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HABITAT SELECTION AND CON- AND HETEROSPECIFIC ASSOCIATIONS OF WINTERING WHOOPING CRANES AT WHEELER NATIONAL WILDLIFE REFUGE, ALABAMA

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Abstract: Winter ecology of the Eastern Migratory Population of whooping cranes (*Grus americana*) has received less detailed study than that of other life stages or the Aransas-Wood Buffalo Population. Increased winter use of novel sites by these cranes makes understanding the mechanisms contributing to habitat selection and use important for efficient conservation. As a subset of a larger and ongoing project, this study examined the individual and temporal variations of occupancy times, habitat types used, and co-occurrence with con- and heterospecifics during winters 2014-15 and 2015-16 at Wheeler National Wildlife Refuge, Alabama, while considering the effect of individual life histories (e.g., breeding status, release method). In total, 27 and 21 whooping cranes were observed during the 2 winters, respectively. Individuals varied in their habitat preference and in co-occurrence with con- and heterospecifics. Mated pairs showed a higher use of wetlands than unmated individuals, which were found more in crops left for wildlife use. Unmated individuals were more often found associating with other whooping and sandhill cranes (*G. canadensis*) than mated pairs. Compared to the first winter in 2014-15, the warmer temperature in 2015-16 likely influenced delayed arrival times while reduced wetland availability may be linked to shorter duration of stay and other temporal variation in habitat selection and co-occurrence. Our findings suggest that multiple management strategies would be needed for effective conservation because of varied habitat preference among individuals. Additionally, understanding environmental influence on occupancy times could offer managers management tools by being able to better predict crane arrival and duration of stay.

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Key words: Alabama, co-occurrence, *Grus americana*, habitat, Wheeler National Wildlife Refuge, whooping crane, wintering.

Captive breeding and the attempts to establish reintroduced populations of whooping cranes (*Grus americana*) have been conservation tools that have helped the number of whooping cranes grow from 21 individuals in winter 1944-45 (CWS and USFWS 2005) to over 600 individuals in 2013 (Harrell and Bidwell 2013). Although the success of these efforts has been mixed (Wells et al. 1998, Harrell and Bidwell 2013), the Eastern Migratory Population (EMP), which started in 2001, is still an ongoing effort (Harrell and Bidwell 2016). Understanding the mechanisms influencing the habitat selection and use and how environmental variables influence these choices is critical for effective management of these new populations.

The original management design for the EMP was to establish breeding grounds in Wisconsin with winter grounds in west-central Florida (Horwich 2001). Over the years, the EMP has extended its winter range beyond the latter area; in winter 2014-15 as much as 85% of the 103 individuals in the population was distributed from Indiana through the southeastern United States outside of Florida (WCEP 2014). Increased use of new

sites warrants investigation to identify the areas being used, the mechanisms driving habitat selection, and if temporal variations in selection occur.

Weather during the winter season can influence temporal variation in bird behavior in different ways. Temperature and rainfall could influence food availability, which can affect arriving and departure times for winter migration (Gordo 2007) and spring migration (Marra et al. 2005, Gordo 2007). Winter weather conditions (e.g., wind and temperature) can influence foraging behaviors in some species (Grubb 1975), and cranes of the Aransas-Wood Buffalo Population (AWBP) have been observed using different habitats in times of inclement weather (Wright et al. 2014). Rainfall can affect the habitat availability for cranes that are reliant on wetlands for foraging, as observed in red-crowned cranes (*G. japonensis*) (Ma et al. 1999); draining of flooded areas, a typical practice in areas managed for waterfowl (Smith et al. 1989), can affect the availability of roosting sites, as seen in sandhill cranes (*G. canadensis*) in California (Pogson and Lindstedt 1991).

Whooping cranes are known to associate with heterospecifics; approximately one-third of all AWBP roosting and feeding areas during migration were associated with sandhill cranes (Austin and Richert 2005), and members of the EMP have been found associating with sandhill cranes as well (Urbanek et al. 2014). In general, negative impacts could occur when competition for resources increases from conspecifics (Goss-Custard 1980, Vahl et al. 2005), and heterospecifics (see Pieman and Robinson 2010). However, social cues given by con- and heterospecifics can play a role in habitat selection, and offer benefits such as reducing predation risk and indications of habitat quality (Thomson et al. 2003).

Other factors including age, reproductive status, and in the case of reintroduction efforts, breeding and release techniques, can also influence differences in habitat selection and use. Adult common cranes (*G. grus*) tend to be more vigilant and partake in resting and preening activities while juveniles forage, but adults tend to be less vigilant when in larger flocks (Alonso et al. 2004). Avilés et al (2002) also found differences in habitat selection between the adults with juveniles and those without in common cranes. Among the sandhill cranes, family units have been found in less densely populated areas more often than non-family units in winter (Lovvorn and Kirkpatrick 1982). Also, the EMP is mostly captive bred and most of the releases into the wild have been coupled with aided migration (USFWS 2001). Additional rearing and release techniques (CWS and USFWS 2005) were used as this program grew (e.g., DAR [direct autumn release] and parent-rearing). It is plausible that some individual variation of overwintering behaviors could be a byproduct of different release methods (see McDougall et al. 2006).

