

NEST HABITAT SELECTION AND NEST SUCCESS OF GREATER SANDHILL
CRANES IN NORTHWESTERN MINNESOTA

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Abstract. - We studied Greater Sandhill Cranes (Grus canadensis tabida) in northwestern Minnesota to document nest habitat selection and nest success, and to determine whether nest success was related to nest habitat characteristics. We located 62 crane nests. At each nest and a matched random site in the same wetland, we recorded 15 habitat characteristics. We used multiple conditional logistic regression to determine whether habitat characteristics differed between matched pairs of nests and random sites. Only the low height concealment index and sedge (Carex spp.) stem density predicted whether a location was a nest site. The odds of a location being a nest site (vs. a random site) decreased 2.8 times for each 10% increase in concealment score and increased 3.1 times for each unit decrease in \ln (sedge stem density). Overall nest success was 39.6% (95% CL = 23.4%, 51.7%). Nests initiated in April were less likely to be depredated than those initiated in May ($P = 0.03$). All but one of 23 depredated nests appeared to have been destroyed by mammalian predators. Nests in large wetland basins (>2.2 ha) were not more likely to hatch than those in small basins (≤ 2.2 ha) ($P = 0.29$). The dominant vegetation within a 5 m radius of the nest did not differ significantly between hatched and depredated nests ($P = 0.63$). We tested for an association between 10 other habitat variables and the probability that a nest would be depredated by fitting an unconditional logistic regression model to data from the 62 nest sites. Only low height concealment score, water depth, and their interaction were statistically significant. The odds of depredation at nests in shallow water (≤ 9.7 cm) were 3.7 times greater than at

nests in deeper (> 9.7 cm) water regardless of the low height concealment score. At deeper water nest sites, the odds of depredation increased 1.2 times for each 10% decrease in concealment score.

Maintenance of essential habitats for Sandhill Cranes (*Grus canadensis*) is a primary need for crane populations throughout North America (Tacha et al. 1992). Because humans frequently alter shallow marshes and bogs which are important Sandhill Crane nesting habitats, land managers and planners need to better understand Sandhill Crane nest habitat preferences and whether habitat changes influence nest success. In the Great Lakes region, nesting Greater Sandhill Cranes have been studied in Ontario (e.g., Tebbel 1981), Michigan (e.g., Walkinshaw 1973, Urbanek and Bookhout 1988), Wisconsin (e.g., Howard 1977, Bennett 1978), and Minnesota (e.g., DiMatteo 1991, Provost et al. 1992). Herr and Queen (1993) and Baker et al. (1995) studied Greater Sandhill Crane nesting habitat at larger spatial scales. However, only Tebbel 1981, Provost et al. (1992), and Baker et al. (1995) attempted to determine nest habitat preferences by comparing nests with randomly selected sites and only Urbanek and Bookhout (1992) assessed whether nest habitat characteristics influence nest success.

Our objectives were to (1) document patterns of nest habitat use and determine whether Greater Sandhill Cranes select certain habitat components when choosing nest sites, (2) estimate Sandhill Crane nest success, and (3) determine whether nest success was associated with nest habitat characteristics.

STUDY AREA AND METHODS

Study area. - Our study was conducted during April-July, 1989-1991 in portions of Kittson, Marshall, and Roseau Counties of extreme northwestern Minnesota. All sites are within the aspen parkland landscape region of Minnesota (Kratz and Jensen 1983). This area is characterized by flat topography with a mosaic of agricultural land (primarily small grain or Conservation Reserve Program fields), brushlands dominated by willow (Salix spp.), forests dominated by aspen (Populus tremuloides), and shallow wetlands. Portions of the study area are described in further detail by Herr and Queen (1993).

Field Methods. - Sandhill crane nests were located by low-level (10-30 m) helicopter searches of shallow wetlands. Cranes typically flushed a short distance ahead of the helicopter and were readily seen. Nest sites were marked by dropping weighted strips of plastic flagging from the helicopter and by plotting locations on aerial photos. Additionally, locations of several nests were reported to us by Minnesota Department of Natural Resources personnel. Nests were later relocated from the ground and each was marked by tying plastic flagging to vegetation 5 m from the nest. At the initial visit to each nest we floated the eggs to determine their stage of incubation (Fisher and Swengel 1991). We revisited nests shortly after the expected hatch date to determine their fate (Urbanek and Bookhout 1992). Nest success was estimated using the Mayfield method (Klett et al. 1986).

