteristics

Available habitat differences by region

The habitat characteristics of random locations representing available habitat within daily home ranges of wintering Whooping Cranes differed by region. The proportion of locations identified by the CDL as agriculture and wetlands differed by region (*P* < 0.0003 for both analyses, Table 4). There southern region has less available habitat in agriculture and more available habitat in wetlands, compared to the central or northern regions (*P* < 0.006 for all pairwise comparisons of the southern region with the other two regions, Table 4). The distance to wetlands of any type was further in the north than in the south (*P* = 0.02, Table 4), however there was no difference in distance to wetlands between the central region and either the north or south regions (*P* > 0.07 for both pairwise comparisons with the central region, Table 4). The distance from random locations within crane home ranges to emergent wetlands was further in the central region than either the northern or southern regions (*P* = 0.03 and 0.02 for pairwise comparisons of the central region, respectively, $P = 0.87$ comparing north and south, Table 4). There were no significant regional differences in available habitat with respect to protected areas, hydric soils, presence of wetlands identified by the NWI, distance to major roads, or the proportion of grasslands, forests, or developed areas identified by the CDL ($P > 0.05$ for all analyses, Table 4). All subsequent analyses of habitat associations were therefore conducted separately by region.

Habitat selection in the Northern region

In the north region (Illinois, Indiana, and Kentucky), locations used by wintering Whooping Cranes were on average 2.26 (± 1.4) km from the nearest major road, 242.5 (± 268.8) m from the nearest wetland of any type, and 805.9 (± 1069.5) m from the nearest emergent wetland. Of the locations used by cranes, 22.5% were in protected areas (mostly Goose Pond Fish and Wildlife Area in Indiana), 66.3% were in areas with hydric soil, and 11.3% were in wetlands identified by the National Wetland Inventory (USFWS 2016). The land cover category most often used by cranes was agriculture (69.4%), followed by wetlands (15%), forests (7.5%), developed areas (4.4%), and grasslands (3.8%). The top three specific land cover types used by wintering cranes in the north were corn (38.8%), soybeans (30.6%), and open water (14.4%). All other specific land cover types accounted for less than 10% of locations used by cranes.

In the northern region, two of the ten habitat models we tested were well supported, with the top model including land cover category and the presence of hydric soil, and the next best model including only land cover category (Table 5). Based on coefficient estimates from the top model (which was 2x as likely to be the best model as the second ranked model), the odds of a location being used by cranes were 1.6x higher in areas with hydric soil than in areas without hydric soil (P = 0.04, Table 5). The top ranked model also indicated that the odds of a used location occurring in agriculture was 2.8x higher compared to that of a used location occurring in forested areas (P = 0.02, Table 5, Fig. 8). The top two models fit the data reasonably well (Hosmer–Lemeshow goodness-of-fit test: P = 0.98 and 1.00, respectively).

Habitat selection in the Central region

In Tennessee and northern Alabama, or the central region, locations used by cranes were on average 1.6 (± 1.3) km from the nearest major road, 104.9 (± 118.3) m from the nearest wetland of any type, and 1.8 (± 1.3) km from the nearest emergent wetland. Fifty-one percent of the locations used by Whooping Cranes were protected, particularly at the Hiwassee Wildlife Refuge in Tennessee or Wheeler National Wildlife Refuge in Alabama. Eighteen percent of locations used by cranes were in hydric soils, and 31.3% were in wetlands identified by the National Wetlands Inventory (USFWS 2016). Similar to the north region, most locations were in agriculture (48.8%) and wetlands (25.6%), followed by grasslands (16.3%), forests (6.9%), and developed areas (2.5%). The four specific land cover types used most often in the central region were corn (24.4%), open water (22.5%), soybeans (19.4%), and grass or pasture (15.6%). All other specific land cover types accounted for less than 10% of locations used by cranes in this region.

In the central region, three habitat models were best supported, with the top model including land cover category, the second model including distance to emergent wetlands, and the third ranked model including land cover category and the presence of hydric soils (Table 5). Based on the coefficient estimates of the top model in the central region, the odds of a location being used by cranes was 3.0x higher in agricultural areas, and 2.6x higher in wetlands, compared to that of a location being used in forested areas (P = 0.01 and 0.02, respectively, Table 5, Fig. 8). This model fit the data well (Hosmer–Lemeshow goodness-of-fit test: P = 1.0). The second best model indicated the odds of a location being used by cranes increased with the distance to emergent wetlands, however this was not a significant predictor of crane habitat, and did not fit the data as well as the top model (P = 0.12, Table 5, Hosmer–Lemeshow goodness-of-fit test: P = 0.5). The third best model supported the results of the top model, in which the odds of a location being used by cranes was 2.9x higher in an agricultural area, and 2.5x higher in wetlands, compared to forests (P = 0.01 and 0.02, respectively, Table 5, Fig. 8). In addition to land cover category, the third ranked model also suggested the importance of hydric soils in predicting crane use of a location, where the odds of a location in hydric soil being used by cranes was 1.2x that of a location in non-hydric soils, however this result was not significant (P = 0.5, Table 5). This model also fit the data well (Hosmer–Lemeshow goodness-of-fit test: P = 1.0).

Habitat selection in the Southern region

Locations used by cranes in the south (Florida, Georgia, and Louisiana) were on average 2.4 (± 2.8) km from the nearest major road, 75.1 (± 122.9) m from the nearest wetland of any type, and 369.8 (± 289.4) m from the nearest emergent wetland. More than half (64.4%) of the locations used by cranes in the south were on protected lands, mostly at St. Mark's National Wildlife Refuge in Florida. Fifty-eight percent of locations were in areas with hydric soil, and 46.7% were in wetlands identified by the National Wetlands Inventory (USFWS 2016). Unlike the central and northern regions, there were no agricultural locations used by cranes, and most locations were classified as wetlands (54.4%) by the Cropland Data Layer (USDA 2014, USDA 2015). Grasslands, forests, and developed areas accounted for 21.1%, 18.9%, and 5.6% of locations used by cranes, respectively. The specific land cover type used most often by cranes in the south was herbaceous wetlands (33.3%). Aquaculture, grass pasture, and shrubland each accounted for 11.1% of used locations, and all remaining specific land cover types accounted for less than 10% of locations.

In the southern region, model differentiation was not supported, and seven models each had AIC weights ≤ 0.16. Additionally, none of the parameters in these seven models were significant predictors of habitat used by wintering Whooping Cranes ($P > 0.15$ for all parameters, Table 5), suggesting cranes were not using habitat out of proportion to what was available.

Water depth and vegetation height

During the winters of 2015 and 2016 and when data were pooled among all three regions, we found significant differences among all water levels of locations used by cranes (Table 6, Fig. 9). We observed Whooping Cranes most often on dry land (mean proportion of observations = 0.60 ± 0.06), but when in water, we observed cranes in shallow water (mean proportion of observations = 0.38 ± 0.06) more often than in deep water (mean proportion of observations = 0.02 ± 0.01). In the north region (36% of groups) there were significant differences among all pairwise comparisons of water depth (Table 6, Fig. 10). Cranes occurred more frequently on dry land (mean proportion of observations = 0.7 ± 0.3) compared to shallow water (mean proportion of observations = 0.3 ± 0.3), and more often in shallow water compared to deep water (mean proportion of observations = 0. 0 ± 0.0, $P < 0.003$ for all pairwise comparisons, Table 6, Fig. 10). In the central (43% of groups) and south regions (21% of groups) significant differences in pairwise comparisons were limited. Cranes occurred more frequently on dry land (mean proportion of observations = 0.5 ± 0.3 in the central region and 0.6 ± 0.3 in the south region) compared to deep water (mean proportion of observations = 0.0 ± 0.1 in the central region and 0.0 ± 0.1 in the south region), and more frequently in shallow water (mean proportion of observations = 0.5 ± 0.3 in the central region and 0.3 ± 0.3 in the south region) compared to deep water ($P < 0.04$ for all pairwise comparisons, Table 6, Fig. 10).

Vegetation height at crane locations was measured using crane anatomy as a reference point (Fig. 4) and categorized as no vegetation, short vegetation (maximum height below their hock), and high vegetation (minimum height above their hock). Pooling among regions and years we found significant differences among vegetation heights of crane locations ($P = 0.03$, Table 6, Fig. 11). Cranes occurred most frequently in areas with short vegetation (mean proportion of observations = 0.44 ± 0.06, Fig. 11) compared to areas with tall vegetation ($P = 0.02$, Table 6, Fig. 11). There was no difference in crane locations in areas with short vegetation or bare ground, or in areas with tall vegetation compared to bare ground (*P* > 0.3 for both pairwise comparisons, Table 6, Fig. 11). When analyzed separately by regions, there were no significant differences in the proportion of observations of cranes on bare ground, in short vegetation, or in tall vegetation (*P* > 0.07 for all analyses, Table 6, Fig. 12).

Behavior

We found no significant difference in the number of foraging observations per group per day among agriculture, grassland, and wetland land classifications when data were pooled among regions and years ($F_{(2,90)} = 1.15$, $P = 0.3$, Fig. 13). Significant differences occurred in the number of loafing observations per group per day ($F_{(2,90)} = 5.9$, $P = 0.004$). The number of observations of cranes loafing were higher in wetlands compared to agriculture (*P-adjusted* = 0.03) or grasslands (*P-adjusted* = 0.005, Fig. 14).

When analyzed by region, there were different patterns of the number of observations of cranes foraging or loafing in the three habitat types. In the north, cranes exhibited behaviors differently in agriculture than in wetlands (overall $\chi^2_2 = 11.71$, $P = 0.003$, post-hoc test *P-adjusted* = 0.004), and slightly differently in agriculture compared to grasslands (*P-adjusted* = 0.064, Fig. 15, Table 7). In the north, there were more observations of cranes foraging than loafing in agriculture (mean number of observations = 3.6 and 1.4 respectively, Fig. 15). In the central region, cranes foraged or loafed in similar proportions when in agriculture, grasslands, or wetlands (overall $\chi^2_2 = 3.16$, $P = 0.21$, Fig. 15). In the south region, there were no observations of cranes foraging or loafing in agriculture, and there were no differences in the pattern of foraging compared to loafing in grasslands or wetlands (overall χ^2_1 = 1.56, *P* = 0.21, Fig. 15).