This study examined the individual and temporal variation in habitat selection by whooping cranes and possible contributing mechanisms at Wheeler National Wildlife Refuge (WNWR), Alabama. This was the first study of its kind at this site, and our goal was to provide some scientific foundation for ongoing and future studies at this site, while contributing to knowledge of the wintering ecology of this population. This site was chosen due to its relatively large number of wintering whooping cranes, roughly 25% of the EMP during winter 2013-14 (WCEP 2013), and its heterogeneous land cover. Additionally, whooping cranes co-occupy the Refuge with >15,000 wintering sandhill cranes

(WNWR, unpublished data). Our objectives were to: 1) identify habitats used by whooping cranes and determine if individual and temporal differences existed; 2) quantify the co-occurrence with con- and heterospecifics; 3) determine if habitat selection and co-occurrence varied among individuals with different individual life history traits; and 4) examine the relationship between weather and habitat availability and how that affected crane behaviors such as occupancy times, habitat selection, and co-occurrence.

STUDY AREA

The study site, WNWR, is located in Madison, Limestone, and Morgan counties of northern Alabama (Fig. 1). The Refuge encompasses 14,614 ha, with 1,653 ha being within the boundaries of Redstone Arsenal, a U.S. Army installation; a portion of this shared boundary is administered by the Marshall Space Flight Center, a center for the National Aeronautics and Space Administration (USFWS 2007). The WNWR was established in 1938 primarily for waterfowl and was the first NWR superimposed on a hydro-electric

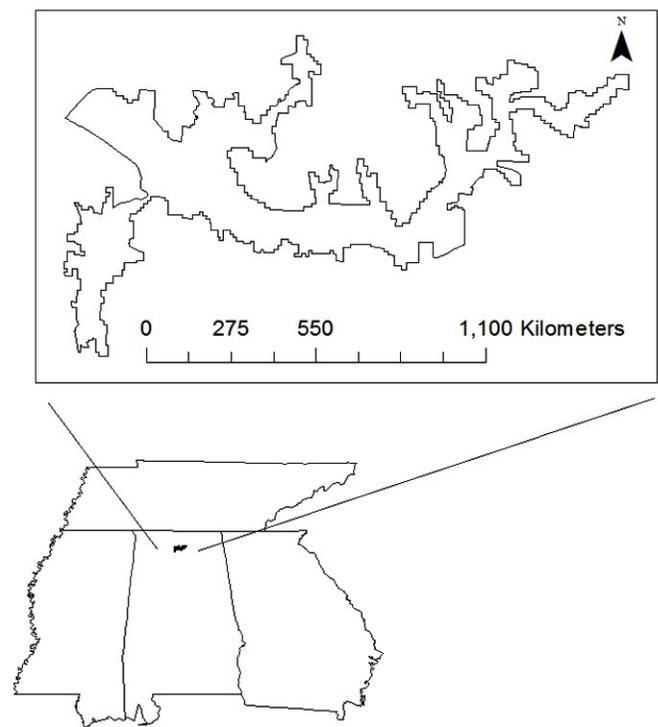


Figure 1. Location and boundary of Wheeler National Wildlife Refuge, Alabama, where whooping cranes were surveyed during the winters of 2014-15 and 2015-16.

impoundment. The WNWR is intersected by the Tennessee River, governed by the Tennessee Valley Authority, which flows centrally through from east to west, dividing the WNWR into north and south sections. Naturally occurring wetlands are present, ranging from small ephemeral ponds to large rivers and sloughs that directly flow into the Tennessee River. There are also 16 impoundments managed to provide approximately 809 ha of open water and flooded field habitat, some of which are permanent water bodies whereas others are low lying croplands or fields that are flooded during the winter and typically drained before the next planting season (USFWS 2007). The WNWR is also composed of upland and bottomland forests and agricultural lands. Cooperative farming supplies additional food resources to wildlife by means of harvest gleanings and crop shares; crop shares are patches of or whole crops, typically corn, that are left unharvested but usually knocked down to serve as a supplemental food resources for wildlife during the colder months (USFWS 2007).

METHODS

We collected data during winters 2014-15 and 2015-16. Individuals were observed at least 3 times a week after each individual's arrival until departure from WNWR. All observations were made during the day, and efforts were made to obtain observations across different times of day (e.g., early morning, mid-afternoon, late day). Cranes were located by using radio telemetry, visual searches, and data obtained from satellite tags enabled with global positioning system (GPS). We identified individuals from recording unique leg band combinations. All GPS transmitters, VHF transmitters, and leg bands were attached to birds by other entities (see Urbanek et al. 2014). Once an individual was located, the habitat type was recorded as 1 of the following: wetland, harvested soybean, harvested corn, or crop share.

