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# HABITAT SELECTION BY BREEDING SANDHILL CRANES IN CENTRAL WISCONSIN

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**Abstract:** We used compositional analysis to describe habitat use for a dense population of breeding sandhill cranes (*Grus canadensis tabida*) in central Wisconsin at 2 spatial scales: selection of home range within a study area and selection of habitats within the home range. Habitat use and home range size were estimated from radio-telemetry data from 12 breeding sandhill crane pairs. Research in Wisconsin that was performed on the landscape level suggests that breeding cranes depend on wetlands and do not select upland habitats. Evaluating habitat selection at different spatial levels, such as during different stages of the breeding season, can better illustrate the hierarchical nature of selection by breeding sandhill cranes. In establishing home ranges, breeding cranes selected wetland habitat over all other land-use categories. Within home ranges, breeding cranes still selected wetland habitat above all other habitat types; however, row crops and tall grass were also important. During daylight hours, habitats that were used consisted primarily of wetland ( $38.7\% \pm 4.5$  [mean  $\pm 1$  SE]), row crop ( $24.3\% \pm 5.7$ ), and short crop ( $14.0\% \pm 4.6$ ). Home range size as well as the selection of habitat type was not constant during the breeding season. On average, home range size during the post-fledging stage was 3 times greater than pre-fledging stage. Wetlands were used daily (97.4% of all days) throughout the breeding season but for a greater percentage of each day when chicks were small than when large. Wetland accounted for 50.1% of all locations during the pre-fledging stage and for 30.6% of all locations during the post-fledging stage. The knowledge that breeding cranes require emergent wetlands at all spatial and temporal scales, but that the presence of both upland and wetland habitat within a home range is important, provides a greater refinement to the understanding of habitat needs of breeding sandhill cranes in Wisconsin.

## PROCEEDINGS OF THE NORTH AMERICAN CRANE WORKSHOP 13:1-12

**Key words:** compositional analysis, greater sandhill crane, *Grus canadensis tabida*, radio-telemetry, seasonal habitat shifts.

Resource selection studies are common in wildlife research because determining which resources are selected provides basic information about the ecology of animals and how they meet their needs for survival (Manly et al. 2004). Resource selection studies have become an important tool in conservation biology and wildlife management (Leopold 1933, Pulliam and Dunning 1997, Garshelis 2000). Though frequently conducted, resource selection studies often produce contradictory results. A common problem of these studies is unclear definitions of basic terms (Jones 2001). Hall et al. (1997) reviewed 50 recent articles to compare how these studies defined habitat terms such as “use” and “availability” and found only 18% followed standard terminology.

Defining the appropriate geographical and temporal scales is another common problem with many resource selection studies. Resource selection can be categorized at a hierarchical order of spatial scale from geographic range (first order), to individual home range (second

order), to habitats within the home range (third order), and to selection of certain items within a habitat (fourth order) (Johnson 1980). The criteria for selection of specific resources may be different at each level (Johnson 1980, Alldredge et al. 1998). If selection within the home range, for example, is the only geographical scale evaluated, the results may not indicate the actual criteria for the animal’s choice of habitats if it is only selecting among individual food items within a field. Likewise, if temporal scale is not defined, results may also be inconclusive because changes in habitat composition may be related to some, but not all, portions of the annual cycle (Schooley 1994, Arthur et al. 1996).

Habitats are the resources and conditions present in an area that are needed by an organism to survive (Krausman 1999). In our study, habitat use is defined as an animal’s use of the physical and biological resources in a habitat (Krausman 1999). Different habitat uses include foraging, sleeping (roosting), social interaction, and nesting. We define habitat availability as the accessibility of physical and biological components in a habitat (Krausman 1999). Habitat selection refers to the hierarchical process of behavioral responses (Jones 2001) that results in habitats being used disproportionately to their availability (Johnson 1980,

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Manly et al. 2004).

Several methods have been used to analyze habitat selection (Alldredge and Ratti 1986, 1992; Alldredge et al. 1998; McClean et al. 1998; Alldredge and Griswold 2006). Results produced by these methods are variable and are affected by several components of the study not necessarily tied to selection (Alldredge and Ratti 1986). We selected compositional analysis (Aebischer et al. 1993) as the most appropriate method to analyze habitat selection by breeding greater sandhill cranes (*Grus canadensis tabida*) because of the high variability in habitat use between home ranges and the potential for non-independence of radio-telemetry points. This method of analysis also addresses some of the shortcomings of other resource selection functions such as solving the problem of non-independence of proportions by using their log ratios (Aitchison 2003) and addresses the problem of defining habitat availability by conducting the analysis on several geographical scales. Finally, we did not correct for bias in habitat selection created by territorial species, which violates the assumption of independence between individuals. Since sandhill crane territories are maintained over multiple years (Hayes 2015), habitat selection that we measured should be relatively unbiased.