After nest fate was determined, 15 measurements of habitat structure were recorded at each nest. Any current-year plant growth was ignored during these

measurements because it was not present when nests were constructed and was not a factor in site selection. We used a 25 x 99 cm density board divided into three 33 cm height increments to measure nest concealment (Provost et al. 1992). Each height increment was subdivided into 25 rectangles. The density board was placed on the nest and orientated to the cardinal directions. All rectangles more than 50% visible at a distance of 5 m and eye height of 1 m were counted. Totals from the four directions were summed and subtracted from 100 to yield a concealment index for each of the three height increments. The three indexes were intended to represent vegetative concealment of the following: low = crane incubating with head down, mid = crane incubating with head up, high = crane standing at nest. A 0.25-m² quadrat was randomly located within each of four 1-x 5-m strips radiating from the nest in the cardinal directions. Within each quadrat, counts of residual stems of each herbaceous species were recorded. For analysis, herbaceous species were pooled into the following categories: cattail (Typha spp.), bulrush (Scirpus spp.), phragmites (Phragmites australis), sedge (Carex spp.), grass (Poacea exclusive of Phragmites), and other. We visually categorized the dominant vegetation within a 5 m radius of the nest as cattail, bulrush, phragmites, sedge, or grass. Mean water depth was computed from measurements made 1 m from the nest in each of the cardinal directions. (At most nests, water depth was also measured when the nest was initially visited.). The number of shrub stems ≥ 4 mm in diameter that were within 1.5 m of the nest and the number of trees ≥ 3 cm in diameter within 5 m were recorded. We also estimated basin size and measured distance to the nearest upland and distance to the

nearest tree.

Immediately after completing habitat measurements at a nest, we made the same measurements at a randomly selected site within the same wetland basin. Random sites were selected in two ways. When nests were in large wetlands, a transparent grid was placed over an air photo and each square falling inside the basin was numbered. One square was randomly selected and the approximate center of this square was then located in the wetland. From this point we walked a randomly predetermined direction and distance (1-10 m) to a second point which became the random site. In small wetlands, which did not show up well on air photos, we divided the basin into quarters in the field. One quarter was randomly selected. From the center of this quarter we walked a randomly predetermined direction and distance (1-10 m) to the random site.

Statistical methods. - We used Pearson correlations to test for an association between basin size and distance to nearest upland and between distance to nearest tree and distance to nearest upland. A Mantel - Haenszel χ^2 test (Agresti 1996:38-39) was used to determine whether there was a trend in the proportion of nests depredated from late April through late May. Chi-square homogeneity tests were used to determine whether nests were more likely to hatch in large versus small wetland basins and whether dominant vegetation within 5m of a nest differed between hatched and depredated nests. We used a paired t-test to compare mean water depth at nests when initially visited versus after nest fate was determined.

We used a multiple conditional logistic regression model to determine whether

habitat characteristics differed between matched pairs of nests and random sites. Based on box and whisker plots of the distribution for each habitat variable, we selected 10 variables whose distributions differed most between nests and random sites for entry into the model. These included: concealment indexes at low, mid, and high density board height increments, total stems of cattail, bulrush, phragmites, sedge, and grass within the four 0.25-m² quadrats, mean water depth, and distance to the nearest upland. Strength of association between the 10 habitat variables and the conditional probability that one member of each matched pair was actually the nest site was estimated by exponentiation of the model parameters (Hosmer and Lemeshow 1989: 178-201, Clayton and Hills 1993: 290-297, Agresti 1996). Regression diagnostics for the matched pairs analysis indicated that the linearity assumption was satisfied for all habitat variables except sedge stem counts; however, this problem was corrected by a log transformation. Likelihood ratio tests determined the best reduced model. The final model included any significant ($\alpha = 0.10$) two-way interactions among significant habitat variables in the reduced model; small sample size precluded testing for higher order interactions. When significant interactions occurred, one of the interacting habitat variables was dichotomized based on its median value and the odds for the second variable were estimated separately at each level of the dichotomy. We report results as the odds ratios with 90% confidence limits.

We tested for an association between the same 10 habitat variables and the probability that a nest would be depredated by fitting an unconditional logistic regression model (Hosmer and Lemeshow 1989: 36-76) to nest site data. The final reduced model,

interaction assessment, and odds ratio estimates were obtained as per the matched pairs analysis. Tests of goodness of fit and of the assumption of linearity in the log-odds and residual analyses were made for all models (Hosmer and Lemeshow 1989: 135-173).