We determined if there were differences of co-occurrence with con- and heterospecifics by recording the presence and number of both whooping cranes and sandhill cranes that were within an estimated 50 m from an individual whooping crane. In the case of a mated pair (defined as any pair that either nested or was paired during the previous breeding season) or flock, a single central point that best represented the location of the individuals was visually estimated from

which co-occurrence data were collected. The central point method was used as there is a lack of statistical independence with mated individuals and those associating as a flock.

Temporal differences were determined between and within the years. For each winter, the year was divided into 3 seasons including early (1 Nov-20 Dec), middle (21 Dec-8 Feb), and late period (9 Feb-31 Mar). These equally divided dates were based on data of whooping crane occupancy collected by WNWR (WNWR, unpublished data) and mirror other studies such as Zhou et al. (2010). We also examined whether breeding status (unmated individual or mated pair) and reintroduction method (ultralight-aided, direct autumn release, or parent-reared [CWS and USFWS 2005]) influenced habitat use and co-occurrence with con- and heterospecifics. Both the individuals from the ultralight-aided and direct autumn release programs were costume-reared but were separated based on the different migration strategy.

A standardized date value was set using 1 November as day 1 to assist in the analyses related to seasonal time; 1 November was used because whooping cranes would start arriving in November but never prior to that date (WNWR, unpublished data). We obtained measures of total daily rainfall (cm) and average daily temperature (°C) from a locally based weather station (Global Historical Climatology Network Data: USW00003856). During this study we observed several rain events that made water levels too high for cranes to inhabit natural wetlands, warranting the need for some quantification of wetland availability (i.e., wetlands with water depths appropriate for crane use). With 1 exception, whooping cranes did not use managed impoundments but used natural wetlands connected to the Tennessee River. Daily water depth data (feet) were obtained from a local stream gauge along the Tennessee River (U.S. Geological Survey, 03577150). We used data from the stream gauge to develop a daily standardized wetland score for these natural wetlands which ranged from 0 to 100, with 100 being the most available (i.e., lowest water depth) and 0 being the value when water levels were determined too high for cranes, which we found to be when the water depth at the gauge reached 2.18 m; at this level cranes no longer used nearby natural wetlands for roosting or foraging.

All units were converted to metric when needed and statistics were performed using SPSS v. 24 (IBM Corp., Armonk, NY, USA). Independent *t*-tests were performed

to evaluate differences in temperature, rainfall, and wetland availability for each winter. The standardized date values of returning individuals were analyzed to determine differences in arrival, departure, and duration times with paired *t*-tests. Two separate analyses were done to examine habitat selection and co-occurrence. First, general linear multivariate models were used to explore the differences of habitat types used and co-occurrence parameters across individuals and life history traits using Pillai's trace (*V*) as the test statistic, followed by analysis of variance (ANOVA) and Tukey multiple comparisons. To examine yearly and seasonal differences and their interactions in habitat types used and co-occurrence parameters, we used linear mixed models for repeated measures with individuals being the subject and season being the repeated measure. Linear mixed models also helped to deal with incomplete data through the season for some individuals. All tests were declared significant at $P < 0.05$.

RESULTS

During winters 2014-15 and 2015-16, a total of 27 and 21 whooping cranes, respectively, used WNWR; 78% and 90%, respectively, were returning individuals from previous years (Table 1). Those returning individuals arrived on average 8 days earlier ($t_{13} = -2.94$, $P = 0.012$) and departed on average 32 days later ($t_{13} = 4.1$, $P = 0.001$), resulting in a 184% longer duration of stay the first winter compared to the

second ($t_{13} = 4.76$, $P < 0.001$) (Table 1). The average temperature was 3.7°C colder ($t_{225} = -4.78$, $P < 0.001$), and had an 84% higher average wetland score ($t_{155} = 11.49$, $P < 0.001$) during the first winter compared to the second, though there was no difference in the amount of rainfall between the 2 winters ($t_{170} = -1.49$, $P = 0.139$) (Table 1).

A season-by-year interaction was detected (Table 2) for harvested cornfield use, indicating a reversal pattern of use between the 2 winters. Use of harvested cornfields increased across the 3 seasons during the first winter but decreased across seasons in the second winter (Fig. 2; $F_{2,43} = 4.17$, $P = 0.022$). Harvested soybean fields were used more during the early and mid-seasons and not used at all during the late season ($F_{2,42} = 19.13$, $P < 0.001$); however, the interaction between season and winter indicated that in the second year, harvested soybean fields were used 46% more in the early season with a 63.6% increase during the mid-season, whereas a 73.3% decrease was observed between the 2 seasons during the first winter (Table 2, Fig. 3; $F_{2,36} = 12.91$, $P < 0.001$). Crop share use was 147% higher in the second winter than the first (Table 2, $F_{1,68} = 48.81$, $P < 0.001$). Crop share usage increased 87% from early to mid-season during the first winter and 52.8% in the second winter, ($F_{2,50} = 27.92$, $P < 0.001$), but a season-by-winter interaction indicated that crop share use at the late season decreased during the first winter but increased in the second winter (Table 2, Fig. 4; $F_{2,50} = 49.6$, $P < 0.001$). Wetland use only differed by year,