The eastern population of greater sandhill cranes that breed in central Wisconsin is an ideal study subject for resource selection analysis because of its accessibility and high density of individuals. Once categorized as rare (U.S. Fish and Wildlife Service 1966), this population is now abundant throughout much of its historic range (Lacy et al. 2015). There has been a gradual decline in the growth rate of the population (Meine and Archibald 1996) in the Central Sands region of Wisconsin, an area with the state's greatest density of birds (Su et al. 2004). Individual cranes primarily enter the breeding population through replacement of mates on existing territories (Hayes 2015), further evidence that most potential breeding territories are occupied.

Several components are necessary for sandhill crane breeding success. Though sandhill cranes are commonly seen using upland habitats during summer, the most important component of a breeding crane territory is thought to be a secure nest site associated with water (Armbruster 1987, Safina 1993). Research in Wisconsin supports this result and suggests that on a landscape level, breeding crane distribution is linked to wetland type and distribution (Su 2003). Su (2003) also found a clear spatial separation between territorial pairs

and non-breeding flocks, indicating social status may be another factor affecting habitat selection in cranes (Hayes 2015). Pairs tend to stay close to the wetland while non-breeding flocks forage farther from wetland areas (Su 2003). Yet sandhill cranes have increased most dramatically in agricultural areas (Lacy et al. 2015), which suggests that upland habitats may also be important for territorial cranes in summer.

Walkinshaw (1949) found that most sandhill crane territories consist of areas used for nesting, roosting, and feeding and that the size of each area varies with time and crane density. Austin et al. (2007) suggested that water depth influenced daily nest survival for migratory sandhill cranes nesting at Grays Lake National Wildlife Refuge, Idaho. Nesbitt and Williams (1990) also observed that territory size of non-migrating, territorial Florida sandhill cranes (*Grus canadensis pratensis*) changed during the year, but they also found that whereas upland pastures were used more than predicted by their availability, wetland sites were not. Although breeding cranes return to the same location each year (Walkinshaw 1949), territorial boundaries are somewhat dynamic and may change based on the needs of the pair or based on availability of critical habitat components within the home range. The roles of wetland and upland habitats, as well as the role of spatial and temporal variation in these habitats, are thus not completely defined and suggest the importance of including these elements in developing the most accurate understanding of resource needs for sandhill cranes.

Evaluating selection at 2 different spatial levels within the same study population can better illustrate the hierarchical nature of habitat selection by breeding sandhill cranes while deemphasizing the difficulty of defining availability (Miller et al. 1999). Considering temporal variation in habitat selection also broadens the scope at which the needs of these pairs can be assessed. The objective of our study was to analyze habitat selection of breeding sandhill cranes in central Wisconsin using radio-telemetry and land cover data. Habitat selection was evaluated at 2 geographical scales: home range within a study area and habitats within a home range (Johnson 1980). We tested the null hypotheses that the selection of habitats at both of these scales was not different from random. We also evaluated temporal variation in selection of habitats within the home range by accounting for the influence of different stages of breeding season. Temporally, 2 null hypotheses were tested: 1) home range size did

not vary during the breeding season, and 2) selection of habitats during the different stages of the breeding season was random.

## STUDY AREA

The study area is located at the intersection of Marquette, Columbia, and Adams counties in central Wisconsin (Figure 1). Our study area was 7,531 ha and consisted of a heterogeneous landscape of wetlands, row crops, grassland, forest, and low-density residential areas. The wetlands in this area are predominantly palustrine with flow-through hydrology (Cowardin et al. 1979).

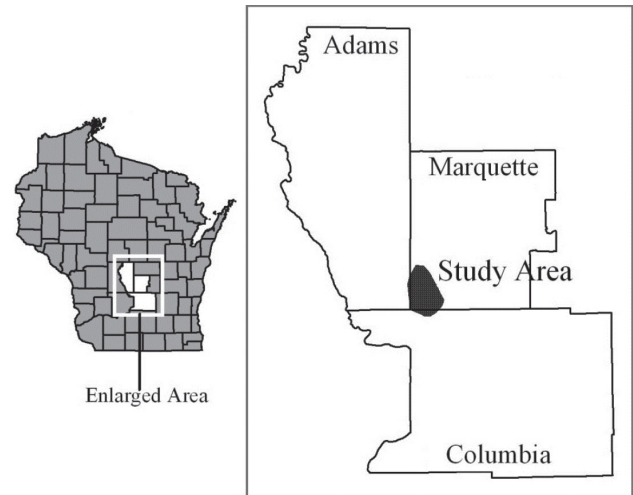
## METHODS

### Capture and Banding

Breeding pairs included in our study were captured on territory in the fall seasons of 1997, 1999, and 2000. We tracked these birds for the breeding season during the year following capture. We used alpha-chloralose, an oral tranquilizer, to sedate family groups for capture after baiting them with corn (Bishop 1991, Hayes et al. 2003). Each individual was marked with a U.S. Geological Survey (USGS) Bird Banding Laboratory band, a 7.62-cm-high numbered band, and a unique combination of 2.54-cm-high color bands (Dickerson and Hayes 2014). Advanced Telemetry Systems (ATS, Isanti, MN) radio transmitters (Series A3500 Model) were attached to the 2.54-cm color bands. Each bird was uniquely marked through transmitter frequency, color combination of plastic bands, or the USGS band number.

