2016

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Abstract: We conducted aerial surveys to determine nest locations of greater sandhill cranes (*Grus canadensis tabida*) in central Wisconsin, 2001-2003. Helicopter flights covered 8.90 km^2 of wetlands in each year, and we found 41 nests in 2001, 50 nests in 2002, and 48 nests in 2003 from 11 wetlands. Our best estimate of nest density (n = 14) included wetlands containing 5 or more nests and averaged 5.25 ± 0.36 (1 SE) nests/km^2 of wetland. Maximum nest density of larger wetlands in any 1 year was 7.80 nests/km^2. As some nests had likely failed by the time we completed our surveys, our measure of nest density likely under-estimated the total number of territories in each wetland. Minimum distances between nests averaged 222 ± 70 m (range 33-666 m) among all wetlands and 151 ± 41 m (range 33-571 m) for wetlands with 5 or more nests. Nest locations differed from a random distribution ($P < 0.05$) and were clustered within wetlands and within years. Nest locations were found more than expected in the wetland habitat type (Jacob's Index D = 0.72 in 2001, 0.66 in 2002 and 0.76 in 2003) and less than expected in open water, open shrub, and closed shrub. No nests were found in wetland forests. Crane nests also tended to occur on the outside margins of the wetlands. Nest density in central Wisconsin was greater than any previous estimate for any other crane population yet recorded and likely represents a breeding population at carrying capacity as well as a species that utilizes both upland and wetland habitats together.

PROCEEDINGS OF THE NORTH AMERICAN CRANE WORKSHOP 13:13-24

Key words: carrying capacity, eastern population, *Grus canadensis tabida*, habitat selection, territoriality.

Throughout North America, many populations of sandhill cranes (*Grus canadensis*) have recovered from population nadirs of the early 20th century (Meine and Archibald 1996). The Eastern Population (EP) of greater sandhill cranes (*G. c. tabida*) in Wisconsin was thought to have declined to as low as 25 breeding pairs (Henika 1936) and was lamented by Leopold (1966) as being on the brink of extirpation. Low densities of isolated breeding pairs occurred in very large, isolated wetlands (Henika 1936, Meine 2004), and this early description of nesting habitat has persisted. It was not until the 1970s that biologists began to describe a recovering sandhill crane population in Wisconsin (Hunt and Gluesing 1976, Howard 1977, Bennett 1978). Since then, the EP in Wisconsin has increased dramatically (Harris and Knoop 1987, Windsor 1990, Dietzman and Swengel 1994, Su et al. 2004, Lacy et al. 2015). Now, a different question arises: What is the limit of crane nesting territories that a wetland can hold?

Current studies suggest that sandhill cranes are strongly wetland dependent during their breeding season, utilizing wetlands both to place their nests and to roost at night while often foraging in uplands during the day (Walkinshaw 1973*a*, Melvin 1978, Hoffman 1983, Herr and Queen 1993, Su 2003, Miller and Barzen 2016). In turn, nest and fledging success of sandhill cranes has depended upon hydrologic characteristics and land management activities (e.g., predator control, prescribed burning, grazing, row-cropping) that occur in wetlands (Littlefield and Paullin 1990, Austin et al. 2007, Ivey and Dugger 2008) or adjacent uplands. Finally, sandhill cranes are large territorial birds that utilize the same territory perennially (Walkinshaw 1965, Drewien 1973, Hayes 2015) and this behavior might further constrain how many nesting crane pairs can utilize any single wetland (Brown 1969, Brown and Orians 1970, Maher and Lott 2000). Territorial cranes exclude non-territorial cranes from nesting areas of wetlands but not from night roosting areas of the same wetlands (Su 2003).

Measuring nest densities in populations that may be at or near carrying capacity (Hayes 2015) helps to elucidate maximum nest densities and formulate hypotheses on factors that limit the abundance of nests in any 1 wetland. Specifically, our objectives here were to: 1) describe nesting density of sandhill cranes in central Wisconsin, 2) explore environmental correlates

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with nest density, and 3) compare sandhill crane nest density in our population with other crane populations.

STUDY AREA

Our study area was located near Briggsville, Wisconsin, where Marquette, Columbia, and Adams counties meet (Figure 1). The study area for our long-term research project was 98 km^2 and located in areas created by recessional moraines and inter-moraine low areas (Martin 1965, Devaul and Green 1971). Farmland (about 60%) mixes with scattered wetlands (about 20%) predominantly in the low areas, and patches of forest (about 20%) occur mostly on the moraines. This study area is known for its high number of territorial and non-territorial cranes (Harris and Knoop 1987, Dietzman and Swengel 1994, Su 2003, Hayes 2015).

Our study focused only on a subset of wetlands within this larger long-term study area. Among 3 years we surveyed 24 wetlands totaling 20 km^2 but only 11 wetlands were surveyed consistently in all 3 years (Figure 1). Except where noted, we restricted our analysis to these 11 wetlands.