DISCUSSION

The availability of habitats differed among the landscapes of the northern, central, and southern regions, and cranes appeared to use habitat differently among these regions. The results of this study clearly showed a strong use of agricultural landscapes by Whooping Cranes wintering in the northern and central regions, and use of shallow wetlands throughout the winter distribution of the EMP, particularly for loafing habitat. For example, cranes in the north used locations with hydric soils that may have been seasonally inundated, cranes in the central region used locations in wetlands, and daily home ranges in the south were comprised of more than 50% wetlands.

One tool to inform managers of the scale at which to implement conservation and management actions for cranes is the estimation of home range sizes. Assuming home range sizes are determined by resource abundance, dense resources or habitat of high quality should result in smaller home ranges (Village 1982, Rothstein et al. 1984). Home range sizes are commonly estimated during the breeding season and are positively correlated with habitat quality across a wide array of avian species (Stenger 1958, Anich et al. 2010, Ponjoan et al. 2012, Godet et al. 2018). During the winter season, birds also use smaller home ranges in areas with increased food availability or habitat quality (Siffczyk et al. 2003; Bautista et al. 2017) but home range size may also be less constrained during the nonbreeding season when individuals are not constrained to a nest site or required to guard or provision young.

Daily home ranges of wintering Whooping Cranes were largest in the northern region and were approximately 1.8 and 2.6 times larger than in the central and southern regions, respectively. If home range size is inversely related to habitat quality in wintering cranes, then the north to south gradient we observed in home range size suggests that the quality of wintering habitat increases as cranes migrate south. Whooping Cranes are a wetland-dependent species (Stehn and Johnson 1987, Pickens et al. 2017, Barzen et al. in press). Although cranes in the southern region did not select wetlands out of proportion to their availability, home ranges in the south had the highest proportion comprised of wetlands compared to the north and central regions, another indication of high habitat quality in the southern region. Home ranges of Whooping Cranes in the northern region also may be larger compared to those in the central and south due to climactic differences. Colder temperatures can increase energetic costs of thermoregulation on a daily basis that must be offset by increased consumption (Fitzpatrick et al. in press). If habitat quality (i.e., food availability) is lower, cranes may establish larger home ranges to meet energy demands. However, cranes in the north may also be reducing energy expenditures during the non-breeding season by migrating shorter distances from the breeding grounds. If so, this may suggest a trade-off between habitat quality and migration effort (Bell 2005, McKinnon et al. 2015).

In addition to differences in size of daily home ranges, habitat characteristics within home ranges of Whooping Cranes differed by region. Wetlands were more common and agricultural lands less common in the southern region. Furthermore, wetlands not within home ranges also were closer in the southern region and the distance to specifically emergent wetlands was furthest in the central region. Wetlands were therefore more available both within and nearby the daily home ranges we surveyed in the south. Whooping Cranes use open water or emergent wetlands as roosting habitat and often spend daytime hours in or near the same wetlands (AWBP on migration, Austin and Richert 2001, Faanes et al. 1992; EMP on breeding areas, Van Schmidt et al. 2014; EMP on wintering areas, Urbanek et al. 2010a). The relative abundance of wetlands in the southern region and the smaller home range sizes there suggest that habitat quality is suitable for cranes.

Previous studies of Whooping Cranes in the EMP during the breeding season have found a strong dependence on wetlands and agricultural areas (Maguire 2008, Van Schmidt et al. 2014, Barzen et al. in press). Within the breeding range in Wisconsin, territorial Whooping Cranes from the EMP (from 2011 – 2012) most often used emergent wetlands (43%), open water (27%), or agriculture (11%), within their home ranges (Barzen et al. in press). Non-territorial cranes also used agriculture (42%), emergent wetlands (30%), and open water (15%) during the breeding season (from 2011 – 2014, Barzen et al. in press). During the breeding season, cranes avoid forested or developed areas which may provide cover for predators, or are a source of other threats to cranes (e.g. powerline and vehicle collisions; Stehn and Wassenich 2008, Van Schmidt et al. 2014). We found that during wintering periods in the northern and central regions, land cover category was a strong predictor of habitat use within a home range. Similar to habitat use during the breeding season, cranes in the northern and central regions used agriculture habitat more often compared to forests, and in the central region cranes used wetlands more often than forests. In the northern region, cranes also used areas with hydric soil that had the potential to be seasonally inundated (McCauley and Jenkins 2005). Use of agricultural areas in the northern and central regions may be driven in part by the availability of agricultural food items. Fitzpatrick et al. (In press) modeled the energetic requirements of cranes wintering throughout the distribution of the population and found cranes in the north and central regions need to acquire food with a higher density of energy to offset the costs of wintering in colder climates. During our study, cranes wintering in the northern region were not using wetlands more often than available, but used flooded agricultural areas with moist soil in which they could forage for invertebrates or other food items (Fitzpatrick 2016). Agricultural food items provide higher energy via a higher carbohydrate content compared to wetland food resources (i.e. amphibians, molluscs, fish, crustaceans) which also may be unavailable to cranes in the north (Fitzpatrick 2016, Barzen et al. 2018, Fitzpatrick et al. in press). Fitzpatrick et al. (In press) reported cranes need to consume less corn per day (26-71 g/day) compared to other food types (87-338 g/day) to offset additional thermoregulatory costs of wintering in the north compared to the south. Shorter day lengths in the north also limit the total activity time for this diurnal species, and potentially also limit the amount of time spent foraging. The results of our study support the prediction of a high use of agricultural areas in the north and central regions, based on the energetic model (Fitzpatrick et al. in press). Furthermore, cranes wintering in the southern region did not use or avoid any habitat type out of proportion to its availability, but instead exhibited a greater use of wetlands than in the north or central regions. High use of wetlands in the south may be due to a greater availability of wetlands, combined with lower energetic costs of wintering in warmer climates, and thus less dependence on agricultural areas for high energy food items.

We expected Whooping Cranes to avoid areas of human disturbance (i.e., areas without any legal protection, or near major roads) based on behaviors of other species of cranes (wintering Eurasian Cranes, Franco et al. 2000; migrating Sandhill Cranes, Pearse et al. 2017; breeding Sarus Cranes, Sundar 2009), and of Whooping Cranes in the AWBP while on migration (Belaire et al. 2014). In this study, we did not find any evidence of habitat use based on presence of protected areas or distance to major roads. The lack of significance of these habitat variables may have been due in part to the scale at which we assessed habitat use. For example, we assessed habitat characteristics within a crane's home range (3rd order selection, Johnson 1980), much of which was either completely within or outside of a protected area. Therefore, the scale at which we assessed habitat use may not have been ideal for detecting an association with protected areas if one did occur. Whooping Cranes in the EMP may instead choose home range locations within protected areas when choosing an area in which to winter (2nd order, Johnson 1980). Additionally, there may be circumstances in which the presence of a protected area may increase human disturbance of cranes if birds are subjected to anthropogenic pressure either acutely or chronically. Although we used the distance to major roads as a measure of human disturbance, that variable may not completely represent human disturbances of cranes. Disturbances may occur differently throughout time and causes of disturbance need not be consistently present at a winter site to be disruptive. For example, cranes have been flushed by approaching humans on private property in the northern region > 800 m from the nearest road. Such a disturbance may not be captured in our measure of human disturbance, nor were the humans that caused the disturbance always present at that site. Additionally, privately-owned lands with large parcel sizes and minimal human disturbance may be functioning similarly to protected lands. Assessing the levels of human disturbance on both public and privately-owned properties may be an important aspect of crane habitat that should be examined further.

Throughout the winter distribution of the EMP, there were similarities in the water depths and vegetation heights of used areas. In all three regions, cranes were either in shallow water or on dry land more often than in deep water. In the north, cranes were on dry land more often than in shallow water, however this is likely a result of their dependence on upland agricultural areas in that region. Cranes also used areas with short vegetation more often than areas with tall vegetation. Shorter vegetation provides for easier locomotion by cranes as they spend substantial time walking and stepping while foraging (Barzen et al. 2018). Shorter vegetation also is likely to increase vigilance and the opportunity to observe predators or disturbance.

Each habitat component within a crane's home range may provide different resources (i.e. specific food items or safe habitat for loafing, 4th order selection, Johnson 1980). Across the winter distribution of the EMP, we observed cranes foraging in similar proportions in wetlands, agriculture, and grasslands. In the northern region, cranes had a higher use of agricultural areas within their home range, and preferred to use this habitat for foraging. In the southern region, cranes were foraging in wetlands or grasslands instead of in agriculture. These differences may be due to a difference in availability of habitat or specific food types by region. For example, specific types of agricultural fields available to cranes may differ by region (i.e., corn and soybeans in the north, cotton and citrus in the south). Additionally, throughout the winter distribution of the EMP, cranes tended to loaf more frequently in wetlands than in upland habitats. Although wetlands were not used more often than they were available in each region, wetlands were an important component of habitat used for loafing by cranes wintering in all regions.

Although not statistically different, our data appeared to suggest cranes winter in larger groups in the north region, compared to the central or southern regions. Spending time in larger groups may provide greater protection from predators, can increase chances of finding food in novel habitats, and by spending less time on territorial defense behaviors, individuals can spend more time foraging or loafing (Pulliam and Caraco 1984, Davies and Houston 1984). Common cranes wintering in Spain were either territorial or gregarious, and territorial birds spent more time being vigilant and had lower food intake rates (Alonso et al. 2004). However, territorial cranes defended higher quality habitat, had the same overall food consumption as cranes in flocks, and had higher average breeding success (Alonso et al. 2004). Similarly, Whooping Cranes of the AWBP wintering in Texas showed territoriality strictly in saltmarsh habitat (Stehn and Johnson 1987, Chavez-Ramirez and Slack 1999). However, Whooping Cranes were gregarious in upland habitats, suggesting there were abundant and defendable resources in wetlands, and food availability in wetlands is positively related to breeding success in this population (Pulliam and Caraco 1984, Chavez-Ramirez and Slack 1999, Gil-Weir 2006). In the EMP, Whooping Cranes in the north may be wintering in larger groups due to an abundance of agricultural foraging areas, and no defendable concentration of resources as there is in saltmarshes used by the AWBP.