### Classification of Habitats

Habitat boundaries were digitized in ArcView 3.2 (Environmental Systems Research Institute, Inc., Redlands, CA) using 1-meter-resolution aerial photographs taken in spring 2000 (Figure 2). For a concurrent study conducted by the International Crane Foundation (ICF), land-use changes were recorded every week each year to follow the progression of the crops throughout the growing season (ICF, unpublished data). For our analysis, we used land-use classifications from the middle of June of each year of the study to reflect the primary land-use for the season.



**Figure 1.** Breeding sandhill crane study area located within Adams, Columbia, and Marquette counties in the Central Sands Region of Wisconsin, 1997-2001.

We grouped 32 existing land-use classifications into 8 categories based on vegetation structure and hydrology: developed (DEV), vegetable crop (VC), row crop (RC), short crop (SC), tall grass (TG), upland forest (UFOR), wetland forest (WFOR), and wetland (WET). Developed included areas dominated by man-made features such as residential areas, ditches, roads, and Lake Mason. VC included crops such as beets, carrots, onions, peas, and potatoes. RC included corn, soybeans, wheat, oats, rye, and unidentified agriculture. SC included mowed grass, grazed grass, mint, and alfalfa. TG included grass, grass with less than 50% shrubs, fallow fields, and planted trees. UFOR included either hardwood, mixed hardwood pine, or pine forests. WFOR included any wetland area with tree cover, including grazed areas. The WET land use classification included emergent wet meadow wetland areas plus open water that was shallow enough for wading by cranes.

### Radio-telemetry

Individual birds outfitted with radio transmitters were located using either a handheld or roof-mounted, 4-element Yagi antenna (ATS) with a portable receiver. Each individual was tracked once per week from sunrise to sunset, March-October. Location, behavior, and habitat data were recorded at 1.5-2-hour intervals. When bird locations were not visually confirmed, 3 compass bearings were recorded and then triangulated (White and Garrott 1990) on USGS 7.5-minute topographical