METHODS

Aerial Nest Surveys

Crane nest searches occurred 2-3 May 2001, 25-26 April 2002, and 23-24 April 2003. A team consisting

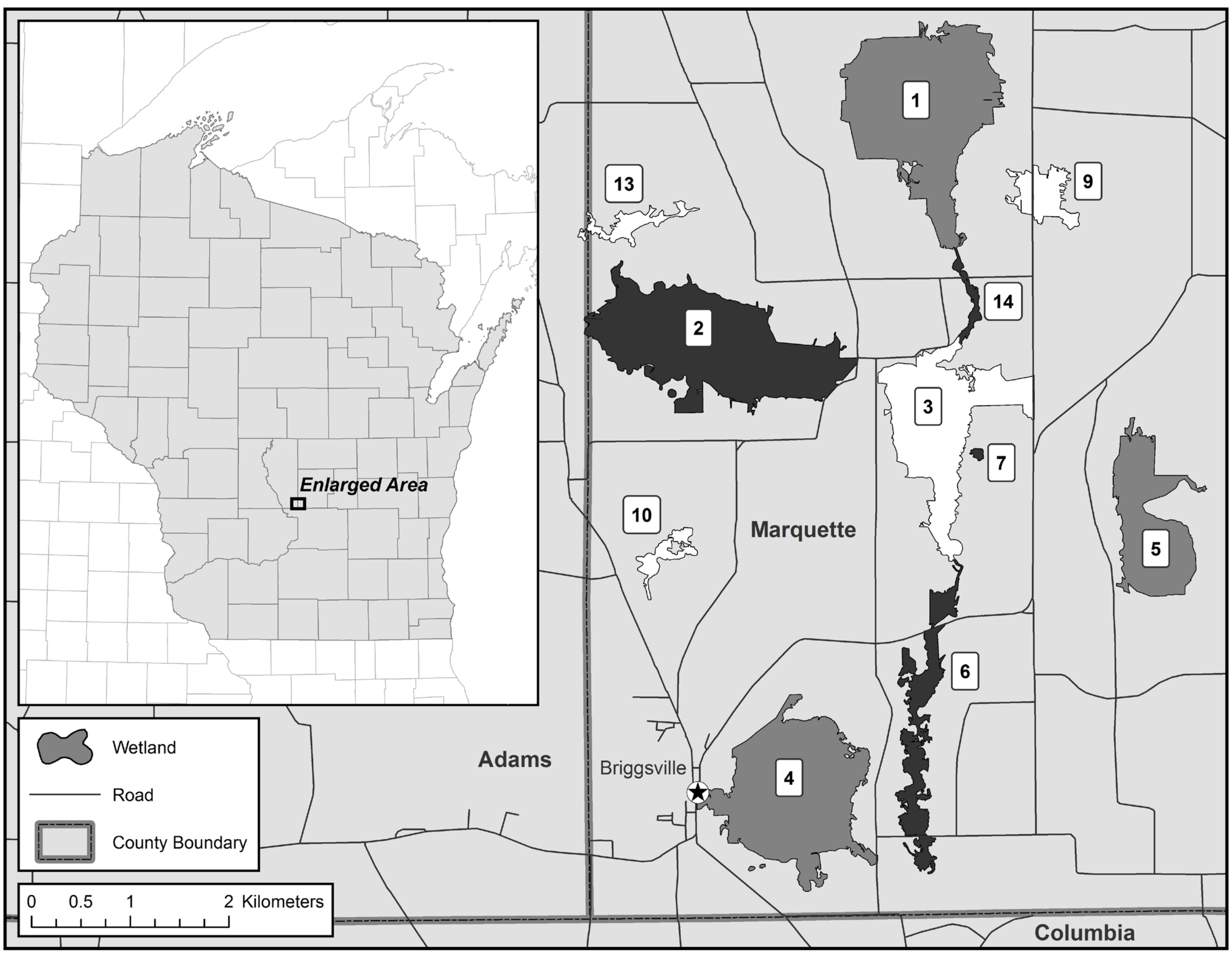

Figure 1. Locations of 11 wetlands surveyed for sandhill crane nest locations near Briggsville, Wisconsin, 2001-2003. Numbers denote wetland identifiers used throughout the text.

of pilot, videographer, mission coordinator, and 4 observers flew in a Bell 206 helicopter at an altitude of 175 m above the ground with transects spaced 100 m apart and running lengthwise over all wetlands. Flight speeds were 10 km/hr while nest searching. Once a nest was spotted, we took video images of each nest to verify whether it was active and to record habitat composition surrounding the nest. Only data for nests containing 1 or 2 whole eggs and having an adult flushing from, or guarding, a nest were presented here. Nests destroyed by predators prior to our flight were seen but were not included. GPS coordinates of nests were plotted on the air-photos with 1-m resolution.

Calculation of Nest Density

Even though sandhill crane territories in Wisconsin usually include both upland and wetland habitats (Miller and Barzen 2016), most nest sites occur in wetlands alone (Bennett 1978, Miller and Barzen 2016). We calculated nest density by dividing the number of nests found in each wetland complex by the area (km^2) of the wetland surveyed. Upland habitats were not included in these estimates even if they were located within territories.

Statistical Analysis of Spatial Patterns for Nest Locations

We used the G-test analysis in R (R Development Core Team 2014) to compare point-to-point nearest neighbor distances from nest locations to random points (Mohan and Tobias 2015), resulting in a complete partial randomness process (Kaluzny et al. 1996). Each location of a crane nest was considered as 1 point. Each wetland was defined as a specific region with the boundary being the outline of the entire wetland area. We did 100 simulations for each data set (where more than 5 nests were found) for each wetland and plotted simulation envelopes to compare $\hat{g}$ values of the crane data. These envelopes gave 98% confidence intervals ($\alpha = 0.02$) of $\hat{g}$ values for the crane data. This test qualitatively indicates whether the distribution pattern of the crane nest locations in wetlands conforms to random, regular, or clustered distributions (Mohan and Tobias 2015) and quantitatively tests whether distributions differ significantly from the random model. Levels of significance were set at $P < 0.05$.