During this study, we collected habitat use and behavior data across 16 sites in eight states during our two study years. These data represent the most widespread survey of wintering habitat use for Whooping Cranes in the EMP to date, and therefore present a unique opportunity to assess habitat use throughout the winter distribution of this population. While it is possible that cranes used sites outside of our spatial and temporal sampling window, and thus that additional data on habitat use could alter our conclusions, this appears unlikely. For example, the spatial coverage of our sites included every state known to include a wintering site of Whooping Cranes during our study years (WCEP 2015, WCEP 2016). During winter 2015 – 2016, there were only six Whooping Cranes in the EMP whose winter locations were unknown to the Whooping Crane Eastern Partnership, and our study included sites at all major wintering areas (WCEP 2016). There was one individual who was reported early in the winter north of our northernmost site in Indiana, however it appears that report was of a migrating crane who continued to move south before we arrived at that site. Similarly, the temporal coverage of our sites represented the winter season for cranes in the EMP. None of the cranes in our study were known to make large-scale movements during our study periods, thus we are confident our data represent winter habitat and not migratory stopover habitat. At the daily temporal scale, we collected location data on the focal cranes every 30 minutes throughout one day per group. During our study cranes did not tend to change locations more often than every 30 minutes, so we are confident in our estimates of home range sizes and habitat use of the focal cranes for that particular day. Daily home range sizes of groups of Whooping Cranes were a snapshot of the area used by cranes, and are likely not representative of the entire area used throughout the winter season, but is a measure comparable by regions.

Previous studies of winter habitat selection of Whooping Cranes in the EMP have assessed habitat at a higher order of selection (2nd order selection, Johnson 1980), i.e., how cranes are selecting habitat within the winter range of the population (Fondow 2013, Urbanek et al. 2014). However, these studies either addressed habitat selection prior to the expansion of the winter range of this population (Fondow 2013), or only include general habitat characteristics such as overall cover of grain crops, habitat loss to development, average temperatures, and drought indices (Urbanek et al. 2014, Teitelbaum et al. 2016). Our study focuses on habitat selection within a crane's home range (3rd order selection, Johnson 1980), which allows us to assess habitat characteristics of used areas at a smaller spatial scale. While we did not address how cranes are selecting winter areas from what is available in the flyway, we provide descriptions of habitat use within a site, at a wide array of sites throughout the wintering distribution of the population.

Our data highlight differences as well as similarities in habitat use by cranes throughout the population's winter distribution that may be relevant to management of cranes in the EMP. For example, agriculture does not appear to be used by cranes wintering in the south compared to the north, but all cranes throughout the winter distribution use some type of shallow wetlands (flooded agricultural areas in the north, wetlands in the central and south). Upland foraging grounds and loafing habitat in wetlands are both important components of crane wintering areas. Our data suggest that upland areas with bare ground or short vegetation, and areas with shallow water, are more likely to provide foraging habitat compared to deep water or tall vegetation.

If winter temperatures increase in future years, and if juvenile birds continue to learn from adults to winter further north, then a greater proportion of the EMP may winter in the northern region (Urbanek et al. 2014, Teitelbaum et al. 2016). Under such a scenario, strategies to improve habitat may be considered in the north and central regions. For example, habitat quality could be improved by restoring emergent wetlands that cranes use for roosting and loafing. Improved diet data from cranes in upland agricultural areas would also inform land managers of how best to provide resources to cranes during winter. Resources gained during winter affect spring migration timing or fat reserves used during nesting, and have the potential to impact a population’s reproductive success (Fitzpatrick et al. In press). The EMP of Whooping Cranes is currently sustained through releases of captive-reared juveniles, and although there are nesting pairs in the population, recruitment is not high enough for the population to be self-sustaining. Improving our understanding of winter habitat selection, energetics, and food resources used by this population will contribute to the knowledge of the species as well as inform management actions taken to encourage successful reproduction.

TABLES AND FIGURES

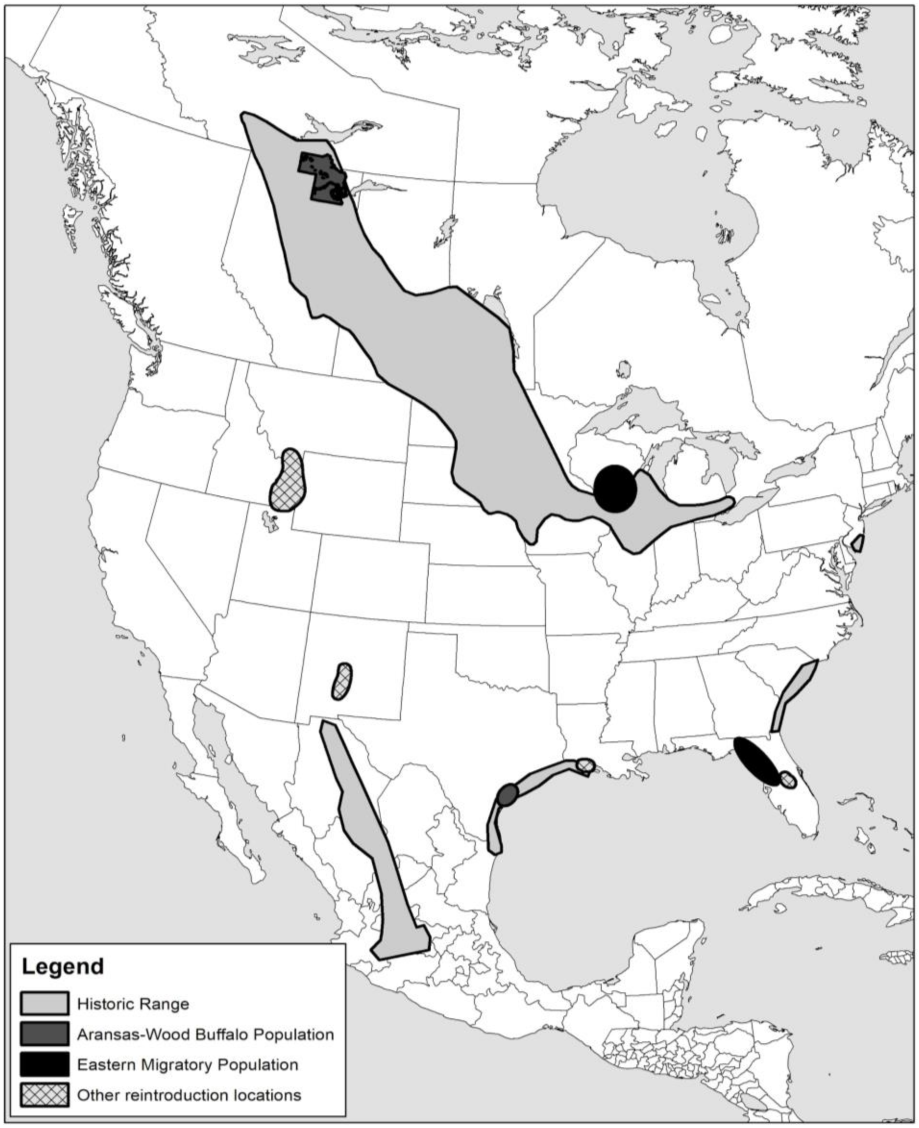

Figure 1. Map of the historic range of Whooping Cranes (both migratory and non-migratory populations, Allen 1952), the current extent of the wild Aransas - Wood Buffalo Population, the original range of the reintroduced Eastern Migratory Population, and the ranges of other reintroduced populations (extirpated Grays Lake Migratory Population between Idaho and New Mexico, Florida Non-migratory Population, and Louisiana Non-migratory Population).

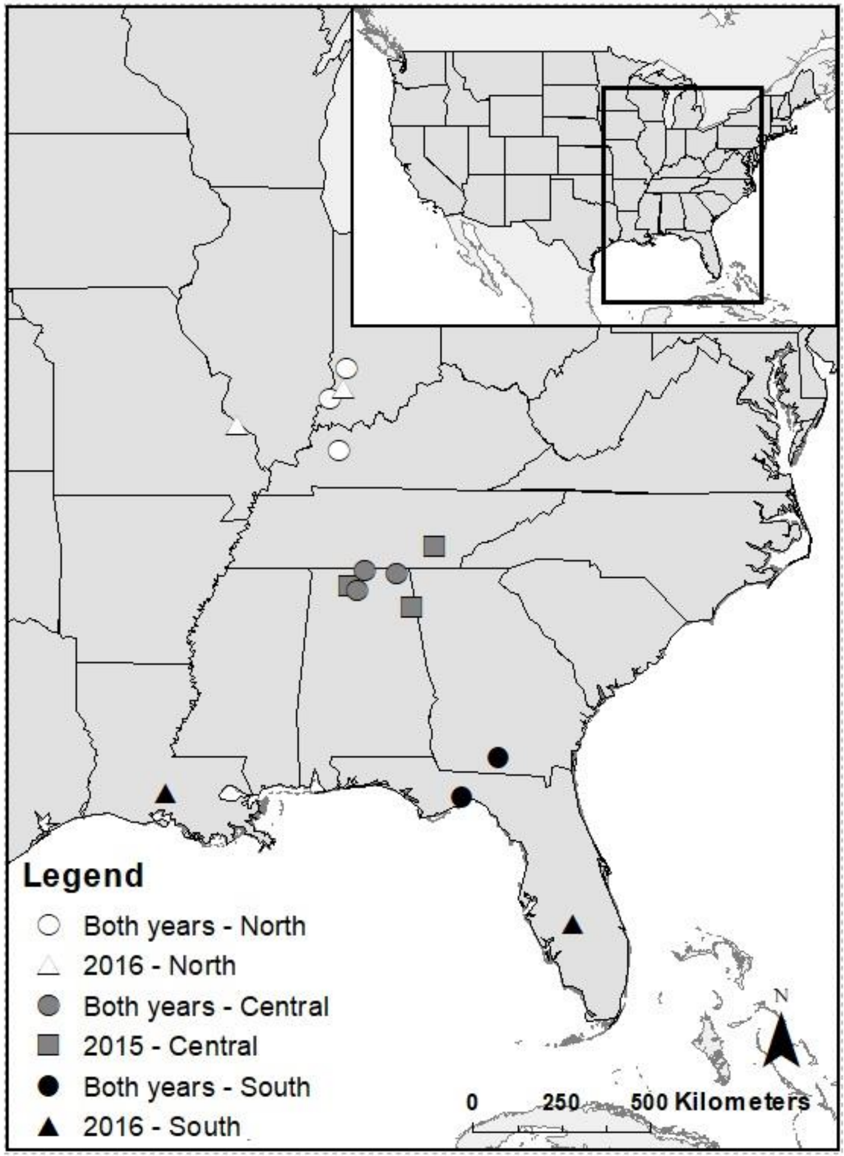

Figure 2. Locations of Whooping Cranes in the eastern USA during winter 2015 (December 2014 – January 2015) represented by squares, winter 2016 (January 2016 – February 2016) represented by triangles, or during both years represented by circles. For analyses, data were grouped into three regions by latitude: North (Illinois, Indiana, Kentucky) represented by white symbols, Central (Tennessee, Alabama) represented by gray symbols, and South (Louisiana, Georgia, Florida) represented by black symbols.