Table 1. Number of whooping cranes and differences of occupation timelines (days) for reoccurring individuals and environmental factors (mean ± SE) at Wheeler National Wildlife Refuge, Alabama, during the winters of 2014-15 and 2015-16. Arrival, departure, and duration times are based on a standardized date value starting with 1 November = 1. Environmental data were collected from U.S. Geological Survey and National Oceanic and Atmospheric Administration databases; wetland availability is a standardized score of 0-100, where 0 represents when water levels were too high for cranes and 100 being when wetlands were most available.

	2014-15	2015-16	<i>n</i>	<i>t</i>	<i>P</i>
No. of whooping cranes	27	21			
No. of new individuals	7	3			
Arrival	51.6 ± 6.7	59.1 ± 6.0			
Departure	117.0 ± 6.7	79 ± 6.3			
Duration	66.4 ± 11.0	21.0 ± 5.9			
Arrival ^a	49.6 ± 5.5	57.5 ± 6.6	14	-2.94	0.012
Departure ^a	110.4 ± 4.7	78.2 ± 7.1	14	4.1	0.001
Duration ^a	61.8 ± 9.0	21.7 ± 6.6	14	4.76	0.000 ^b
Daily wetland availability	71.5 ± 1.3	39.5 ± 2.9	94, 103	11.5	0.000
Total daily rainfall (cm)	0.3 ± 0.1	0.6 ± 0.2	119	-1.49	0.139
Average daily temperature (°C)	6.3 ± 0.5	10.0 ± 0.6	119	-4.78	0.000

^a Statistical test performed on individuals that were present during both winters.

^b *P* values reported as 0.000 indicate $P < 0.001$.

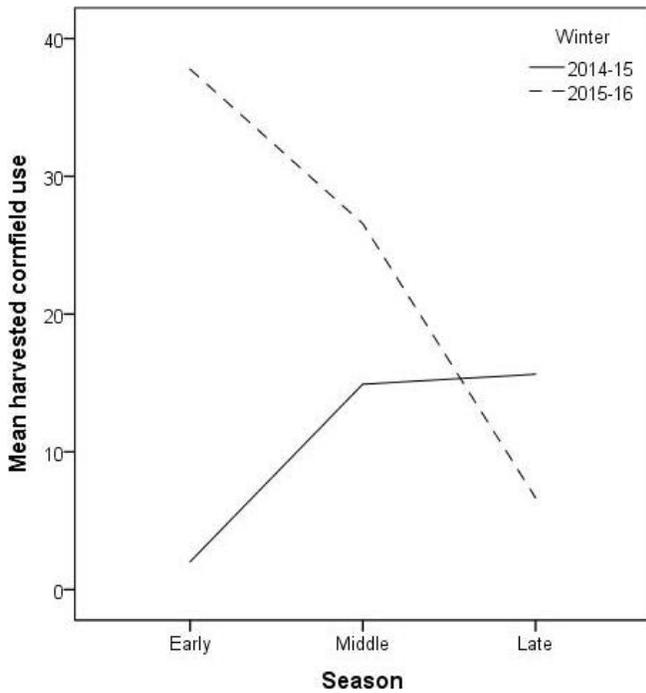


Figure 2. Seasonal and yearly differences in the mean number of observations that whooping cranes used harvested cornfields at Wheeler National Wildlife Refuge, Alabama, during the winters of 2014-15 and 2015-16.

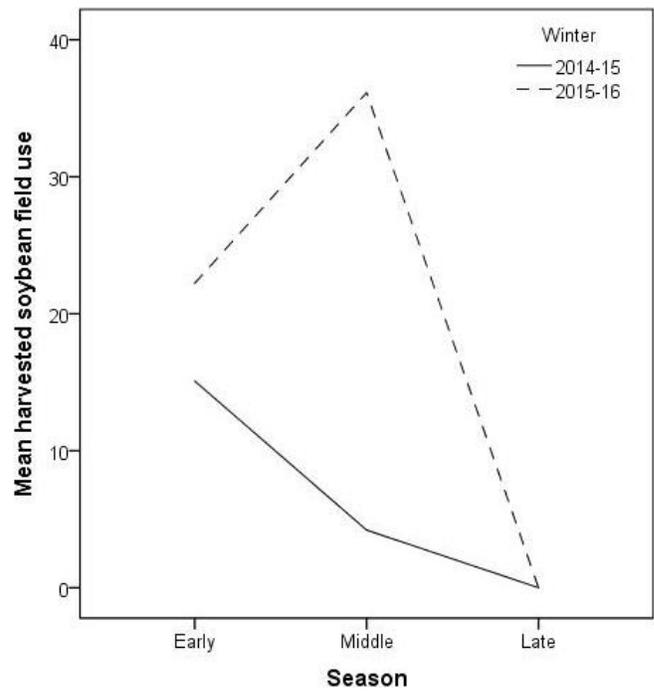


Figure 3. Seasonal and yearly differences in the mean number of observations that whooping cranes used harvested soybean fields at Wheeler National Wildlife Refuge, Alabama, during the winters of 2014-15 and 2015-16.

decreasing 88.6% in the second winter (Table 2, $F_{1,49} = 65.38, P < 0.001$).