Once the patterns of spatial distribution for nests were described, we quantitatively explored 2 factors that may have created the distribution of nests found. First, we examined nest site selection to see if nest distribution was influenced by the distribution of habitat types found within the wetlands. Wetland habitat types were interpreted from a geo-registered 1995 aerial photo with 1-m resolution and were digitized. Habitat types considered were: 1) open water or ditches (wetland areas containing no vegetation or only submerged aquatic macrophytes), 2) wetland (inundated areas dominated by emergent, non-woody wetland vegetation), 3) wetland shrub open (inundated areas where wetland shrubs had a dominant cover but emergent vegetation could still be seen between patches of shrub), 4) wetland shrub closed (inundated areas where only wetland shrubs could be seen in the aerial photo, and 5) wetland forest (inundated areas containing closed tree canopy). Once digitized, habitat types were verified through ground surveys. Although in each year the area covered by water varied slightly due to variation in the water budget, we assumed that the wetland boundaries and wetland habitat types did not change over the period of this study because dominant wetland vegetation is mostly composed of perennial species (Fassett 1940). The habitat type that each nest was located in was determined by estimating the dominant habitat type within a 5-m radius of each located nest.

Habitat selection was quantified with Jacob's Index: $D = (r - p)/(r + p - 2rp)$, where r was the proportion of a given habitat class that each nest was located in and p was the proportion of this habitat available within the studied wetlands. Following the definition of Aarts et al. (2008), we refer to habitats receiving more usage than expected by availability (taking into account accessibility) as "preferred" and areas receiving less as "avoided." A Jacob's Index value of 1 indicated complete preference and −1 indicated complete avoidance (Jacobs 1974).

Second, territorial behavior of sandhill cranes (Hayes 2015) suggests that nest locations within a territory, replicated over 3 years, might well be clumped. We used 2 GIS techniques to examine this behavioral influence on nest distribution. We overlaid nest locations from all 3-year surveys on classified digital land cover maps. Linear distance between nests in each wetland was measured to compare how close nests were likely to be located to each other in different wetlands but within the same year and how consistent nest location was between years. Closest nests for each wetland within a year was a simple calculation of linear distance between nest locations for each wetland.

To calculate the frequency of nests located near other nests for each wetland and within each year, we used a spatial consistency index (SCI) to measure the spatial consistency pattern of nest locations in a wetland where SCI = $1/M \sum (n_t.w_t)$. Here:

M = mean number of nests found in a wetland over the years of this study.

t = consecutive years: 3, 2 (if the study was longer than 4 years, T, T-1, T-2, … 2. T = total years of surveys in a wetland).

n_t = number of nest locations found in t consecutive years on approximately the same site. We analyzed the spatial consistency of the nest locations at 2 different proximity scales, (within) 50-m and 150-m radius.

w_t = weighted index for consecutive year t, $w_t = t/T$.

SCI values were regressed against nest density for the same wetland using least squared regression (Sokal and Rohlf 1981) to see if SCI increased as nest density increased.

RESULTS

Nest Density

The 11 wetlands surveyed in 2001-2003 varied in size from 0.006 km^2 to 2.05 km^2, collectively totaling 8.90 km^2, and were situated close to each other (Figure 1). In total, we counted 65 nests in 2001, 74 nests in 2002, and 63 nests in 2003 in the 24 wetlands of the area, but we considered 42 nests located in 2001, 51 nests located in 2002, and 48 nests located in 2003 that were found in the same 11 wetlands surveyed in all 3 years (Table 1). Only wetland 14 had no nests located in it during any of the 3 years of the study.

Nest density was calculated for each wetland complex and varied by the size of wetland in which cranes nested as well as from year to year (Table 1). Overall mean density (± 1 SE) of the 3 years was 11.55 ± 5.22 nests/km^2 of wetland and ranged from 2.40 to 103.1 nests/km^2 for all wetlands. Compared to all 11 wetlands, nest density in wetlands 1-5, in years that contained 5 or more nests, averaged 5.25 ± 0.36 nests/km^2 and reflected a more precise measure of density. Maximum nest density found in wetlands 1-5 for any of the 3 years was 7.80 nests/km^2 when 16 nests were located in wetland 2 (2.05 km^2), the largest wetland of the 11 that we studied.

Spatial Patterns of Nests

The distribution of nests in all 11 wetlands, surveyed for all 3 years combined, was clustered (Figure 2). Only wetlands 1-5 contained a sufficient number of nests to test further. Within each of these 5 wetlands, distributions of nests differed significantly from random when all 3 years were combined and for each year when data from all 5 wetlands were combined (Table 2). Nest distribution for each of the 5 wetlands in each of 3 years, however, did not differ from random. Still,

Table 1. Number and density of sandhill crane nests observed in wetland habitat from 11 surveyed wetlands near Briggsville, Wisconsin, 2001-2003.