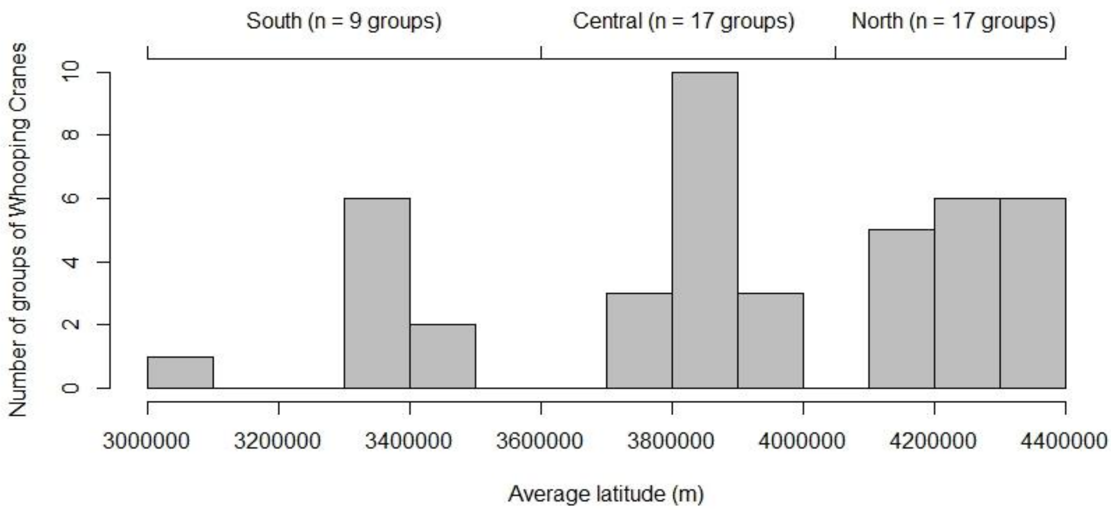

Figure 3. Frequency distribution of groups of wintering Whooping Cranes in the Eastern Migratory Population during two winters (2015 - 2016) within 100 km latitude bins. Average latitude was calculated in meters in a projected coordinate system (projection: NAD 1983 UTM Zone 16N). Natural clustering of cranes was used to create three regions for subsequent analyses; south, central, and north.

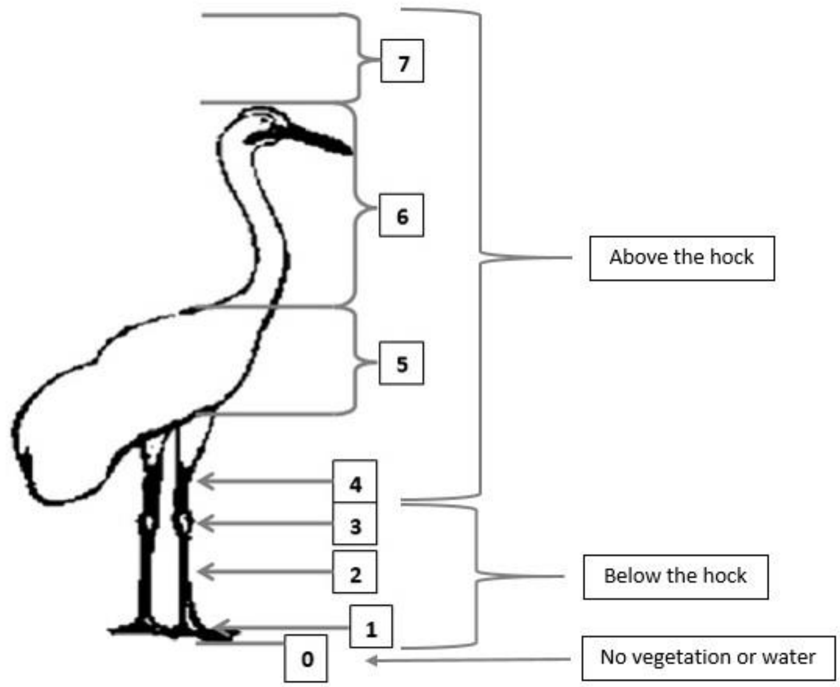

Figure 4. From Fitzpatrick et al. (2015): Categories used to measure water depths and vegetation heights relative to Whooping Cranes in the Eastern Migratory Population during two winters (2015-2016). We recorded the category closest to the depth of the water or the height of the vegetation in which the crane was standing. We subsequently grouped Fitzpatrick et al.'s (2015) categories into three broader categories: vegetation or water was absent, was above the crane's hock (tibiotarsal joint), or was below the hock.

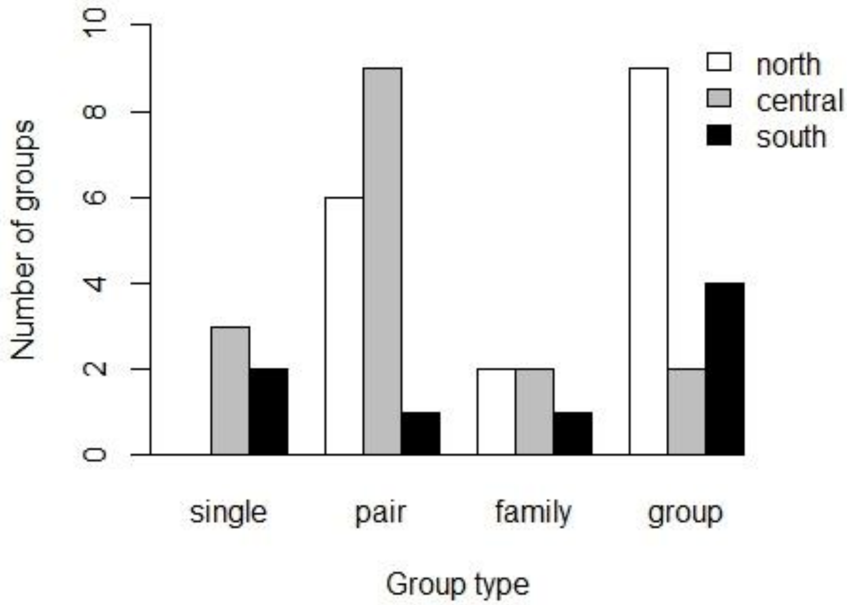

Figure 5. Number and social grouping of wintering Whooping Cranes in the Eastern Migratory Population in three regions (north shown in white, central shown in gray, and south shown in black) during two winters (2015 - 2016).

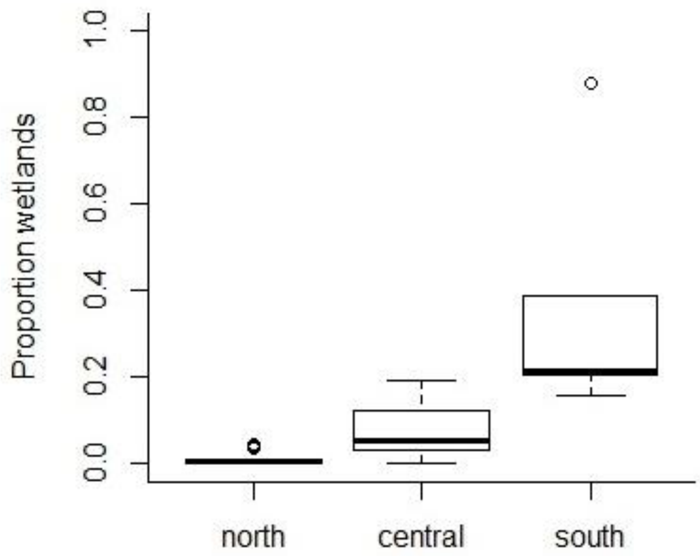

Figure 6. Proportion of the daily home ranges comprised of wetland habitats of Whooping Cranes in the Eastern Migratory Population during two winters (2015 - 2016) in three regions (north, central, south). Bolded horizontal lines represent the median, upper and lower borders of boxes represent quartiles, and 1.5 * Interquartile range (upper quartile minus the lower quartile) are within the whiskers outside of the boxes. Outliers are represented as open circles.