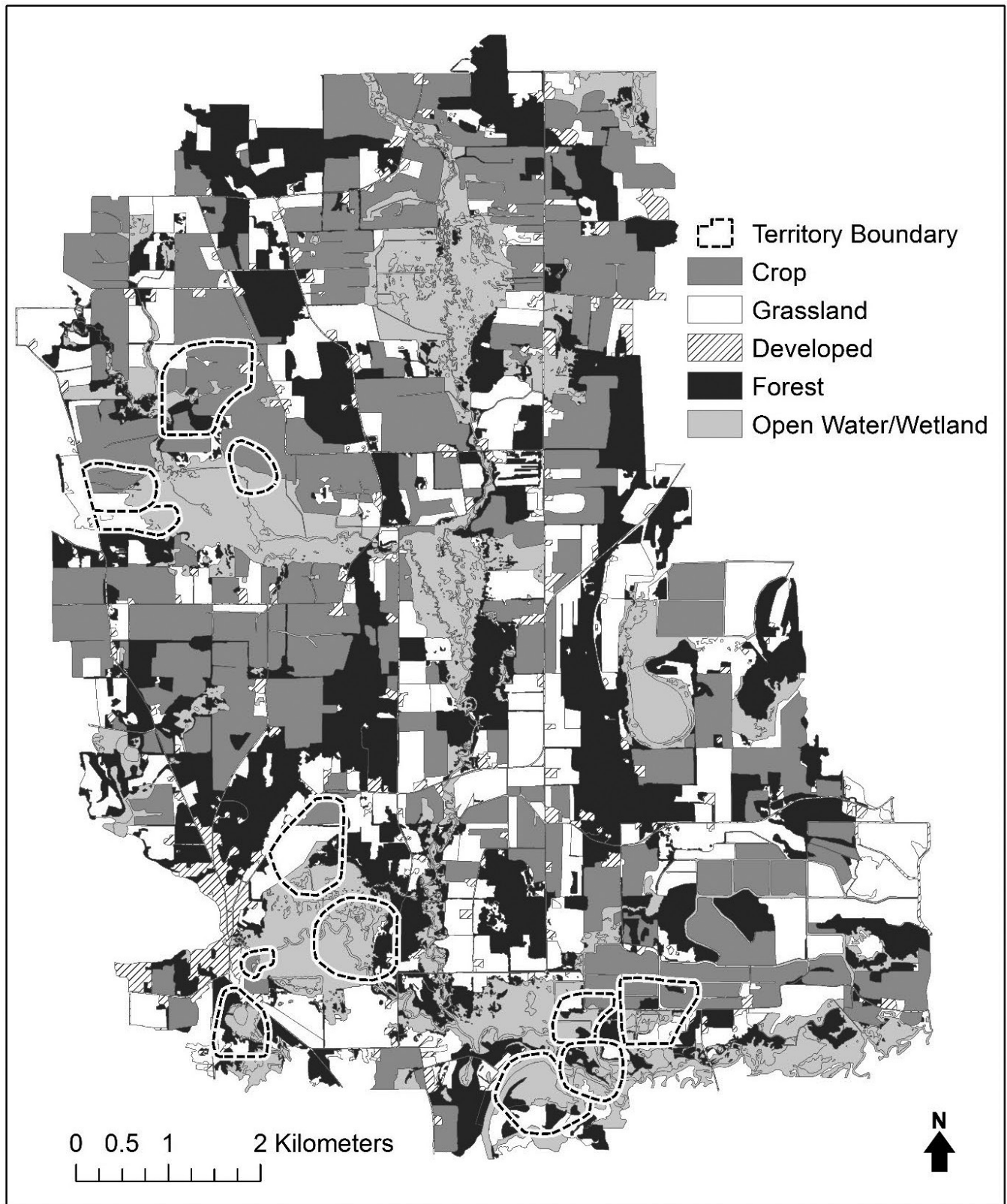


Figure 2. Distribution of general land use categories across the study area and within 12 territories of breeding sandhill cranes in the central Wisconsin study area during 1998, 2000, and 2001.

quadrangle maps. All locations were converted to the Wisconsin Transverse Mercator (WTM) coordinate system by plotting locations on quadrangles within an Access (Microsoft Corporation, Redmond, WA) database. These telemetry points were used to estimate home range size and to represent habitat use in the analysis of habitat selection within the home range.

Visual locations were plotted directly onto topographical maps using aerial photos as reference and were accurate to 0.5 ha. Triangulations with error polygons >3.5 ha were not used. Locations with only 2 bearings (termed bi-angulation here) had no error polygon. Error polygons >3.5 ha were excluded because this number represents over half the area of the average land-use polygon in the study area. The proportions of locations using bi-angulations were noted for each estimate.

Home range was calculated by the fixed kernel method, using least squares cross validation to select the smoothing parameter (Seaman and Powell 1996, Seaman et al. 1999). Calculations were made with the animal movement extension (Hoodge and Eichenlaub 1997) of ArcView 3.2 (Environmental Systems Research Institute 1992-1999). The home ranges estimated habitat use for home range selection within the study area and availability in the analysis of selection of habitats within the home range.

Habitat availability in the analysis of home range within the study area was defined by connecting the outermost points of the 12 individual home ranges. Location data from 36 additional color-marked breeding pairs in our study area were also included to construct the final habitat availability polygon. These additional pairs were part of an unrelated study and were entered into a Microsoft Access database similar to the radio-telemetry database. Adding these pairs increased the sample size sufficiently to enable us to measure availability, which better represented the population within our study area.

Roost-to-roost tracking (following a bird from its dawn roost to its evening roost for 1 diurnal day of tracking) allowed us to describe daily rhythms of habitat use. We could examine whether habitats were used in a clumped fashion such as when a food source becomes temporarily available and is used for several days before being abandoned or on a uniform basis such as habitats that are utilized each day. We examined frequencies of daily use of each habitat component for all pairs using pair days (the total number of days of observation for

each pair combined) as our sample size. The days that a bird was not tracked for a full day and where the roost location was missed were excluded from this analysis.

## Statistical Analysis

To compare home range size of breeding cranes during different stages of the annual breeding cycle we used a 1-way analysis of variance (ANOVA). *A posteriori* comparisons of means were made with Bonferroni's test (Sokal and Rohlf 2011). Breeding stages were combined if there was no significant change in size of the home range ( $\alpha = 0.05$ ).

We used compositional analysis (Aebischer et al. 1993) to evaluate habitat selection of radio-tracked breeding sandhill cranes. This resource selection analysis method addressed 3 of the 4 common difficulties with habitat selection studies. To overcome the problem of non-independent bird locations, the individual was the sample unit. Since all birds in the study were members of a breeding pair and territories did not overlap, their territorial behavior minimizes overlap of used habitats. Proportions were log-transformed to rectify non-independence of use and availability ratios. This method tested between-group differences by referencing within-group and between-animal variation (DeHaan 1999).