Wetland ID[a]	Area (km^2)	2001		2002		2003		Mean nests/km^2	SE
		Nests/km^2	No. nests	Nests/km^2	No. nests	Nests/km^2	No. nests		
14	0.006	0	0	0	0	0	0	0	0
7	0.009	0	0	103.10	1	103.10	1	68.73	34.36
10	0.103	9.50	1	28.40	3	28.40	3	22.10	6.30
13	0.123	8.10	1	0.00	0	8.10	1	5.40	2.70
9	0.231	4.30	1	0.00	0	8.60	2	4.30	2.48
6	0.473	0.00	0	3.80	2	0.00	0	1.27	1.26
5	0.877	2.28	2	6.80	6	5.70	5	4.93	1.36
3	1.256	4.70	6	3.98	5	5.40	7	4.69	0.41
4	1.754	5.10	9	6.20	11	4.00	7	5.10	0.64
2	2.047	7.80	16	4.90	10	6.30	13	6.33	0.84
1	2.015	2.40	5	5.80	12	4.40	9	4.20	0.99
Total	8.895	4.02	41	14.82	50	15.82	48	11.55	5.22

[a] See Figure 1 for wetland locations.

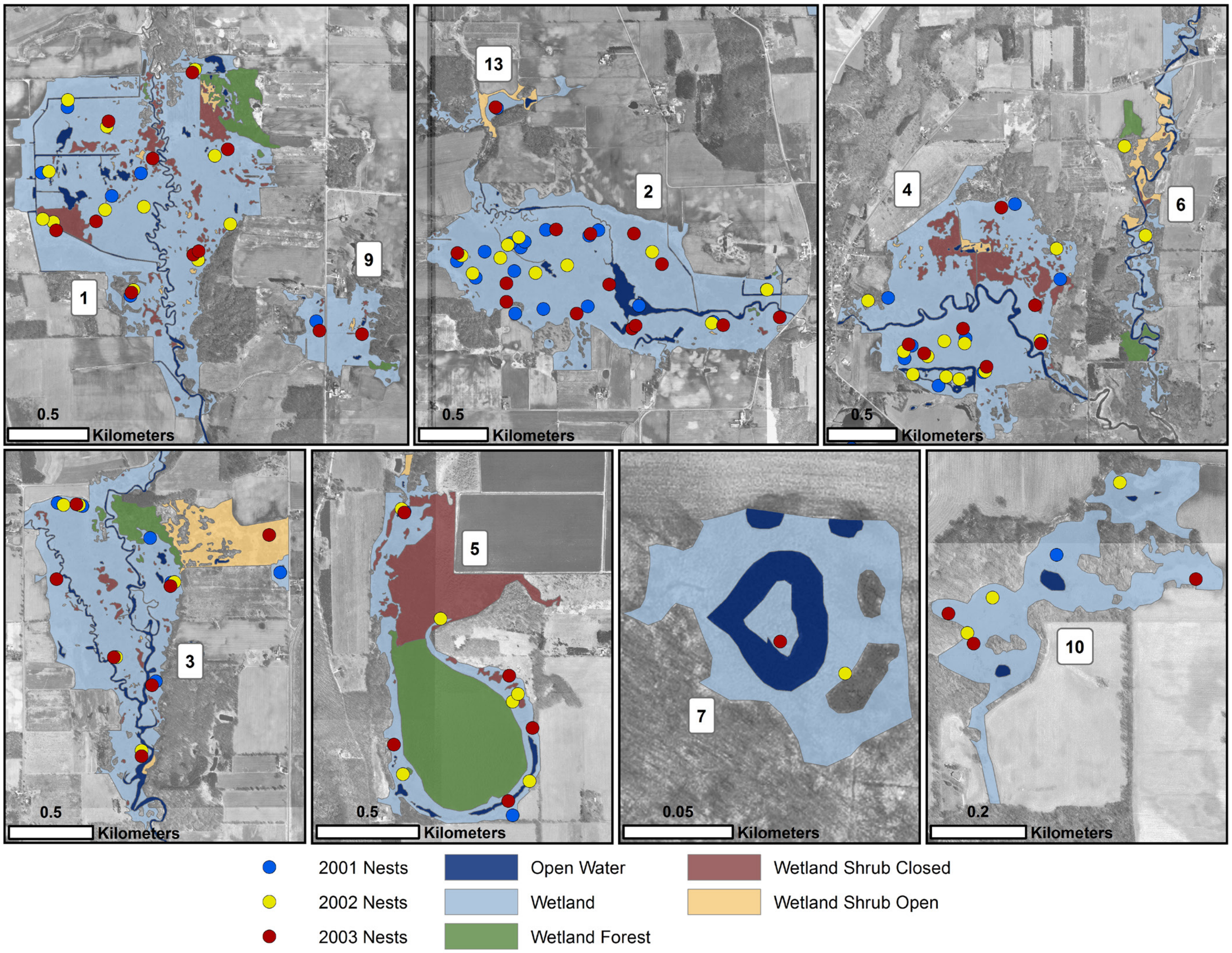

Figure 2. Habitat types and sandhill crane nest locations for each of the 11 wetlands surveyed near Briggsville, Wisconsin, 2001-2003. Nest locations vary by color for each of the 3 years studied while habitat types are denoted by color but did not change in each of the 3 years. Note that the spatial scale depicted was the same for all wetlands except wetlands 7 and 10.

qualitative evidence of patterning was seen for some of the 5 wetlands in each year. Spatial point pattern analysis for these 5 individual wetlands also showed greater variation in spatial distribution of nests at different spatial scales among some years. For example, during 2001, the nest distribution pattern in wetland 2 was clustered at small scale and was regular at a large scale whereas the reverse was true for wetland 1. Spatial patterning in wetlands 3-5 varied among years.