Individuals differed in their preference of habitat types ($V = 2.12, F_{29,156} = 1.9, P < 0.001$), with the different usage being in wetlands ($F_{29,49} = 2.44, P =$

0.003) and crop shares ($F_{29,49} = 2.59, P = 0.002$); further analysis showed that individuals of different breeding status differed in use among habitat types ($V = 0.20, F_{4,72} = 4.48, P = 0.003$). Unmated individuals were observed 143% more often in crop shares than mated

Table 2. Temporal differences in whooping crane (WC) habitat use and co-occurrence with con- and heterospecifics (i.e., sandhill cranes [SC]) at Wheeler National Wildlife Refuge, Alabama, during the winters of 2014-15 and 2015-16. Data presented as mean \pm SE of the number of observations of whooping cranes in a specific habitat type, and the number of observations co-occupying areas with con- and heterospecifics, and their abundance.

	2014-15			2015-16			P		
	Early	Middle	Late	Early	Middle	Late	Season	Year	Season by year
Corn	2.0 \pm 1.4	14.9 \pm 4.1	15.6 \pm 3.4	37.8 \pm 20.1	25.6 \pm 12.8	6.7 \pm 6.7	0.267	0.055	0.022
Soybeans	15.1 \pm 6.4	4.2 \pm 1.7	0.0 \pm 0.0	22.2 \pm 7.0	36.1 \pm 10.1	0.0 \pm 0.0	0.000 ^b	0.078	0.000
Wetland	64.2 \pm 9.9	52.3 \pm 7.2	74.8 \pm 5.2	17.8 \pm 7.0	4.8 \pm 1.8	0.0 \pm 0.0	0.320	0.000	0.133
Crop share ^a	14.7 \pm 2.8	27.4 \pm 6.6	6.7 \pm 2.6	21.1 \pm 6.8	32.3 \pm 8.8	93.3 \pm 6.7	0.000	0.000	0.000
WC %	59.9 \pm 10.0	65.8 \pm 7.3	73.8 \pm 8.4	54.4 \pm 20.8	65.9 \pm 13.1	80.0 \pm 20.0	0.369	0.977	0.917
No. WC	1.0 \pm 0.2	2.4 \pm 0.3	4.5 \pm 0.5	1.3 \pm 0.4	1.4 \pm 0.3	2.2 \pm 0.6	0.018	0.000	0.054
SC %	70.9 \pm 9.0	68.8 \pm 3.9	72.9 \pm 6.6	57.2 \pm 11.0	74.4 \pm 13.0	93.3 \pm 6.7	0.16	0.584	0.241
No. SC	94.0 \pm 40.3	88.8 \pm 17.4	46.4 \pm 6.4	126.2 \pm 40.0	157.3 \pm 36.15	235.33 \pm 42.72	0.533	0.001	0.008

^a Crop share fields are areas of unharvested corn used for supplementary food management.

^b P values reported as 0.000 indicate $P < 0.001$.

individuals ($F_{1,75} = 10.85, P = 0.002$), while mated pairs were observed 71.4% more often in wetlands (Table 3, $F_{1,75} = 7.19, P = 0.009$). No differences were detected for individuals with different introduction methods.

Whooping cranes were observed associating with a greater number of other whooping cranes during the first winter ($F_{1,38} = 6.09, P = 0.02$) while co-occupying areas with a greater number of sandhill cranes the second winter (Table 2, $F_{1,31} = 14.67, P = 0.001$). A season-by-year interaction ($F_{2,32} = 5.61, P = 0.008$) revealed the number of sandhill cranes utilizing the same area around whooping cranes decreased over the seasons during the first winter but was the opposite the second year, including an 49.6% increase between the mid- and late season (Table 2, Fig. 5). Whooping crane shared use with conspecifics increased through the seasons ($F_{2,34} = 10.0, P < 0.001$), though this trend was more ambiguous during the second winter, resulting in a non-significant season-by-year interaction (Table 2, $F_{2,24} = 3.18, P = 0.054$).