Analysis of habitat selection within the study area was carried out on the 8 habitat categories described above. The analysis of habitat selection within the home range was carried out on the 6 habitat types available to all birds (DEV, UFOR, RC, SC, TG, WET). A value of 0.0001 was substituted for habitats with no use. We used Systat 9.0 (SPSS Inc., Chicago, IL) and command files available from the Game & Wildlife Conservation Trust (Fordingbridge, Hampshire, UK; Aebischer et al. 1993) to test the hypothesis that habitat use was proportional to availability. First, we tested if the use of habitats was non-random. To do so, we calculated the differences between the log-ratio transformations of the used and available proportions for each habitat using wetland as the denominator, then tested whether the average differences were jointly equal to zero using multivariate analysis of variance (MANOVA) (Aebischer et al. 1993). The level of rejection for a null hypothesis was  $\alpha = 0.05$ .

The second step in the analysis was to rank the habitat categories based on selection. Following Aebischer et al. (1993), we generated matrices of the means and standard errors of all possible log-

ratio differences between telemetry locations (use) and habitat composition (availability). The sign of each value from the mean matrix was extracted and placed in a simplified ranking matrix that provided an indication of relative selection. A triple sign represented significant deviation from random at  $P < 0.05$ . Habitat categories were then ranked based on the number of positive signs compared to all other habitat types in the pair-wise comparison matrix. For 8 habitat categories, the rankings ranged from 0 to 7 with 0 being the least selected and 7 being the most selected.

Analysis of habitat selection was evaluated at 2 geographical levels: home range within the study area and habitats within the home range (Johnson 1980). Habitat use was also evaluated during the different stages of the breeding season. The breeding season was divided into 4 stages: 1) pre-nesting, 2) nesting (i.e., nest construction, egg laying, or incubation), 3) pre-fledged chick, and 4) post-fledged chick or pairs with no chick. Dates for these 4 reproductive stages were different for each pair and based on visual observations and movement patterns.

## RESULTS

### Radio-telemetry Error

For all 3 years of the study, the proportions of observations confirmed visually were similar and represented one-fourth to one-third of the sightings (Table 1). The percent of observations used in the analysis that were bi-angulations varied from 1.7 to 17.3%. All bird locations were checked against recorded land-use as well as with habitat observations made at the time of data collection. Errors in plotting the location of the point were corrected. In most cases, 2-azimuth bi-

angulations in 1998 followed or preceded triangulated locations and birds had not moved significantly. Most error polygons were less than half the size of the average field polygon in the study area.

### Habitat Use and Availability

The composition of habitats within the study area remained relatively constant during all 3 years of the study: UFOR (23.2%  $\pm$  0.03 [ $\pm$  1 SE]), RC (25.0%  $\pm$  0.57), and WET (17.9%  $\pm$  0.00, Table 2). The mean home range size for breeding sandhill cranes over the entire season was 284.7 ha  $\pm$  59.7 ( $n$  = 12) and ranged from 24.9 to 794.0 ha (Table 3).

Home range size differed among the 4 temporal stages of the annual breeding season ( $F_{3,51} = 5.55$ ,  $P = 0.002$ ). Home range sizes for pre-nesting, nesting, and chick stages did not differ, so these 3 stages were combined into 1 category, defined as pre-fledging (Bonferroni adjustment). On average, home range size during the post-fledging stage was 3 times greater than during the pre-fledging stage. Of the 12 individuals sampled, only 1 had a home range that was smaller during post-fledging.

Habitat composition during the entire breeding season was variable between individual home ranges (Table 2). Major habitats available to breeding sandhill cranes within their home ranges (habitat composition of the home range), March-October, were WET (35.6%

**Table 1. Percentage of sightings (grouped by degree of potential error in the source data) used to estimate habitat use by sandhill cranes in central Wisconsin where a visual confirmation had the minimum error (0.5 ha) and 2-azimuth bi-angulations had undefined error.**

Year	Visual confirmation	Error Polygon <3.5 ha.	Error Polygon >3.5 ha	Bi-angulation
1998	36.2	44.7	1.8	17.3
2000	34.4	56.1	7.4	2.1
2001	26.0	62.7	9.6	1.7

**Table 2. Land-use composition of the study area, home range, and telemetry locations as defined for 12 breeding, radio-tracked sandhill cranes and 36 color-marked territorial pairs during 1998, 2000, and 2001 in central Wisconsin. Home range composition represents the average percentage of habitats within the 12 radio-tracked individuals' home ranges. Telemetry locations represent the used proportion in the compositional analysis of habitat use.**