Given the non-random distribution of nests, what factors influenced this distribution? First, Jacob's Index described extensive preference for nests to be located in wetlands and avoidance of open water, open shrub, and closed shrub habitat types. No nests were located in forested wetland areas (Table 3). Not all wetlands contained all habitat types, but both the wetland habitat type (76% of all wetlands) and open water habitat type (6.46% of all wetlands) did occur in all wetlands (Table 4).

Yet even for the larger wetlands of this study (wetlands 1-5), clumping of nests occurred even within wetland habitat types. Some of the nests from different territorial pairs were separated by as little as 33 m (Table 5), and the mean minimum distance between nests among all 11 wetlands was 222 ± 70 m while among the 5 largest wetlands (wetlands 1-5) the mean minimum distance between nests was 151 ± 41 m. Among all 24 wetlands surveyed, the minimum distance between 2 active nests was 11 m. Wetland 2, the largest of 11

Table 2. G-test results[a] for 5 wetlands near Briggsville, Wisconsin, 2001-2003. Pattern is the qualitative description of nest distribution (random, cluster or regular[b]) while distance denotes the scale at which that pattern occurs. It is possible to have 2 patterns of nest distribution occur in the same wetland but at different spatial scales.

Wetland ID	2001		2002		2003		All years combined
	Pattern	Distance[c]	Pattern	Distance	Pattern	Distance	
1	regular cluster	<100 >100	regular		random cluster	<120 >120	cluster
2	cluster regular	<150 >150	cluster regular	<100 >100	very close to random		cluster
3	regular		random		regular		cluster
4	very close to random		cluster regular	<300 >300	very close to random		cluster
5	regular		cluster regular	<180 >180	regular to random		cluster
All wetlands combined	cluster		cluster		cluster		cluster

[a] All tests for each wetland, within a year, did not differ significantly from random. When data were combined by year or by wetland, nest locations significantly differed from random and were clustered in their distribution.

[b] A regular pattern describes nest locations that are equidistant from each other.

[c] Units of distance are measured in meters.

wetlands studied, had the lowest minimum distance between nests (61 m).

Maximum SCI values ranged from 0 to 1 and a low number would reflect a random distribution of nests while a high number would reflect a clumped distribution among years. We expected to find a clumped distribution of nests because territories are shaped to include both wetlands and uplands, so the wetland portion, where nests would be located, is relatively smaller. We compared each individual nest with a radius of 50 m and 150 m to see how likely it was to have another nest located within the chosen radius in different years. When using a 50-m radius, the mean SCI was 0.27 (Table 6). This increased to a mean of 0.51 when a 150-m radius was used. When SCI using a 150-m radius was compared to nest density using regression, however, there was no relationship (H_0: Slope = 0, $F = 2.18$, $P = 0.19$).

DISCUSSION

Interpreting Nest Density

Nest densities for the 11 wetlands in the Briggsville area varied from 2.3 to 103.1 nests/km^2, with smaller wetlands having a larger range in density estimates than larger wetlands (Table 1). The smallest wetland containing a nest was 0.9 ha which, when compared to mean territory size of 285 ha for 12 cranes in this area (Miller and Barzen 2016), suggests that, though wetlands may be important for nest location and night roosting (Su 2003), wetlands can comprise a small portion of the overall territory composition of sandhill cranes. Thus, a few nests in small wetlands can skew nest density estimates upward because our estimate of density is based on the number of nests found per unit area of wetland habitat only. A more biologically meaningful measure of density would include the number of territorial pairs per region that encompasses all territories within the study area (which includes upland components of territories if they exist). This estimate, however, cannot be procured without having individually marked birds because home ranges of non-territorial and territorial cranes in summer overlap, especially in wetlands (Su 2003, Hayes 2015). Though several studies have estimated the number of territorial crane pairs in summer (e.g., Hoffman 1983, Austin et al. 2007, Ivey and Dugger 2008), they did not estimate territory size per pair because they did not have enough marked

Table 3. Values for Jacob's Index, D = (r-p)/(r+p-2rp), to measure selection (range –1 to 1) within each habitat type for all 11 wetlands combined, within each year surveyed, near Briggsville, Wisconsin, 2001-2003. The number of nests found refers to the dominant habitat type within a 5-m radius of the nest location.

Habitat type	Number of nests found			*r*			*p*[a]	Jacob's index (*D*)		
	2001	2002	2003	2001	2002	-.07	2001-2003	2001	2002	2003
Open water	1	0	1	0.02	0	0.02	0.06	−0.47	−1	−0.53
Wetland	39	47	46	0.95	0.94	0.96	0.76	0.72	0.66	0.76
Wetland forest	0	0	0	0	0	0	0.07	−1	−1	−1
Shrub closed	1	3	0	0.02	0.06	0	0.07	−0.50	−0.08	−1
Shrub open	0	0	1	0	0	0.02	0.04	−1	−1	−0.30
Total	41	50	48							

[a] The proportion of habitat types was assumed constant for the 3 years of the study.

birds to observe, especially using the same nesting wetlands.