Individual whooping cranes differed in the number of times observed co-occupying areas with other whooping cranes ($F_{29,49} = 301.92, P < 0.001$) and

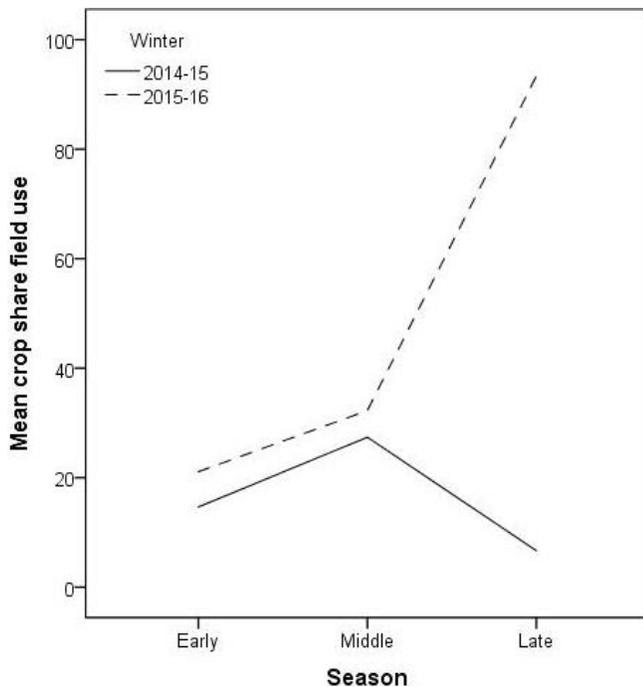


Figure 4. Seasonal and yearly differences in the mean number of observations that whooping cranes used crop share fields at Wheeler National Wildlife Refuge, Alabama, during the winters of 2014-15 and 2015-16. Crop shares were cornfields that were left unharvested and typically knocked down to provide supplementary food resources.

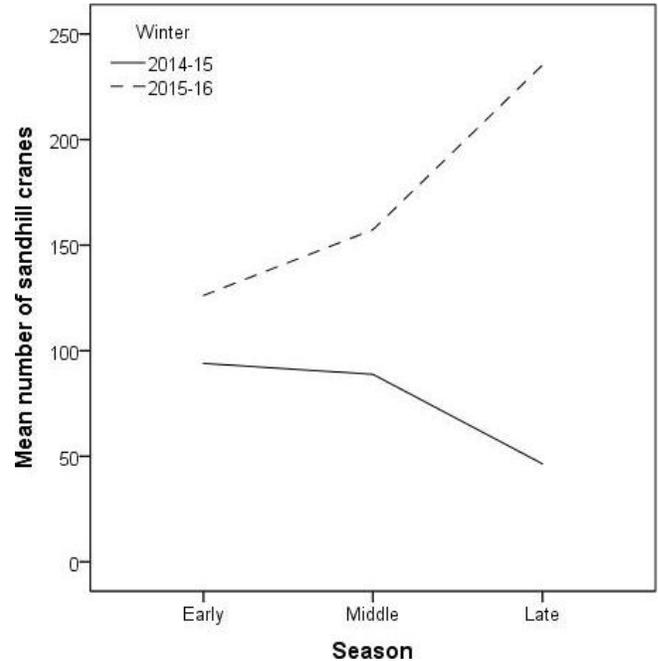


Figure 5. Seasonal and yearly differences in the mean number of sandhill cranes observed within 50 m of whooping cranes at Wheeler National Wildlife Refuge, Alabama, during the winters of 2014-15 and 2015-16.

sandhill cranes ($F_{1,49} = 638.0, P < 0.001$), and in the number of co-occurring sandhill cranes ($F_{29,49} = 3.27, P < 0.001$). No differences were detected based on release method, but differences were detected among individuals of different breeding status (Table 3, $V = 0.24, F_{4,72} = 5.65, P = 0.001$). Unmated individuals were 44.8% more frequently occupying areas with other whooping cranes ($F_{1,75} = 6.6, P = 0.012$) and 31.5% more frequently with sandhill cranes ($F_{1,75} = 11.42, P = 0.001$), and the number of associating sandhill cranes was 143% higher ($F_{1,75} = 18.02, P < 0.001$) than what was observed for mated pairs (Table 3).

DISCUSSION

We found that members of the EMP at WNWR showed both individual and temporal variation in habitat selection and shared use with con- and heterospecifics. Understanding how members of this population select and use areas across a heterogeneous landscape and quantifying the variation within those areas are pivotal for effective management. In the case of the EMP, the majority of the population winters across several eastern

Table 3. Whooping crane (WC) habitat use and co-occurrence with con- and heterospecifics (i.e., sandhill cranes [SC]) by breeding status and release method at Wheeler National Wildlife Refuge, Alabama, during the winters of 2014-15 and 2015-16. Data presented as mean \pm SE of the number of observations of whooping cranes in a specific habitat type, and the number of observations co-occupying areas with con- and heterospecifics, and their abundance.