Land-use category	Study area composition (%)		Home range composition (%)		Telemetry locations (%)	
	Mean	SE	Mean	SE	Mean	SE
Developed	6.15	0.01	4.44	0.8	2.35	0.7
Upland forest	23.23	0.03	12.52	2.6	5.99	2.1
Vegetable crop	1.14	0.27	3.36	1.5	2.02	1.0
Row crop	25.02	0.57	21.31	3.8	24.29	5.7
Short crop	9.56	1.07	9.43	2.5	13.96	4.6
Tall grass	10.89	0.21	6.50	1.6	4.63	1.9
Forested wetland	6.15	0	6.79	2.1	8.07	3.8
Wetland	17.87	0	35.64	3.2	38.70	4.5



**Table 3. Fixed kernel home range estimates (95%) calculated for the entire season (Mar-Oct), pre-fledge, and post-fledge/no chick seasons for 12 radio-tracked breeding sandhill cranes in central Wisconsin tracked during 1998, 2000, and 2001. The length of each stage in the breeding season was defined based on the reproductive cycle of each crane.**

Identification frequency	Area (ha)		
	Entire season (Mar-Oct)	Pre-fledge	Post-fledge/no chick
148.053	132.5	108.6	124.7
148.054	114.0	29.1	130.6
148.082	331.8	243.6	333.5
148.115	93.2	86.4	101.6
148.135	318.2	147.7	539.3
148.152	195.4	111.1	217.7
148.213	241.8	53.5	569.4
148.333	794.0	180.3	904.7
148.354	330.4	195.8	570.4
148.373	458.9	148.3	451.5
148.880	380.7	197.7	509.0
149.011	24.9	28.0	16.6
Mean $\pm$ SE	284.7 $\pm$ 59.7	127.5 $\pm$ 20.2	372.4 $\pm$ 75.8

$\pm 3.2$ ), RC (21.3%  $\pm 3.8$ ), and UFOR (12.5%  $\pm 2.6$ ). During daylight hours, habitats that were used consisted primarily of WET (38.7%  $\pm 4.5$ ), RC (24.3%  $\pm 5.7$ ), and SC (14.0%  $\pm 4.6$ ). On average, major habitats available in a home range during the pre-fledging stage were WET (43.0%  $\pm 4.5$ ) and RC (19.7%  $\pm 5.2$ ) (Table 4). Habitats used within the home range during the pre-fledging stage consisted primarily of WET (50.1%  $\pm 4.9$ ) and RC (20.8%  $\pm 6.2$ ). The composition of home range habitats during post-fledging was WET (30.3%  $\pm 2.3$ ), RC (24.6%  $\pm 3.5$ ), UFOR (12.5%  $\pm 1.9$ ), and SC (11.1%  $\pm 2.8$ ) (Table 4). On average, habitats used were WET (30.6%  $\pm 3.2$ ), RC (26.3%  $\pm 5.1$ ), and SC (20.5%  $\pm 5.4$ ).

With roost-to-roost tracking we could also measure absolute frequencies of habitat use within each day. Wetlands were used in 97.4% of the days on which we observed pairs ( $n = 469$  pair-days), uplands (all habitats except WET and WFOR) were used in 83.6% of observed days, and 15.8% was unknown land-use (Table 5). Row crops and SC, whose relative importance is defined below, were used 60.8% and 32.6%, respectively. The total exceeds 100% as a tracked individual used multiple land uses in 1 day.

## Habitat Selection

Selection of home ranges within the study area was not random ( $\lambda = 0.072$ ,  $F_{7,12} = 9.18$ ,  $P = 0.013$ ). A ranking matrix (Table 6) ordered the habitat types in the sequence WET>RC>SC>DEV>TG>UFOR>WFOR. Wetland was used significantly more than any other habitat. There was no detectible difference in use of the 6 other habitats, implying that the order of their assigned ranks was not distinguishable ( $P > 0.05$ ).

Analysis for habitat selection within home ranges

**Table 5. Absolute frequency of daily use for wetland, upland, and unknown land use categories by 12 breeding sandhill cranes over the entire season (Mar-Oct) in central Wisconsin during 1998, 2000, and 2001. The total exceeds 100% as tracked individuals used multiple land use categories in 1 day ( $n = 493$  pair-days).**

Land-use category	Frequency of use (%)
Wetland	97.4
Upland	83.6
Row crop	60.8
Short crop	32.6
Unknown	15.8

**Table 4. Mean composition of habitats and habitat use within the home ranges of 12 radio-tracked breeding sandhill cranes during the pre-fledged chick season and the post-fledged/no chick season in central Wisconsin during 1998, 2000, and 2001.**

Land-use category	Pre-fledged chick season				Post-fledged/no chick season			
	Home range composition (%)		Telemetry locations (%)		Home range composition (%)		Telemetry locations (%)	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Developed	3.5	1.1	2.0	0.9	5.4	1.3	3.1	1.0
Upland forest	8.8	1.7	6.2	2.1	12.5	1.9	6.1	2.0
Row crop	19.7	5.2	20.8	6.2	24.6	3.5	26.3	5.1
Short crop	6.2	2.4	6.2	2.4	11.1	2.8	20.5	5.4
Tall grass	6.9	1.9	4.6	2.0	6.2	1.6	4.6	1.8
Wetland	43.0	4.5	50.1	4.9	30.3	2.3	30.6	3.2