RESULTS

Nest habitat selection. - Habitat data were obtained from 62 Greater Sandhill Crane nests and an equal number of matched random sites. Nests were in wetland basins ranging from 0.01-601 ha (Median = 2.2 ha). Most nests (58.0%) were in habitats dominated by cattail while 21.0% were in sites dominated by phragmites. Sites dominated by bulrush, sedge, and grass accounted for only 11.3%, 8.1%, and 1.6% of nests. Nests were not found where mean water depth exceeded 35.7 cm. (Table 1). Water depths of zero were recorded at eight nests. Two were on small upland islands within marshes while the other six were in wetlands that were dry when nests were found in early - mid May. The distance from nests to the nearest upland varied considerably (Table 1), but was positively correlated with basin size ($r = 0.784$). Distance to the nearest tree was positively correlated with distance to nearest upland ($r = 0.853$) because trees often lined the upland edges of wetlands. Only one nest and one random site had trees within 5 m. Similarly, only seven nests and five random sites had any shrub stems within 1.5 m. Concealment scores were quite variable (Table 1), but decreased from low to high density board height increments for 87% of nests and 100% of random sites as the number of plant stems decreased with increasing height.

Cattail occurred (i.e., was present in one or more 0.25-m² quadrats) at both nests

and random sites more frequently than any other plant type (Table 2). At sites where it occurred, cattail was usually present in all four quadrats. Sedge occurred at more than half the nests and random sites while bulrush and phragmites occurred at 1/4 -1/3 of the locations. Grass and “other” plant stems occurred at few locations and in relatively few quadrats at each site.

Stem counts (total from all four 0.25-m² quadrats combined) for each of the five main plant types varied considerably (Table 3). Cattail had the highest stem count at 29 nests and 26 random sites. In contrast, grass had the highest counts at only two nests and one random site.

Only two variables, the density board concealment index at low height and sedge stem density, predicted whether a location was a nest site (vs. a random site). The fit of this reduced model was quite good ($R^2 = 0.81$). The odds of a location being a nest site were decreased 2.8 (1.8, 4.5) times for each 10% increase in the low height concealment score and increased 3.1 (1.7, 5.7) times for each unit decrease in \ln (sedge stem density).

Nest success. - Dates of nest initiation (i.e., date the first egg was laid) were estimated for 53 nests and ranged from 23 April - 29 May. Total nests initiated during the last week of April was similar to the number begun during the first half of May, but nest starts dropped off sharply during the latter half of May (Table 4). The proportion of nests depredated exhibited an increasing trend from April through late May (Mantel-Haenszel $\chi^2 = 4.53$, $df = 1$, $P = 0.03$).

Clutch size was either 1 or 2 ($\bar{x} = 1.86$). Of 63 nests, 36 hatched, 23 were

depredated, and four had infertile or addled eggs. Mayfield nest success was 39.6% (57 nests, 788 exposure days, 95% CL = 23.4%, 51.7%). Based on evidence remaining at depredated nests (e.g., Rearden 1951, Trevor et al. 1991) it appeared that only one nest was destroyed by avian predators (likely Common Ravens, Corvus Corax or American Crows, C. brachyrhynchos). The remaining 22 nests were likely depredated by mammals. Potential local predators included raccoons (Procyon lotor), striped skunks (Mephitis mephitis), red foxes (Vulpes vulpes), coyotes (Canis latrans), and gray wolves (Canis lupis). Ten nests contained no remnants of eggs suggesting that the eggs were removed and eaten elsewhere, a pattern typical of coyotes (Littlefield 1995) and sometimes red foxes (e.g., Trevor et al. 1991).

Association of nest fate with nest habitat. - For comparisons of nest fate and nest habitat, we included the four nests having addled/infertile eggs in the hatched category because all were incubated longer than the normal incubation period and would have hatched had the eggs been viable. Nests in large basins (>2.2 ha) were not more likely to hatch than those in small (≤ 2.2 ha) basins ($\chi^2 = 1.11$, $df = 1$, $\underline{P} = 0.29$). The dominant vegetation within a 5 m radius of the nest did not differ significantly between hatched and depredated nests ($\chi^2 = 2.61$, $df = 4$, $\underline{P} = 0.63$).