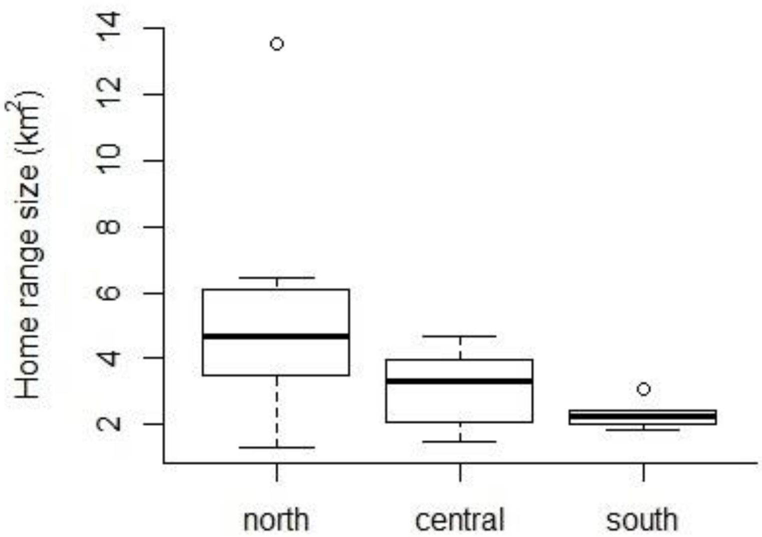

Figure 7. Daily home range sizes of groups of Whooping Cranes in the Eastern Migratory Population during two winters (2015-2016) in three regions. North (n = 17 groups), central (n = 13 groups), and south (n = 5 groups) regions were delineated based on natural clustering of winter areas. Bolded horizontal lines represent the median, upper and lower borders of boxes represent quartiles, and 1.5 * Interquartile range (upper quartile minus the lower quartile) are within the whiskers outside of the boxes. Outliers are represented as open circles.

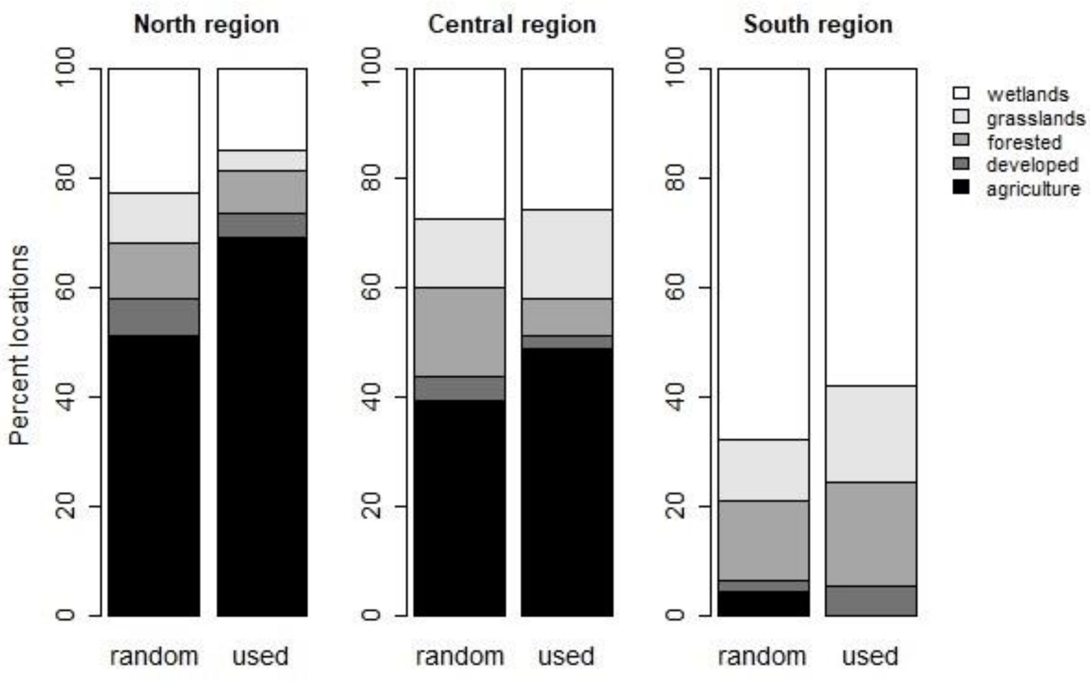

Figure 8. Percent of randomly generated and used locations of wintering Whooping Cranes in the Eastern Migratory Population during two winters (2015 - 2016) in each land cover category from the Cropland Data Layer (wetlands shown in white, grasslands shown in light gray, forested areas shown in medium gray, developed shown in dark gray, and agriculture shown in black) in three regions (north, central, south). Random locations were generated within 100% minimum convex polygon daily home ranges of wintering cranes. Regions were delineated based on natural clustering of wintering areas.

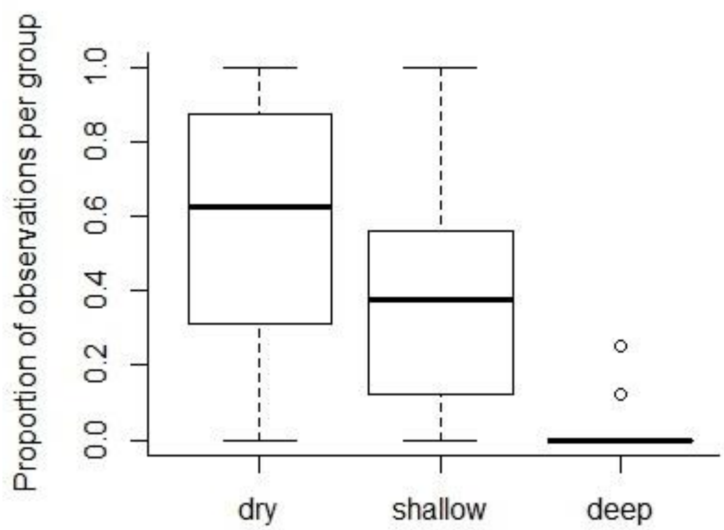

Figure 9. Proportion of visual observations of wintering Whooping Cranes (n = 28 groups) in the Eastern Migratory Population in three regions (north, central, south) during two winters (2015 – 2016) in each water depth category (dry, shallow, deep). Bolded horizontal lines represent the median, upper and lower borders of boxes represent quartiles, and 1.5 * Interquartile range (upper quartile minus the lower quartile) are within the whiskers outside of the boxes. Outliers are represented as open circles.

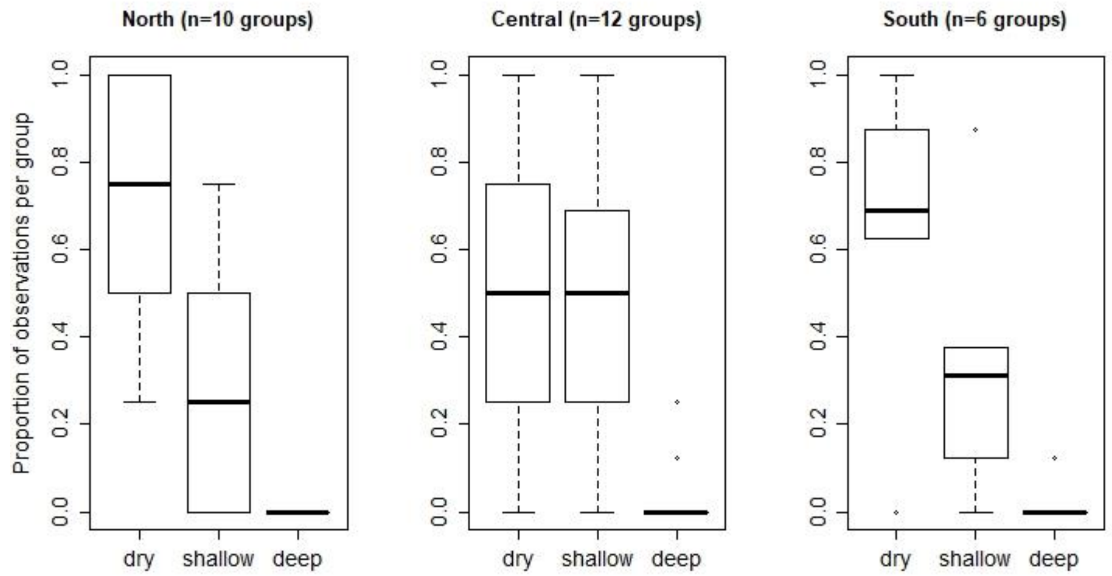

Figure 10. Proportion of visual observations of wintering Whooping Cranes in the Eastern Migratory Population in each water depth category (dry, shallow, deep) during two winters (2015-2016), separated by regions (north, central, south). Bolded horizontal lines represent the median, upper and lower borders of boxes represent quartiles, and 1.5 * Interquartile range (upper quartile minus the lower quartile) are within the whiskers outside of the boxes. Outliers are represented as open circles.

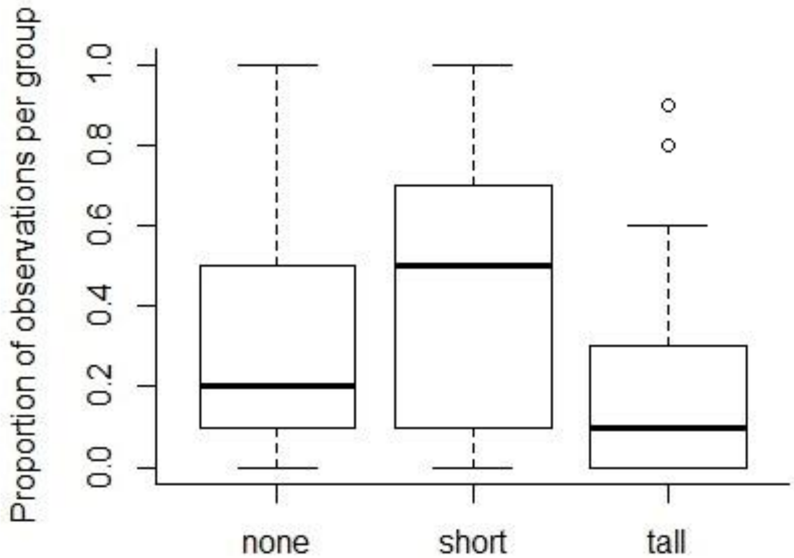

Figure 11. Proportion of visual observations of groups of wintering Whooping Cranes in each vegetation height category (none, short, tall) in all regions during two winters (2015 - 2016). Bolded horizontal lines represent the median, upper and lower borders of boxes represent quartiles, and 1.5 * Interquartile range (upper quartile minus the lower quartile) are within the whiskers outside of the boxes. Outliers are represented as open circles.