**Table 6. Simplified ranking matrix for 12 breeding sandhill cranes over the entire season (Mar-Oct) based on comparing proportional habitat use within the home range with the proportions of total available habitat type in the entire study area, central Wisconsin, during 1998, 2000, and 2001. The disproportionate use of a habitat to its availability indicates an animal's preference or avoidance of that habitat. Each mean element in the matrix was replaced by its sign; a triple sign represents significant deviation from random at  $P < 0.05$ .**

Habitat type	Habitat type								Rank
	DEV	UFOR	VC	RC	SC	TG	FW	WET	
Developed (DEV)		+	+	–	–	+	+	---	4
Upland forest (UFOR)	–		+	–	–	–	+	---	2
Vegetable crop (VC)	–	–		–	–	–	–	---	0
Row crop (RC)	+	+	+		+	+	+	---	6
Short crop (SC)	+	+	+	–		+	+	---	5
Tall grass (TG)	–	+	+	–	–		+	---	3
Forested wetland (FW)	–	–	+	–	–	–		---	1
Wetland (WET)	+++	+++	+++	+++	+++	+++	+++		7

was carried out on 6 habitat types available to all birds. Vegetable crop and WFOR were not considered because they did not occur in 50% and 25% of the home ranges, respectively. Both of these habitat categories also did not have a significant relationship with other categories and they were at the bottom of the ranking matrix. Habitat use within the fixed kernel home range was not random ( $\lambda = 0.073$ ,  $F_{7,12} = 15.22$ ,  $P = 0.002$ ). At this scale, WET was ranked highest and was selected over all habitats ( $P < 0.05$ ), and RC was ranked second highest and significantly different from the remaining rankings ( $P < 0.05$ ).

Analysis of change in seasonal habitat selection was carried out on the same 6 habitat categories as the analysis of habitat selection within the home range over the entire breeding season (March-October). Habitat use within the kernel home range during the pre-fledging stage did not differ from random ( $\lambda = 0.416$ ,  $F_{5,12} = 1.97$ ,  $P = 0.201$ ), whereas habitat use during the

post-fledging stage approached significance ( $\lambda = 0.2695$ ,  $F_{5,12} = 3.79$ ,  $P = 0.056$ , Table 7). A ranking matrix was not created for the pre-fledge stage since overall the test for habitat use was not significant. We did explore the ranking matrix in the post-fledging stage and sequenced the habitat types as  $SC > WET > RC > TG > UFOR > DEV$ . The top 3 habitats, SC, WET, and RC were used more than the lowest 2 habitats, UFOR and DEV. There was no detectable difference in the use of the top 3 habitats, implying that the order of their assigned ranks was indistinguishable.

## DISCUSSION

Central Wisconsin has one of the highest densities of breeding sandhill cranes in North America (Barzen et al. 2016), and this population is likely saturated with breeding birds (Hayes 2015). Individuals lost from breeding pairs are quickly replaced with adults from

**Table 7. Simplified ranking matrix for habitat selection of 12 sandhill cranes during the post-fledged/no chick seasons based on comparing proportions of radio locations of each of the 12 radio-tracked sandhill cranes in each habitat type with the proportion of each habitat available within the animal's home range, central Wisconsin, 1998, 2000, and 2001. Each mean element in the matrix was replaced by its sign; a triple sign represents a significant deviation from random at  $P < 0.05$ .**

Habitat type	Habitat type						Rank
	DEV	UFOR	RC	SC	TG	WET	
Developed (DEV)		–	---	---	–	---	0
Upland forest (UFOR)	+		---	–	–	---	1
Row crop (RC)	+++	+++		–	+	–	3
Short crop (SC)	+++	+	+		+	+	5
Tall grass (TG)	+	+	–	–		–	2
Wetland (WET)	+++	+++	+	–	+		4

local, non-breeding flocks without missing a breeding season (Hayes and Barzen 2006, Hayes 2015). Some nests are located as close as 11 meters apart and nest density of this population was 5.25 nests/km<sup>2</sup> of wetlands at the time of this study (Barzen et al. 2016). Thus most viable breeding territories were occupied, leaving little room for new territory establishment (Hayes 2015) and our habitat use estimates were not likely biased by the presence of unused, high-quality habitat.

In our study, the selection of habitats within the study area was not random. Breeding sandhill cranes selected wetland habitats over all other land-use categories, and upland habitat did not appear to influence the distribution of breeding pairs. These results support previous and current studies that concluded wetlands are the most important component of a breeding crane's territory (Safina 1993, Su 2003, Lacy et al. 2015). Unlike other studies, however, the analysis of habitat selection within the home range suggested that breeding cranes selected wetland habitat over all other habitat types but also selected row crops at this finer geographic scale. Daily use of wetland habitats within home ranges, however, suggests the importance of wetlands to breeding cranes even when upland habitats are also used and preferentially selected.