	Breeding status			Release method			
	Unmated	Mated	<i>P</i>	Ultralight	DAR ^a	Parent-reared	<i>P</i>
Corn	12.9 \pm 5.0	18.2 \pm 3.8	0.473	18.0 \pm 4.2	11.3 \pm 4.3	23.7 \pm 13.4	0.499
Soybeans	11.2 \pm 3.9	10.3 \pm 3.0	0.721	11.1 \pm 3.6	10.0 \pm 3.0	10.5 \pm 6.9	0.931
Wetland	31.8 \pm 6.8	54.5 \pm 5.2	0.009	48.3 \pm 5.7	47.8 \pm 7.2	26.4 \pm 14.6	0.318
Crop share ^b	39.9 \pm 5.3	16.5 \pm 4.1	0.002	21.6 \pm 4.6	27.5 \pm 5.5	39.0 \pm 13.9	0.577
WC %	83.2 \pm 5.7	57.5 \pm 5.6	0.012	60.3 \pm 5.9	80.9 \pm 5.8	59.0 \pm 18.6	0.22
No. WC	2.8 \pm 0.3	2.2 \pm 0.3	0.252	2.3 \pm 0.3	2.6 \pm 0.3	2.5 \pm 1.0	0.934
SH %	84.4 \pm 5.1	64.19 \pm 3.8	0.001	69.3 \pm 4.0	76.1 \pm 6.0	70.1 \pm 13.2	0.321
No. SH	162.3 \pm 23.5	66.8 \pm 9.5	0.000 ^c	87.5 \pm 13.3	121.3 \pm 23.7	124.3 \pm 44.6	0.468

^aDirect autumn release.

^bCrop share fields are areas of unharvested corn used for supplementary food management.

^c*P* value reported as 0.000 indicates *P* < 0.001.

states (WCEP 2013a), and these areas likely vary in terms of habitat types and quality, weather patterns, food resources, and predation pressure. Because the EMP is a reintroduced population utilizing areas not known for use by whooping cranes historically, increased research is needed on how and why these cranes select and use these areas. This study was the first dealing with whooping cranes on WNWR, so this information could help fill some knowledge gaps and potentially aid in future research and management decisions on WNWR and other areas, where applicable.

Migratory birds are influenced by a profusion of endogenous and environmental factors affecting migration timing and selection of wintering areas (Jenni and Schaub 2003). Results of the arrival and temperature suggest that members of the EMP vary in both their endogenous programming and their responses to temperature. Some individuals tended to consistently arrive early at WNWR, implying that WNWR is their intended winter site, while others, based on reports and satellite data, tended to arrive from more northerly stopover sites during times of colder weather, which tended to occur in late December-mid January during this study. The temperature during the second winter of this study was much warmer than that of the first winter and probably resulted in delayed arrival times and more individuals remaining on sites north of WNWR.

Another environmental factor that differed between the winters was wetland availability, which was lower during the second winter. There was no statistical difference in daily rainfall between the 2 winters;

however, many periods of heavy rain occurred during the second winter and caused less wetland availability for cranes (i.e., water levels were too high) and even periodically flooded fields. During these events both natural wetlands and impoundments were inundated, cresting above the flood stage, further inundating surrounding areas including croplands used for foraging; the cranes that remained on WNWR were found roosting on the edges of flooded fields, which were atypical roosting sites. Reduction in wetland availability probably caused many individuals to leave WNWR and seek habitat elsewhere during the second winter. It is also likely that these environmental differences prompted other behavioral variations such as differences in co-occurrence with con- and heterospecifics that were documented. Whooping cranes tended to aggregate with other whooping cranes, forming larger flocks over the course of the seasons, but warmer temperatures and less habitat availability during the second winter resulted in fewer cranes occupying WNWR and likely resulted in less aggregations during the second winter. The increased co-occurrence with sandhills during the second winter is likely a circumstance of necessitated aggregation due to reduced habitat availability. Future research should include improved methods to quantify individual wetland availability as our methodology was based on a single stream gauge and only provides a general assessment. Though there is a direct relationship between the wetlands we analyzed and this stream gauge, wetlands likely differ in terms of size and topography and in their availability. However,

this wetland score allowed us to make some assessment when no bathymetric data were available.

We found that individuals selected habitat types differently and that members of the EMP at WNWR could be categorized into 1 of the following categories: 1) those that preferred agricultural lands (i.e., crop shares) with little use of wetlands, 2) those that preferred wetlands with little use of agricultural lands, and 3) those that did not show a clear preference for 1 habitat type over the other. Mated pairs occupied wetlands during the day more frequently than non-mated individuals, which were found to use crop shares more frequently. We observed croplands to typically be more densely occupied by sandhill cranes than were wetlands. Having mated whooping cranes occupying areas less densely occupied is similar to findings of Lovvorn and Kirkpatrick (1982) that family units of sandhill cranes chose less occupied areas.