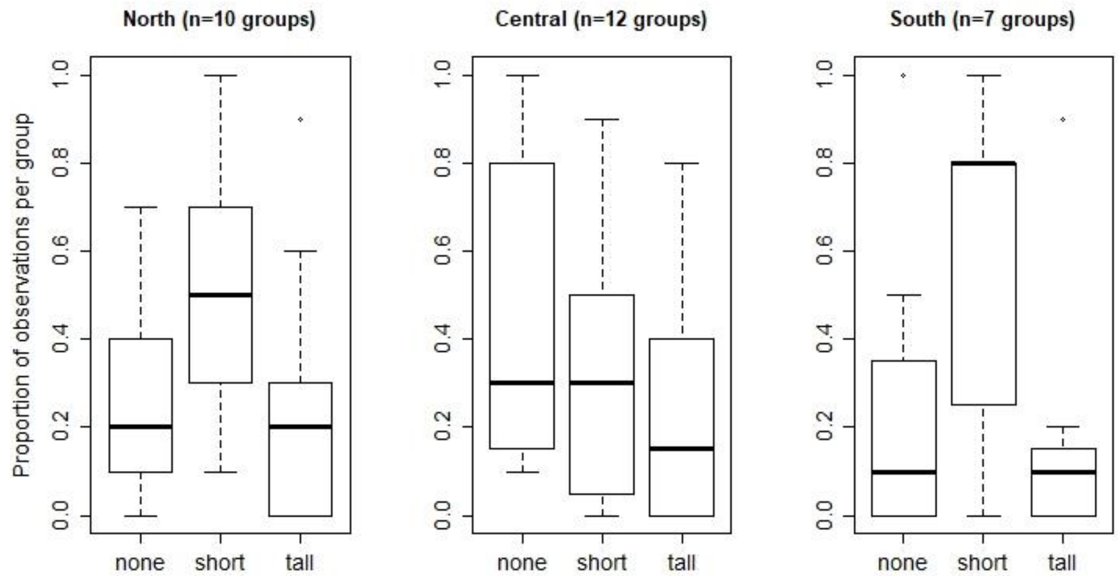

Figure 12. Proportion of visual observations of groups of wintering Whooping Cranes in the Eastern Migratory Population in each vegetation height category (none, short, tall) during two winters (2015-2016), separated by regions (north, central, south). Bolded horizontal lines represent the median, upper and lower borders of boxes represent quartiles, and 1.5 * Interquartile range (upper quartile minus the lower quartile) are within the whiskers outside of the boxes. Outliers are represented as open circles.

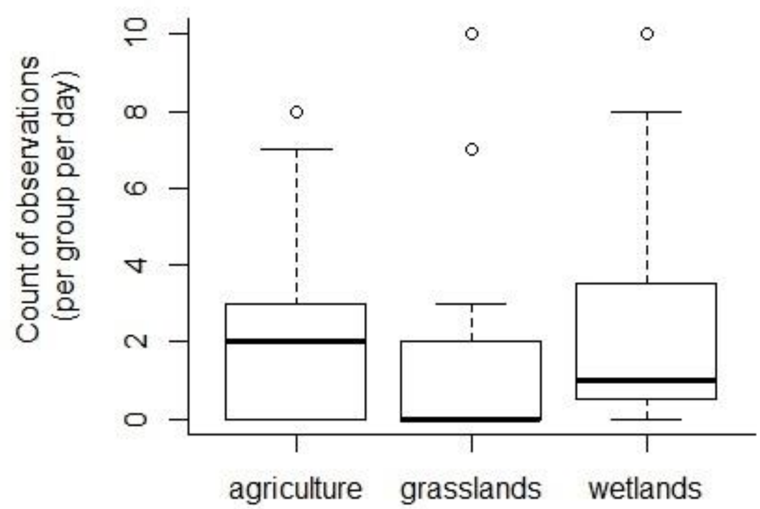

Figure 13. Observations of foraging behavior exhibited by wintering Whooping Cranes during two winters (2015-2016) pooled among all three regions. Bolded horizontal lines represent the median, upper and lower borders of boxes represent quartiles, and 1.5 * Interquartile range (upper quartile minus the lower quartile) are within the whiskers outside of the boxes. Outliers are represented as open circles.

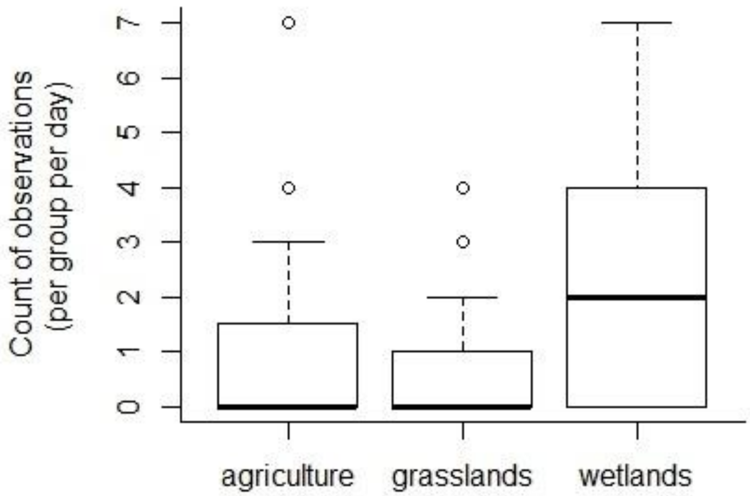

Figure 14. Observations of loafing behavior exhibited by wintering Whooping Cranes during two winters (2015-2016), in three regions (north, central, south). Observations were in agriculture ($\bar{x}$ = 1.0 ± 1.6 observations), grasslands ($\bar{x}$ = 0.7 ± 1.2 observations), or wetlands ($\bar{x}$ = 2.2 ± 2.3 observations). Bolded horizontal lines represent the median, upper and lower borders of boxes represent quartiles, and 1.5 * Interquartile range (upper quartile minus the lower quartile) are within the whiskers outside of the boxes. Outliers are represented as open circles.

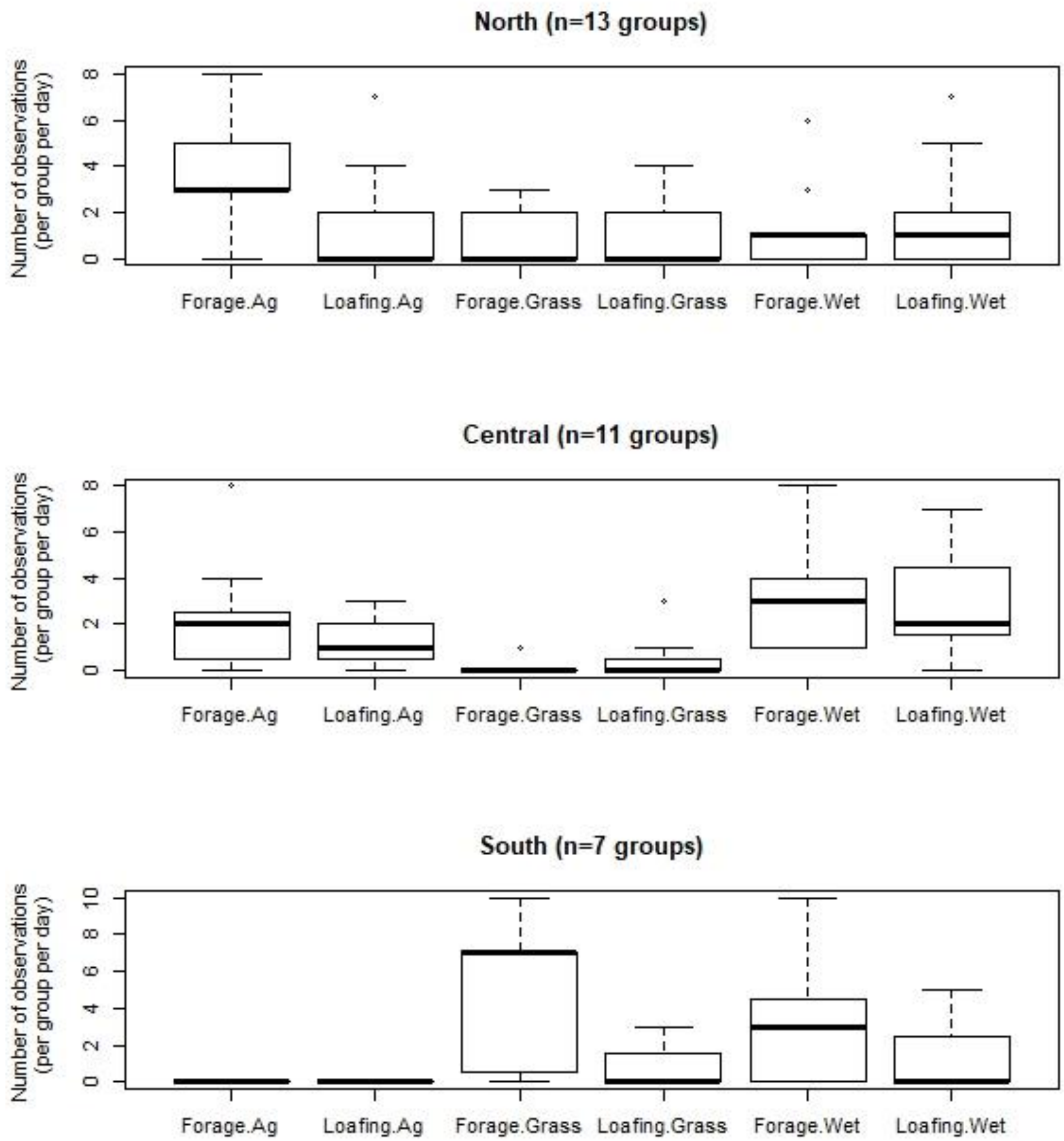

Figure 15. Number of observations of wintering Whooping Cranes in agriculture, grasslands, and wetlands, exhibiting either foraging or loafing behaviors. Data are pooled for two years (2015 - 2016), but separated by region (north, central, south). Bolded horizontal lines represent the median, upper and lower borders of boxes represent quartiles, and 1.5 * Interquartile range (upper quartile minus the lower quartile) are within the whiskers outside of the boxes. Outliers are represented as open circles.