Though the importance of upland habitats for sandhill cranes is often mentioned (Melvin 1978, Armbruster 1987, Su 2003, Austin et al. 2007), before this study, selection for upland habitats has been quantitatively documented only in Florida for non-migratory breeding cranes and wetlands were used in proportion to their availability (Nesbitt and Williams 1990). On a daily basis, uplands were not used as regularly as were wetlands but they were still used with a high daily frequency (83.6%).

Breeding sandhill cranes are territorial (Walkinshaw 1949, Nesbitt and Williams 1990, Hayes 2015) and are behaviorally restricted by other territorial pairs to remain within their home range. Within the home range, however, territorial use (i.e., home range size) can vary throughout the breeding season and may change based on the needs of the pair. In our study the size of the home range during the pre-fledging stage was 3 times smaller than in the post-fledging stage/no chick stage (Table 3), and habitat use as shown in the telemetry data varied between these stages as well (Table 4). The mobility of family groups, as determined by the presence and developmental stage of the chick, and which changes over time, thus serves as an important

modifier to habitat availability. During the pre-fledging stage, breeding pairs showed no selection for certain habitats, presumably because chicks were limited by how far they could travel between night roost areas and daytime foraging areas. Chick mortality is high during this pre-fledge stage (Littlefield et al. 2001; ICF, unpublished data). Post-fledging breeding cranes showed more selection for specific habitats since chicks could travel farther from the wetland and thus habitats no longer needed to be contiguous. The seasonal effect that Nesbitt and Williams (1990) demonstrated compared year-round resident pairs with pairs that left their territories after the breeding season, and so is not comparable to our results. Selection of habitats at the temporal scale that we examined was still weaker than selection over the entire breeding season.

This study supports the hypothesis that breeding sandhill cranes are dependent on wetlands as well as uplands that are adjacent to nesting and roosting habitat. Though the distribution of wetlands can limit the growth and expansion of the sandhill crane population in the Midwest, crane populations are likely to do best where they find an intermixing of wetland and upland habitat that is contiguous within 1 territory. Suitable upland habitat, in turn, appears to require low vegetation structure as upland forested areas ranked low in our selection matrices.

Breeding cranes return to the same home range (territory) over many years (Walkinshaw 1949, Hayes 2015). When breeding habitats are saturated with cranes, territory boundaries are restricted through behavioral interactions with adjacent breeding pairs who compete for similar resources. In areas where wetlands are adjacent to agriculture, land-use of uplands can vary widely year to year while territory boundaries remain relatively constant. The boundaries of a home range do not vary with the changing land-use because pairs need wetland for nesting (Hoffman 1983, Baker et al. 1995, Hayes 2015) and roosting (Iverson et al. 1987). This requirement constrains the extent to which selection for certain habitats can occur within a home range until birds can become more mobile and visit habitats that are not directly adjacent to the breeding wetland.

The longevity of territories makes selection for upland areas within the study area difficult to demonstrate under high-density nesting conditions. If upland habitats change greatly (e.g., switching from low crop to tall grass or shrub after an agricultural field is abandoned), breeding birds may show site

fidelity to territories because there are no other open territories but reproductive productivity may decline as the quality of upland habitats decline (ICF, unpublished data). Though breeding productivity may change as the habitat converts from optimal to sub-optimal conditions (Cody 1985), bird use of the area may persist (Brown 1969, Brown and Orians 1970). This behavior results in significant lags between habitat change and crane habitat use in response to that change when the only alternative to maintaining the now sub-optimal territory is to join the non-territorial flock in which there is no opportunity to breed (Hayes and Barzen 2006). Several examples of this situation have occurred in this study area during the past 10 years (Hayes 2015).

Our data support Su's (2003) hypothesis that, though non-breeding cranes have greater mobility and show strong preference for specific upland habitats, they avoid upland habitats close to wetlands containing territorial birds. This segregation of resources is subtle but important to the manner in which 2 different social classes of cranes allocate resources among themselves within the same landscape.

With the knowledge that breeding cranes require emergent wet meadow wetlands (Hoffman 1983, Baker et al. 1995), we have a better understanding of the relationship between breeding cranes and their habitat requirements within both spatial and temporal scales. The results from our habitat selection analysis may help managers predict where and how crane-human interactions, such as crop damage, may occur in the future. In addition, a dependence on wetlands makes crane populations vulnerable to loss of wetland habitat, particularly where wetlands exist in agricultural-dominated landscapes. Since there is a lag effect between habitat loss and population response, it is important to monitor areas even where sandhill cranes are currently thriving.

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