Our estimate of nest density was most accurate and precise when we used the number of nests per area of wetland habitat in larger wetlands that contained at least 5 nests. With larger wetlands our estimate of nest density averaged 5.25 ± 0.36 nests/km^2. The highest density we encountered was in wetland 2, where 16 nests were found in 2001 (7.80 nests/km^2). Our surveys, conducted late in the initial nesting phase of the population (International Crane Foundation [ICF], unpublished data), likely missed some nests that had been lost during incubation before we searched, so we likely under-estimated nest density.

In Wisconsin the highest density of cranes in summer is concentrated in the central sand counties of which our study area is a part (Harris and Knoop 1987, Dietzman and Swengel 1994, Su et al. 2004). For the entire EP, Wisconsin hosts approximately two-thirds of the birds in summer (Lacy et al. 2015). Our estimate of crane nesting density likely reflects a maximum for the population.

Compared to historical densities, the density of breeding cranes in Wisconsin has recovered rapidly to a saturation point early in the 21st century (Su et al. 2004). The change in nesting density occurred primarily in the 1970s within our study area. For example, only 1 breeding territory occurred in wetland 4 (Figure 2) during 1973 (G. Archibald, personal communication) and 2 territories in 1976 (Bennett 1978; A. Bennett, personal communication), but in 2002, 11 nests were found (Table 1). As of 2015, this density has not changed (ICF, unpublished data).

Early studies on sandhill crane nesting habitat reported a preference for large open wetlands with shallow water and emergent plants (Walkinshaw 1973*b*), far from human

Table 4. Area (km^2) and percentage of area (%) of habitat types for each wetland studied near Briggsville, Wisconsin, 2001-2003.

Wetland ID	Open water		Wetland		Wetland forest		Shrub closed		Shrub open		Total (100%)
	Area	%	Area	%	Area	%	Area	%	Area	%	Area
1	0.118	5.8	1.624	80.6	0.099	4.9	0.157	7.8	0.018	0.9	2.015
2	0.128	6.2	1.911	93.4	0.003	0.1	0.005	0.2	0.001	0.0	2.047
3	0.094	7.5	0.879	70.0	0.067	5.4	0.025	2.0	0.192	15.2	1.256
4	0.107	6.1	1.429	81.5			0.198	11.3	0.020	1.1	1.753
5	0.016	1.8	0.258	29.4	0.364	41.5	0.237	27.0	0.003	0.4	0.877
6	0.084	17.8	0.248	52.5	0.062	13.0	0.005	1.1	0.074	15.6	0.473
7	0.002	23.5	0.007	76.5							0.009
9	0.002	1.1	0.218	94.0	0.006	2.7	0.004	1.6	0.002	0.7	0.231
10	0.003	2.5	0.101	97.5							0.103
13	0.008	6.3	0.085	68.7			0.000	0.3	0.030	24.7	0.123
14	0.017	29.6	0.041	70.4							0.058
Total	0.578	6.5	6.800	76.0	0.601	6.7	0.629	7.0	0.339	3.8	8.946

Table 5. Distances between the 2 closest nests within 11 surveyed wetlands near Briggsville, Wisconsin, 2001-2003. Only wetlands containing 2 or more nests are listed.

Wetland ID	Area (km^2)	Shortest distance (m)			
		2001	2002	2003	Mean
1	2.02	231	70	39	113
2	2.05	53	98	33	61
4	1.75	105	97	131	111
3	1.26	147	93	279	173
5	0.88	571	45	280	299
6	0.47	NA[a]	666	NA	666
9	0.23	NA	NA	267	267
10	0.10	NA	92	85	89
All wetlands			Mean		222
			SE		70
Wetlands 1-5			Mean		151
			SE		41

[a] NA = Not applicable, fewer than 2 nests were found that year.

Table 6. Proportion of adjacent nests that were located within a 50-m or 100-m radius of an individual nest (Spatial Consistency Index [SCI]) near Briggsville, Wisconsin, 2001-2003. Only wetlands containing at least 2 sandhill crane nests from within 1 year were used (see Figure 2).

Wetland ID	SCI	
	50 m	150 m
10	0.21	0.86
9	0.00	0.00
6	0.00	0.00
5	0.32	0.86
3	0.63	0.63
4	0.38	0.70
2	0.23	0.42
1	0.40	0.63
Mean	0.27	0.51

disturbance (Drewien 1973, Gluesing 1974). In contrast, sandhill cranes in our study nested in a broad range of wetland sizes (Table 1), as well as in wetlands with divergent habitat types and proportions (Table 4). Sandhill cranes have now occupied a wide variety of wetland-based territories as the population density has increased.

Environmental and Behavioral Influences on Nest Density

Wetlands at all spatial scales form an important component of habitat for territorial sandhill cranes in Wisconsin (Su 2003), and territorial sandhill cranes utilize both upland and wetland components of their territory on a daily basis during summer (Miller and Barzen 2016) as do non-territorial cranes (Su 2003, Hayes 2015). The strong preference for emergent vegetation in open wetlands (the wetland habitat type) for nest locations occurred in Wisconsin and taller vegetation such as trees and shrubs were avoided, as was open water. Similar results were found for greater sandhill cranes in northern Minnesota (Provost et al. 1992, Herr and Queen 1993). Structure of wetland vegetation also influenced nest success in Oregon (Littlefield and Paullin 1990, Ivey and Dugger 2008) as did hydrologic conditions (Austin et al. 2007, Ivey and Dugger 2008), so the preferred habitat likely links strongly with reproductive potential. Where wetlands contained substantial portions of non-preferred habitat, nest locations appeared to be strongly influenced by the distribution of habitat types (Table 4, Figure 2). Wetlands 4 and 5 presented the most striking examples of the influence that vegetation type may have on the distribution of nests.