The full unconditional logistic regression model included 10 habitat variables (Table 5). The final reduced model contained only the density board concealment score at low height, water depth, and their interaction. The model fit the data (Hosmer and Lemeshow 1989) ($\chi^2 = 1.99$, $df = 8$, $\underline{P} = 0.98$), but there was considerable heterogeneity

in the degree of departure of the observed versus predicted probabilities of depredation ($R^2 = 0.43$). The odds of depredation at nests in shallow (≤ 9.7 cm) water were 3.7 (1.5, 9.2) times greater than at nests in deeper (> 9.7 cm) water regardless of the level of low height concealment. In fact, 69.7% of depredated nests were located in shallow water sites. However, at the deeper water sites the odds of depredation were increased 1.2 (1.0, 1.3) times for each 10% decrease in the low height concealment score.

Because of the importance of water depth to nest success, we compared mean water depths at 51 nests having depth measurements when initially visited ($\bar{x} = 10.8$ cm \pm 1.2 SE) and when nest fate was determined ($\bar{x} = 9.9$ cm \pm 1.1 SE). While water depth tended to decrease during this period ($t = 1.96$, $df = 50$, $P = 0.056$), only 5 nests changed classification from deep to shallow. One nest switched from shallow to deep. Thus, the majority of nests were in either shallow or deep water throughout incubation.

DISCUSSION

Greater Sandhill Cranes in this study and others (e.g., Bennett 1978, Tebbel 1981, Urbanek and Bookhout 1988, DiMatteo 1991, Provost et al. 1992) used a variety of wetland habitats and dominant plant species for nesting. Apparently, habitat selection is based on vegetative structure rather than species composition (e.g., Bennett 1978, DiMatteo 1991, Provost et al. 1992). Selection may also occur beyond the immediate vicinity of the nest at larger spatial scales (Herr and Queen 1993, Baker et al. 1995) although Baker et al. (1995) detected no habitat selection beyond 200 m from a nest site.

Sandhill Cranes exhibit variable nesting habitat selection depending on the

wetland types available. Whereas Tebbel (1982) reported that cranes preferred to nest at sites containing Sphagnum spp. and leatherleaf (Chamaedaphna calyculata) in an area where bogs were prevalent, these plants were not recorded in our study nor at nest sites nearby (Provost et al. 1992). Additionally, Provost et al. (1992) found that crane nests were further from shrubs than were random sites. Provost et al. (1992), using sampling methods similar to ours, did not detect other significant differences between nests and random sites, but their analyses had relatively small sample sizes. We found that the probability of a site being a nest increased as the low height concealment score and sedge stem density decreased. Concealment scores indicated that vegetation was less dense at nests than at random sites. This may be due, in part, to the fact that cranes collect nest construction materials close to their nests (Tacha et al. 1992) and thereby thin out the vegetation; a pattern noted by others (e.g., Bennett 1978, DiMatteo 1991, Provost et al. 1992). Bennett (1978) also noted that potential nesting vegetation was avoided if its density or height impeded free movements by the birds. While crane nests clearly were not in the most dense vegetation available, neither were they in the most open sites. This is supported by the lower sedge stem densities found at nests versus random sites. Residual sedge stems lie close to the ground and would provide virtually no concealment to a nesting crane. None of our nests were in broad expanses of sedge. Thus, Sandhill Cranes appeared to select nest sites that provided some vertical cover (i.e., cattail, phragmites, bulrush) for concealment while also allowing the birds a view of their surroundings and ease of access to and from the nest. This degree of habitat openness

may be important to cranes because it allows them to observe potential predators approaching their nest in time to react appropriately by flight, distraction, or defense.

Although the 62 matched pairs of nest and random sites allowed reasonable power to detect main effects of the 10 habitat variables, we were limited in the number of interactions we could examine. From the 45 possible two-way interactions, we chose to test only those involving one or more significant main effects. Because all nonsignificant odds ratios were within ± 0.13 of 1.0 and none had 90% confidence limits <0.6 or >2.0 , we believe that the null hypothesis was correctly accepted for all “nonsignificant” habitat variable effects (The Journal of Wildlife Management 1995, Maxson and Riggs 1996).

Urbanek and Bookhout (1992) reported different relationships between habitat characteristics and nest fate than we observed. They noted that nests in cattail marshes suffered more predation than nests in sedge marshes. However, water depth or concealment scores were not associated with nest fate in their study. In contrast, we found no differences in nest success among dominant vegetation types, but water depth and low height concealment scores did influence nest survival. Nests in deeper water were much more likely to hatch than those in shallow water. At deeper water sites, an increase in vegetative concealment resulted in a slightly higher nest success rate. However, this difference may not have been large enough to have much biological importance. The increased risk of depredation at shallow water nests overwhelmed any effects of vegetative concealment at those sites.