Breeding status of the EMP did not affect the conspecific group size as documented in the AWBP by Stehn (1997), yet unmated individuals, typically subadults in our study, did tend to associate with other whooping cranes more frequently. Our results could be due to a density-dependent threshold not yet reached (Parrish and Edelstein-Keshet 1999) because the population size is much smaller than the AWBP. This is also consistent with the observation that, although there are exceptions, many EMP cranes do not establish winter territories (Urbanek et al. 2014), unlike what has been observed for members of the AWBP (Chavez-Ramirez 1996). Common cranes have been found to be only territorial when they have young and more social in years when they do not (Alonso et al. 2004). There was only 1 mated pair with young during this study, and that family unit did not associate with other whooping cranes and minimally with sandhill cranes.

This study only examined which habitats were being used but not how they were being used. Determining and quantifying how these habitats are being used would provide more in-depth knowledge of habitat selection and could provide information on how certain mechanisms such as food availability, predator pressure, and inter- and intraspecific competition influence behavior.

MANAGEMENT IMPLICATIONS

The WNWR has been a site of increased use by both whooping and sandhill cranes. Though our study

was only over 2 winters, our findings could assist WNWR management and possibly other wintering areas inhabited by these birds. Finding that individuals differed in their habitat preference is in agreement with Hunt and Slack (1989) that management should focus both on upland and wetland habitat, whether the goals are to increase, improve, or simply conserve these habitats and the food sources contained within. Cooperative farming agreements have proved beneficial to the management of cranes at WNWR, with a large number of both whooping and sandhill cranes utilizing croplands, especially crop shares. However, a balance is needed to make sure that the farmer is given the appropriate time to optimize his yields, which in turn could produce increased yields in crop shares, yet be done on a timeline that will not cause disturbance to waterfowl and cranes; objectives will sometimes not ideally coincide within the same timeline. Therefore, most of our management implications concern the predicting of occupancy timelines and number of cranes.

Environmental factors influence planting times, and crop yields are influenced by environmental factors (Schlenker and Roberts 2009); we found they also potentially influence occupancy timelines and the number of cranes that occupy WNWR. Because weather patterns fluctuate year to year, the use of improved forecasting abilities (e.g., such as being able to better predict dominant climate cycles such as El Niño; Petrova et al. 2017) could help managers to better predict certain occupancy timelines, and estimate number of cranes. If colder weather is predicted, then more individuals will likely arrive at WNWR, and colder weather earlier in the season could indicate earlier arrival. These predictions are likely to be reversed if the prediction is for warmer weather. Also, because the number of sandhill cranes has increased over the last 2 decades (WNWR, unpublished data), it would be beneficial to increase either the number or size of crop shares to accommodate the growing population of cranes, especially if colder weather is predicted.

In the case of WNWR, being able to predict crane occupancy timelines could affect farming activities, such as when to plant the primary crop (i.e., corn or soybeans) in spring, harvest in fall, replant with wintering crops (i.e., winter wheat, where applicable) in fall, and when to knock down existing crop shares. The WNWR attempts to have crops harvested before migrating cranes and waterfowl arrive (USFWS 2007), including the knocking down of crop shares. Knocking

down crop shares too early could result in reduced food sources due to use by non-target species (e.g., species other than cranes and waterfowl). Knocking down these shares should be done within a timeline that maximizes the amount of resources left behind while also making sure it is done before cranes arrive to reduce crane disturbance, though more research is needed to determine the level of impact from such disturbances. Additionally, cranes can have negative impacts on croplands (Aborn 2010, Van Horn et al. 2010), and being able to better predict when cranes arrive and depart could help managers and farmers better plan farming times to reduce this impact by not planting when cranes are expected.

Several of the crops at WNWR were located in impoundments, which were intentionally flooded during the winter. Prolonged flooding of food items, such as corn, reduces the potential caloric value (Ringelman 1990). Though whooping cranes did not utilize these impoundments during the course of this study, with 1 exception, there is potential for future use; therefore, understanding the timing of arrival in relation to flooding should be considered to ensure minimization of this caloric reduction. Impoundments were typically held at water levels too deep for cranes to use, but most of these could be drained to result in more appropriate levels. However, WNWR, like many other refuges, is responsible for managing for waterfowl, so ensuring that water depth remains too high for cranes in certain impoundments may be beneficial by reducing competition for resources.

Lastly, water levels did influence wetland availability in the natural wetlands, and we found suggestive evidence that crane duration of stay and wetland use were influenced by the amount of this availability. Future work is needed to understand at what depth impoundments or natural wetlands need to be maintained for cranes to use them and how depth of these areas relate to quantifiable availability. The latter would likely need to be quantified on a site-by-site basis due to topological and other habitat related differences across each wetland. Also, identifying which wetlands are being used for foraging and roosting should be considered in farming regimes. Though this study did not directly address roosting activity, roosting sites were identified and could provide insights to managers on crop placements with goals to have ample croplands near roost sites to minimize travel time and increase energy reserves (e.g., central foraging theory; Pyke 1984).

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