In addition to habitat selection other behavioral responses by cranes may influence the distribution of crane nests. High SCI values for nest sites being located within 150 m of other nests in our study area (Table 6) suggest other factors may be important. Three conditions for cranes exhibiting a high SCI value in a wetland were met in our study area: 1) pairs returned to the same territory year after year (Hayes 2015), 2) cranes selected the same features for nest sites, presumably the most suitable sites available for nests, each year (Table 3), and 3) habitat features (quality) changed slowly among years (ICF, unpublished data).

Conditions for a high SCI existed in other studies as well. Sandhill cranes have demonstrated strong fidelity for using the same breeding territory each year (Drewien 1973, Walkinshaw 1973*b*, 1989). Walkinshaw (1973*b*, 1989) documented 8 pairs of greater sandhill cranes returning to the same territories and nesting in similar places each year (a few even used old nests) at 3 locations over a period of 13-28 years in Michigan.

Our high SCI values may also have been influenced by the need of sandhill cranes to have both wetland and upland habitats in their territory (Su 2003, Miller and Barzen 2016). Home range size when chicks were flightless was smaller than after chicks attained flight (Miller and Barzen 2016). Flightless chicks must walk between wetland sites and upland sites on a daily basis, which would make nesting toward the outer edge of wetlands advantageous because paths of 1 family group would not cross territories of another family when moving between wetland and upland. Evidence of nesting toward the perimeter of wetlands, independent of habitat patterns, can be seen in the larger wetlands 2, 3, and 4. Though nest distribution in wetland 5 was also strongly orientated toward the wetland perimeter, this likely was due to the distribution of wetland forest (an avoided habitat type).

Littlefield (1976) detected a negative correlation between population density and size of territory among cranes species. Both Maher and Lott (2000) as well as Adams (2001) reviewed studies on territoriality in a variety of taxa and concluded that territory size reflected pressure from adjacent territorial animals, aggressiveness of territorial holders, food abundance, and habitat quality.

With the marked increase in nesting density over the past 40 years, territory size has decreased in Briggsville. Currently, crane territories spatially, but not temporally, overlap one another in our study area (ICF, unpublished data). Now, minimum distance between nests averages 151 m in large wetlands and, when using a radius of 150 m, the SCI for nesting cranes is above 50%, meaning that a majority of nests can be found within 150 m of each other. In general, the territory provides necessary resources for survival and reproductive needs of the territorial birds (Maher and Lott 2000). Presumably, these resources are finite and, at some point become limiting to the population (Adams 2001), especially since non-territorial sandhill cranes do not reproduce (Hayes 2015). Further research is needed to understand the relationships among territoriality, resource characteristics, and breeding success.

Comparison to Other Populations and Species

Maximum densities of territorial greater sandhill cranes have varied across their geographic range in North America (Table 7). In the EP, the Upper Peninsula of Michigan reported the lowest density of 0.43 territories/km^2 (Urbanek and Bookhout 1992) while the Prairie Population had the lowest density of nests (0.25 nests/km^2) reported in northwestern Minnesota (Provost et al. 1992). In contrast, the density of territories in southern Michigan was as high as 4.04 territories/km^2 (Hoffman 1983) and maximum nest density in Wisconsin (7.80 nests/km^2) was almost twice that of Michigan. Density of territorial birds in the Rocky Mountain Population at Grays Lake was comparable to our average (Austin et al. 2007) and higher than that of greater sandhill cranes in the Central Valley Population nesting in Oregon.

Other crane species have experienced strong population recovery after reaching nadirs in the 20th century and may now be approaching or at carrying capacity as well. Though the autecology of other crane species differs from sandhill cranes, the carrying capacity for most species is as yet unknown and maximum nest densities among different species may provide clues regarding the importance of nesting habitat types. The non-migratory population of the red-crowned crane (*G. japonensis*) in Hokkaido, Japan, for example, has reached a maximum density of 1.46 territories/km^2 of wetland (called 'moor' in Masatomi et al. 2007) in the Lake Furen region. Red-crowned cranes are likely more wetland dependent (Masatomi et al. 2007) than are sandhill cranes (Miller and Barzen 2016) and might require more wetland habitat in each territory as a result. Mean distances between nests was 1.72 km at Lake Furen as opposed to a mean of 0.151 km for large wetlands in our study. Likewise, the mean home range size for 13 pairs of whooping cranes (*G. americana*), another species likely more dependent on wetlands than sandhill cranes, was 4.1 km^2 per pair (Kuyt 1993) or 0.24 pairs/km^2. This population of whooping cranes is likely not yet at carrying capacity.