Table 1. Descriptions of land cover datasets used for habitat analysis of wintering Whooping Cranes in the Eastern Migratory Population during two winters (2015 - 2016). Each layer was overlaid on used or random locations using the ArcGIS tool defined in the table.

Variable	Year published	Spatial resolution	Data type	Description	Source	ArcGIS tool
Cropland Data Layer (CDL)	2015 - 2016 (for data from planting seasons in 2014 - 2015)	30 meters	Raster	Crop-specific land cover data set generated annually from satellite imagery with extensive agricultural ground - truthing	USDA National Agricultural Statistics Service Cropland Data Layer, 2014 - 2015	Extract Values to Points
National Wetlands Inventory (NWI)	1980s - 2000s (accessed 2016)	From aerial imagery at 1:12,000 or smaller	Polygon	National inventory of wetlands and deepwater habitats of the United States	U. S. Fish and Wildlife Service, 2016	Generate Near Table, Join
Protected Areas Database (PAD)	Accessed 2016	Varies	Polygon	Inventory of protected space within the United States	Gap Analysis Program of the US Geological Survey, USGS GAP 2016	Join
Soil Survey Geographic Database (SSURGO)	Accessed 2016	1:12,000 to 1:63,360	Polygon	Nationwide soil survey database	Natural Resources Conservation Service, US Department of Agriculture, Soil Survey Staff 2015	Join
USA Major Roads	2006	1:50,000	Line	Map of U.S. interstates, state highways, major streets, and other major thoroughfares	ESRI and TomTom	Generate Near Table

Table 2. Cropland Data Layer (CDL) land cover classifications grouped into five broader categories: agriculture, wetland, grassland, forest, or developed areas. We overlaid the CDL on locations used by wintering Whooping Cranes in the Eastern Migratory Population during two winters (2015 - 2016) and random locations generated to represent available areas to determine habitat selection. Only CDL categories that overlapped with random or used locations are included.

Agriculture	**Wetland**	**Grassland**	**Forest**	**Developed**
Corn	Aquaculture	Fallow/ Idle cropland	Deciduous Forest	Barren
Cotton	Herbaceous wetlands	Grass/ Pasture	Evergreen Forest	Developed Low Intensity
Double crop (winter wheat/ soybeans)	Open water	Other hay/ non alfalfa	Mixed Forest	Developed Open Space
Sorghum	Woody wetlands		Shrubland	
Soybeans				
Winter wheat				

Table 3. Model selection results for generalized linear mixed models assessing factors influencing daily home range sizes of Whooping Cranes in the Eastern Migratory Population during two winters (2015 - 2016). All models included year as a fixed effect. K = number of parameters in the model. Parameter estimates are included only for the top model and derived only from that model.

Model	K	AICc	ΔAICc	AICc weight	Parameter	Estimate	SE	95% Confidence Interval	*P*-value
Region	5	160.82	0.0	0.72	Region - central	-1.81	0.76	-3.29 - -0.32	0.02
					Region - south	-2.56	1.05	-4.61 - -0.51	0.01
Null	3	164.09	3.27	0.14					
Proportion wet	4	164.93	4.11	0.09					
Region + social group type	8	167.88	7.06	0.02					
Social group type	6	168.61	7.79	0.01					
Proportion wet + social group type	7	169.28	8.46	0.01					
Proportion wet * social group type	10	179.53	18.71	0.00					
Region * social group type	13	188.78	27.96	0.00					

Table 4. Assessment of habitat characteristics of random locations within daily home ranges of Whooping Cranes in the Eastern Migratory Population during two winters (2015 - 2016), in three regions (north, central, and south). Region was correlated with multiple habitat characteristics, thus the analysis of habitat selection was conducted by region. Letters in the ‘region differences’ column represent results of post-hoc tests (Tukey HSD and chi-square post hoc tests) assessing pairwise comparisons of regions (i.e. regions with the same letter are not significantly different from each other). For ‘protected’, ‘hydric soil’, and ‘in wetland’ habitat layers, summaries provided are mean ± sd of the proportion by group of locations that were categorized as protected, in hydric soil, or in wetlands, respectively. For ‘distance’ habitat layers, summaries provided are not log-transformed, however statistical tests were conducted on log-transformed variables due to non-normality of the data.

Independent variable	Statistical test	χ^2 / F statistic	Degrees of freedom (df1, df2)	*P*-value	Region differences	Summary by region (mean ± sd) North Central South
Proportion of locations in agriculture	ANOVA	11.38	2, 38	**0.0001**	North - A Central - A South - B	0.6 ± 0.3 0.4 ± 0.3 0.0 ± 0.0
Proportion of locations in development	ANOVA	0.57	2, 38	0.57	North - A Central - A South - A	0.1 ± 0.1 0.0 ± 0.1 0.1 ± 0.1
Proportion of locations in forests	ANOVA	0.74	2, 38	0.49	North - A Central - A South - A	0.1 ± 0.1 0.2 ± 0.2 0.1 ± 0.1
Proportion of locations in grasslands	ANOVA	0.57	2, 38	0.57	North - A Central - A South - A	0.1 ± 0.1 0.2 ± 0.1 0.1 ± 0.2
Proportion of locations in wetlands	ANOVA	10.34	2, 38	**0.0003**	North - A Central - A South - B	0.2 ± 0.3 0.3 ± 0.3 0.7 ± 0.3
Proportion of home range protected	chi-square	22.45	16	0.13	North - A Central - A South - A	0.3 ± 0.4 0.5 ± 0.4 0.7 ± 0.5
Proportion of home range in hydric soil	chi-square	26.76	20	0.14	North - A Central - A South - A	0.6 ± 0.3 0.2 ± 0.3 0.6 ± 0.3
Proportion of home range in wetlands identified by NWI	chi-square	20.61	14	0.11	North - A Central - A South - A	0.1 ± 0.3 0.3 ± 0.3 0.5 ± 0.4
(log) Distance to roads	ANOVA	2.27	2, 38	0.12	North - A Central - A South - A	2.4 ± 1.4 km 1.6 ± 1.2 km 2.3 ± 2.3 km
(log) Distance to wetlands	ANOVA	4.33	2, 38	**0.02**	North - A Central - AB South - B	207.5 ± 133.5 m 112.2 ± 65.8 m 62.9 ± 88.9 m
(log) Distance to emergent wetlands	ANOVA	5.34	2, 38	**0.009**	North - A Central - B South - A	1.0 ± 1.3 km 1.7 ± 1.3 km 0.4 ± 0.3 km

Table 5. Habitat use of Whooping Cranes in the Eastern Migratory Population in three regions (north, central, south) during two winters (2015 - 2016). Models within two AICc of the top model are considered valid and are shown here. Parameters in bold text have $P < 0.05$ and are considered significant. The odds reported for models including CDL category are the odds of a location in that habitat category being used by Whooping Cranes, compared to a reference category of forested areas. K = number of parameters in the model. Parameter estimates are included only for the top models and derived only from that model. Goodness-of-fit of top models was assessed with Hosmer - Lemeshow (HL) tests.

Region	Model	K	AICc	ΔAICc	AICc weight	HL *P*-value	Parameter	Estimate Odds	SE Est SE Odds	95% CI Est 95% CI Odds	*P*-value
North	CDL category + Hydric soil	7	442.23	0.00	0.55	0.98	**Category - Agriculture**	**1.03** **2.81**	**0.45** **1.57**	**0.15 - 1.92** **1.16 - 6.79**	**0.02**
							Category - Developed	0.96 2.62	0.65 1.92	-0.31 - 2.24 0.73 - 9.38	0.14
							Category - Grassland	-0.30 0.74	0.65 1.91	-1.57 - 0.96 0.21 - 2.62	0.64
							Category - Wetland	0.65 1.92	0.51 1.66	-0.34 - 1.64 0.71 - 5.18	0.20
							Hydric soil - Yes	**0.48** **1.62**	**0.24** **1.27**	**0.01 - 0.95** **1.01 - 2.59**	**0.04**
	CDL category	6	444.21	1.98	0.21	1.00	**Category - Agriculture**	**1.04** **2.84**	**0.45** **1.57**	**0.16 - 1.92** **1.18 - 6.83**	**0.02**
							Category - Developed	0.93 2.53	0.65 1.91	-0.34 - 2.19 0.71 - 8.97	0.15
							Category - Grassland	-0.17 0.84	0.64 1.90	-1.42 - 1.08 0.24 - 2.96	0.79
							Category - Wetland	0.67 1.95	0.50 1.65	-0.32 - 1.65 0.73 - 5.22	0.18
Central	CDL category	6	445.97	0.00	0.26	1.00	**Category - Agriculture**	**1.08** **2.95**	**0.39** **1.47**	**0.33 - 1.84** **1.38 - 6.27**	**0.01**
							Category - Developed	1.34 3.89	0.81 2.24	-0.22 - 2.94 0.80 - 18.94	0.09
							Category - Grassland	0.58 1.79	0.46 1.58	-0.31 - 1.48 0.73 - 4.38	0.20
							Category - Wetland	**0.94** **2.56**	**0.41** **1.50**	**0.14 - 1.73** **1.15 - 5.66**	**0.02**
	Dist to emergent wetlands (log)	3	447.11	1.14	0.15	0.51	log(Dist to emergent wetlands)	0.17 1.19	0.11 1.12	-0.05 - 0.39 0.96 - 1.48	0.12