In contrast, the highest density of Eurasian cranes (*G. grus*) in Germany was measured in the Mecklenberg-Western Pomarania region at 39 nesting pairs/100 km^2 (Mewes and Rauch 2012) while Sundar (2009), who used a similar measure for Indian sarus cranes (*G. antigone antigone*), found 0.91 territorial pairs/km^2 (91 pairs/100 km^2). Both Eurasian cranes (Mewes and Rauch 2012) and sarus cranes (Sundar 2009) utilize upland and wetland habitats as do sandhill cranes. Density estimates for both of these species included upland and wetland habitats in their estimates, but the total areas of territories were not clearly defined so they are difficult to compare to our estimate. We believe it likely that the more wetland-dependent a species is, the lower will be the maximum nest density per area of wetland.

Rosenzweig (1991) hypothesized that habitat selection would erode for a single species under a high population density. By studying single species and species co-existing with other closely related

Table 7. Annual maximum nest density measured in crane populations worldwide. This measurement takes the number of nests (not counting renests) or the number of territorial (sometimes called 'breeding') pairs and divides this by the area of habitat in which nests were found. For most species listed, this habitat is wetland habitat even though territories occur in both upland and wetland environs.

Population	Sub-population	Year	Wetland size (km^2)	Max. no. nests	Max. no. territorial pairs	Nest density ($nests/km^2$)[a]	Territory density ($pairs/km^2$)[a]	Reference
Sandhill crane								
Eastern	Central Wis.	2001-2003	8.1	40.3		5.25		This study
Eastern	Central Wis.	2001	2.1	16		7.80[b]		This study
Eastern	Seney NWR[c], Mich.	1987	116.0		50		0.43[d]	Urbanek and Bookhout 1992
Eastern	Waterloo Township, Mich.	1982	8.2		33		3.0 (4.04)[e]	Hoffman 1983
Rocky Mountain	Grays Lake NWR, Id.	1998-2000	52.6	228	256	4.33	4.87	Austin et al. 2007
Central Valley	Sycan Marsh, Oreg.	1982-1984	93.0		126		1.35	Stern et al. 1987
Central Valley	Malheur NWR, Oreg.	1977	122.0		236		1.93	Littlefield 1995
Central Valley	Malheur NWR, Oreg.	1991	122.0[f]		245		2.01	Ivey and Dugger 2008
Prairie	Roseau River WMA[g], Minn.	1989-1991	111.4	28	51	0.25	0.46	Provost et al. 1992[h]
Whooping crane								
Aransas-Wood Buffalo	Wood Buffalo National Park	1991			13		0.24[i]	Kuyt 1993
Red-crowned crane								
Non-migratory	Hokkaido, Japan	2002	327.3		290		0.88[j]	Masatomi et al. 2007
Non-migratory	Hokkaido, Japan	2002	47.9		70		1.46[k]	Masatomi et al. 2007

[a] Density is per km^2 of wetland unless indicated otherwise.
[b] Includes 16 nests found on 1 day in 1 wetland and represents the maximum estimate found.
[c] NWR = National Wildlife Refuge.
[d] Study area consisted of both upland and wetland areas but was approximately two-thirds wetlands.
[e] Hoffman reported 3.0 pairs/km^2, but the 33 pairs he surveyed in 1982 on 8.16 km^2 of non-forested wetlands = 4.04 pairs/km^2.
[f] No wetland area was given in Ivey and Dugger (2008), so estimate of wetland area from Littlefield (1995) for the same wetland area was used.
[g] WMA = Wildlife Management Area.
[h] Study area consisted of both upland and wetlands but was 85% wetlands.
[i] Kuyt (1993) listed mean size of home ranges for 13 nesting pairs in the core breeding area as 4.1 km^2. The reciprocal of this is 0.25 home ranges/km^2, the equivalent of the number of indicated pairs per km^2.
[j] Total number of breeding (territorial) pairs/area of wetlands from all 7 regions studied.
[k] Number of breeding (territorial) pairs/area at the most densely populated wetland region (Lake Furen).

species, Holmes (1961) and Diamond (1978) illustrated that species typically widen their niches under lack of inter-specific competition and increasing intra-specific competition. Under the theory of Ideal Free Distribution, high-quality habitats (territories here) will be occupied before low-quality habitats (Fretwell 1972) and, with territorial species, once all available territories are filled, some sexually mature birds will be unable to breed because they cannot find appropriate territories (Brown 1969). Sandhill cranes have populations of sexually mature, non-territorial cranes that co-mingle with territorial cranes (Su 2003, Hayes 2015) and nest in the highest known density of any crane species. Within our study area the rate of mate switching is high and reproductive rates are depressed for 2-3 years following mate switches (Hayes 2015). This feedback may provide 1 mechanism that drives density-dependent population dynamics (e.g., Sibly et al. 2005). Crane species that are more wetland dependent may be constrained further by habitat requirements and may, therefore, have lower maximum nest densities than do crane species that establish territories in more upland areas as well as wetlands. If our hypothesis is correct, more research is needed to understand this important parameter of population change.

ACKNOWLEDGMENTS

We gratefully thank Windway Corporation for donating all survey expenses. M. Crandall provided excellent piloting skills, M. Voechting produced useful video images of nests, and M. Mauer coordinated flight plans. T. and M. Kohler supported this study throughout. A. R. Barzen, J. J. Barzen, K. Hall, S. Hanuszczak, T. Miller, Z. Rickenbach, and S. Zimorski volunteered as observers. Finally, we thank G. Ivey, R. Urbanek, and an anonymous reviewer for improving this manuscript with their suggestions.

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