	CDL category + Hydric soil	7	447.69	1.72	0.11	1.00	**Category - Agriculture**	**1.06** **2.89**	**0.39** **1.47**	**0.30 - 1.82** **1.35 - 6.16**	**0.01**
							Category - Developed	1.35 3.88	0.81 2.24	-0.23 - 2.94 0.80 - 18.89	0.09
							Category - Grassland	0.55 1.73	0.46 1.58	-0.35 - 1.45 0.70 - 4.26	0.23
							Category - Wetland	**0.93** **2.54**	**0.41** **1.50**	**0.14 - 1.73** **1.15 - 5.63**	**0.02**
							Hydric soil - Yes	0.18 1.19	0.29 1.34	-0.40 - 0.75 0.67 - 2.12	0.54
South	In wetland	3	255.11	0.00	0.16	1.00	In wetland - Yes	-0.22 0.80	0.30 1.35	-0.81 - 0.36 0.45 - 1.44	0.46
	Dist to wetlands (log)	3	255.15	0.03	0.15	0.90	log(Dist to wetlands)	0.03 1.03	0.04 1.04	-0.05 - 0.12 0.95 - 1.12	0.47
	Hydric soil	3	255.29	0.18	0.14	0.98	Hydric soil - Yes	-0.19 0.83	0.31 1.36	-0.79 - 0.41 0.45 - 1.51	0.54
	Protected area	3	255.45	0.34	0.13	1.00	Protected - Yes	-0.15 0.86	0.31 1.37	-0.76 - 0.47 0.47 - 1.59	0.64
	Dist to emergent wetlands (log)	3	255.61	0.50	0.12	0.23	log(Dist to emergent wetlands)	-0.02 0.98	0.08 1.08	-0.17 - 0.13 0.85 - 1.14	0.81
	Dist to roads (log)	3	255.64	0.53	0.12	0.21	log(Dist to roads)	0.02 1.02	0.13 1.14	-0.23 - 0.27 0.80 - 1.31	0.86
	CDL category	5	257.04	1.93	0.06	1.00	Category - Developed	-0.47 0.63	0.75 2.12	-1.94 - 1.00 0.14 - 2.72	0.53
							Category - Grassland	-0.18 0.83	0.55 1.74	-1.27 - 0.91 0.28 - 2.47	0.74
							Category - Wetland	-0.64 0.53	0.44 1.56	-1.51 - 0.23 0.22 - 1.26	0.15

Table 6. Results of ANOVAs with post-hoc Tukey multiple comparisons of means comparing proportions of observations of wintering Whooping Cranes in various water depths and vegetation heights, during two winters (2015 - 2016) in the Eastern Migratory Population. Data from three regions (north, central, south) were either pooled or analyzed separately. Water depth categories were dry, shallow, and deep. Vegetation height categories were none, short, and tall. P-values less than 0.05 are in bold text and are considered significant. There were no differences in observations in three vegetation height categories when analyzed separately by region, so we did not do pairwise comparisons with Tukey tests.

Habitat characteristic tested	**Region**	**Test statistic (F)**	**Degrees of freedom (df1, df2)**	**Overall *P*-value**	**Categories compared**	**Difference in observed means**	**Post-hoc *P*-value**
Water depth	pooled	55.73	2, 81	***P* < 0.0001**	Shallow - dry	-0.453	**0.020**
					Deep - dry	-1.683	**0.000**
					Deep - shallow	-1.230	**0.000**
Water depth	north	32.47	2, 27	***P* < 0.0001**	Shallow - dry	-0.908	**0.003**
					Deep - dry	-2.003	**0.000**
					Deep - shallow	-1.095	**0.000**
Water depth	central	21.07	2, 33	***P* < 0.0001**	Shallow - dry	-0.023	0.995
					Deep - dry	-1.427	**0.000**
					Deep - shallow	-1.404	**0.000**
Water depth	south	8.523	2, 15	**0.003**	Shallow - dry	-0.553	0.391
					Deep - dry	-1.661	**0.003**
					Deep - shallow	-1.108	**0.041**
Vegetation height	pooled	3.826	2, 84	**0.026**	Short - none	0.270	0.402
					Tall - none	-0.307	0.310
					Tall - short	-0.576	**0.019**
Vegetation height	north	2.817	2, 27	0.077	All categories		0.077
Vegetation height	central	1.86	2, 33	0.17	All categories		0.172
Vegetation height	south	2.08	2, 18	0.154	All categories		0.154

Table 7. Post-hoc chi-square analysis results for association between behavior and habitat used by Whooping Cranes in winters 2015 - 2016 in the north region. There were no differences in behaviors associated with habitats in the central or south regions ($P > 0.05$). *P*-values in bold text are < 0.05 and are considered significant.

Comparison	**Raw *P*-value**	**Adjusted *P*-value**
grassland vs. agriculture	**0.0425**	0.0637
grassland vs. wetland	0.6083	0.6083
agriculture vs. wetland	**0.0013**	**0.0039**

Appendix 1. Data for this project were collected for all of the following groups of Whooping Cranes in the Eastern Migratory Population during two winters, 2015 - 2016. Depending on the number of recorded used locations and if the water depth, vegetation height, or behavior were observed, a subset of these groups were used in each of the analyses. In the daily home range size, water depth, vegetation height, behavior, or habitat characteristics columns below, a “y” indicates the group was included in this analysis, while an “n” indicates not enough data were available for the inclusion of this group in that particular analysis.

Group ID (WCEP ID of focal bird)	Year	State / Region	Site name	Social group size/ type	WCEP IDs of other cranes present	Daily home range size	Water depth	Vegetation height	Behavior	Habitat characteristics
A (19_14)	2015	GA south	Lowndes Co	3 / family	7_07, 39_07	y	y	y	y	y
B (4_12)	2015	FL south	St. Marks NWR	8 / group	Semi - captive juveniles	n	y	y	y	y
C (7_13)	2015	FL south	St. Marks NWR	4 / group	2_13, 4_13, 8_13	n	y	y	y	y
D (12_11)	2015	AL central	Wheeler NWR	7 / group	5_11, 1_11, 6_11, 15_11, 59_13, 38_08	y	y	y	y	y
E (19_11)	2015	AL central	Wheeler NWR	2 / pair	17_11	n	n	y	n	y
F (13_02)	2015	AL central	Wheeler NWR	2 / pair	18_02	y	y	y	y	y
G (24_08)	2015	AL central	Madison Co	2 / pair	14_08	y	n	n	n	y
H (7_11)	2015	AL central	Morgan Co	2 / pair	10_11	y	y	y	y	y
I (26_07)	2015	AL central	Cherokee Co	2 / pair	11_02	y	y	y	y	y
J (20_14)	2015	AL central	Jackson Co	3 / family	13_03, 9_05	y	y	y	y	y
K (5_05)	2015	TN central	Hiwassee WR	2 / pair	32_09	y	y	y	y	y
L (22_13)	2015	TN central	Hiwassee WR	3 / group	37_07, 20_11	n	y	n	n	y
M (57_13)	2015	TN central	Hiwassee WR	1 / single	none	n	n	n	n	y
N (24_09)	2015	KY north	Hopkins Co	7 / group	2_04, 25_09, 42_09, 1_10, 27_14, W1_06	y	n	n	n	n
O (36_09)	2015	IN north	Goose Pond FWA	2 / pair	18_03	y	y	y	y	y
P (7_12)	2015	IN north	Goose Pond FWA	6 / group	17_07, 34_09, 8_10, 4_08, 10_09	y	n	y	y	y

Q (6_09)	2015	IN north	Greene Co	3 / group	3_11, 23_10	y	y	y	y	y
R (7_09)	2015	IN north	Gibson Co	3 / group	26_10, 16_04	y	n	n	y	y
S (16_07)	2015	IN north	Gibson Co	2 / pair	16_02	y	y	y	y	y
T (19_09)	2015	IN north	Gibson Co	4 / group	25_10, 14_09, 12_09	y	n	n	n	y
U (39_07)	2016	GA south	Lowndes Co	2 / pair	7_07	y	y	y	y	y
V (20_15)	2016	LA south	St. Martin Parish	1 / single	none	y	n	y	y	y
W (7_14)	2016	FL south	St. Marks NWR	3 / group	4_13, 5_12	y	y	y	y	y
X (4_12)	2016	FL south	St. Marks NWR	3 / group	3_14, 9_14	y	y	y	y	y
Y (4_14)	2016	FL south	St. Marks NWR	1 / single	none	n	n	n	n	y
Z (8_14)	2016	FL south	Highlands Co	unk	unk	n	n	n	n	y
AA (15_09)	2016	AL central	Cherokee Co	unk	11-02, unk	n	n	n	n	n
AB (14_15)	2016	AL central	Wheeler NWR	1 / single	none	y	y	y	y	y
AC (3_04)	2016	AL central	Wheeler NWR	3 / family	9_03, W18_15	y	y	n	y	y
AD (24_08)	2016	AL central	Madison Co	2 / pair	14_08	y	y	y	y	y
AE (27_14)	2016	AL central	Wheeler NWR	1 / single	none	y	n	y	n	y
AF (1_04)	2016	AL central	Wheeler NWR	2 / pair	8_05	y	y	y	y	y
AG (37_07)	2016	AL central	Jackson Co	2 / pair	20_14	y	y	y	y	y
AH (2_04)	2016	KY north	Hopkins Co	3 / family	25_09, W10_15	y	y	y	y	y
AI (13_02)	2016	KY north	Hopkins Co	4 / group	18_02, 1_10, W1_06	y	y	y	y	y

AJ (24_09)	2016	KY north	Hopkins Co	2 / pair	42_09	y	y	y	y	y
AK (67_15)	2016	IL north	Randolph Co	4 / group	61_15, 62_15, 63_15	y	n	n	n	y
AL (16_02)	2016	IN north	Knox Co	3 / group	16_07, 12_05	y	y	y	y	y
AM (29_09)	2016	IN north	Knox Co	2 / pair	12_03	y	y	y	y	y
AN (19_14)	2016	IN north	Knox Co	2 / pair	29_08	y	y	y	y	y
AO (12_02)	2016	IN north	Goose Pond FWA	3 / group	4_11, 19_10	y	y	n	y	y
AP (65_15)	2016	IN north	Goose Pond FWA	3 / family	W3_10, 8_04	y	n	n	n	y
AQ (36_09)	2016	IN north	Goose Pond FWA	2 / pair	18_03	y	n	n	y	y

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