The importance of water depth and the lesser importance of vegetative

concealment for nest success is consistent with studies of nesting waterfowl. Water often constitutes a barrier to many mammalian predators (Sargeant and Arnold 1984) and overwater nesting ducks typically have higher nest success than upland nesters (e.g., Bouffard et al. 1988, Maxson and Riggs 1996). Furthermore, where mammalian nest predators predominate over avian predators, as in our study, nest concealment typically is of little importance to nest success (e.g., Clark and Nudds 1991). Given the apparent high selection pressure to nest in deeper water, why didn't all cranes do so? In fact, not all pairs we studied had the opportunity to do so every year. 1990 was a dry spring and many of the wetlands in our study area were shallow or dry when cranes were nesting. The combination of fewer and shallower wetlands likely made crane nests easier for mammalian predators to find and access.

With only 23 of 62 nests suffering predation, our depredation odds models have substantially less power than the matched pairs analysis. Nonetheless, odds ratio estimates and confidence limits of nonsignificant effects were in the same range as those of the matched pairs analysis. Therefore, we believe that the null hypothesis was correctly accepted for "nonsignificant" habitat variable effects (The Journal of Wildlife Management 1995, Maxson and Riggs 1996).

Interestingly, effects of vegetative concealment and water depth were not consistent in our two analyses. In the nest habitat selection analysis, an increase in low height concealment led to a reduced likelihood of the site being a nest, but an increase in this same concealment score led to increased nest success at nests in deeper water.

Whereas shallow water at the nest site was the major risk factor in nest predation, the nest habitat selection analysis did not indicate that water depth was a significant factor ($\chi^2 = 0.64$, $df = 1$, $P = 0.43$) in nest site selection. A possible explanation for these counterintuitive results is that the 1:1 matched design may not be adequate for wildlife resource selection studies. An implicit assumption in our design is that each random site represents the range of habitat available for selection; i.e., that for each nest site, a sample of $n = 1$ is sufficient to represent characteristics of the surrounding locality. While the nest site itself is essentially a single point of habitat, the available habitat from which the crane presumably made its selection is a much larger and often, a more heterogeneous expanse. Thus the 1:R matched design (Rothman 1986) is probably more appropriate for resource selection studies. Ideally, the value of R (the number of random sites evaluated per nest site) should be determined by the heterogeneity of the wetland. Epidemiologic studies generally employ 2 - 10 controls per case (Kleinbaum et al. 1982: Rosenbaum 1995), and we suggest that ecologists consider similar guidelines for resource selection studies which employ matching.

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Table 1

Habitat characteristics at 62 Greater Sandhill Crane nests and 62 random sites in northwestern Minnesota, 1989-1991.

Habitat Characteristics	Nest sites			Random sites			Mean paired differences ^a	
	\bar{x}	\pm SE	Range	\bar{x}	\pm SE	Range	\bar{x}	\pm SE
Water depth (cm)	10.4	\pm 1.1	0-35.7	9.2	\pm 1.2	0-41.5	1.3	\pm 1.0
Distance to upland (m)	61.2	\pm 7.8	3-245	64.0	\pm 8.8	1-320	-2.8	\pm 5.7
Distance to tree (m) ^a	76.3	\pm 7.3	6-255	77.4	\pm 7.9	12-294		
No. trees within 5 m	0.3	\pm 0.3	0-17	0.3	\pm 0.3	0-19		
No. shrub stems within 1.5 m	2.9	\pm 1.8	0-102	2.8	\pm 2.0	0-116		
Concealment score - low	52.7	\pm 3.1	0-100	78.4	\pm 3.7	0-100	-6.4	\pm 0.9
Concealment score - mid	23.9	\pm 3.1	0-100	44.1	\pm 4.8	0-100	-5.0	\pm 1.2
Concealment score - high	12.1	\pm 2.5	0-84	24.1	\pm 4.0	0-95	-3.0	\pm 1.0

^a Computed as the mean of the 62 nest site - random site differences.

Table 2

Plant type occurrence within four 0.25-m² quadrats at 62 Greater Sandhill Crane nests and 62 random sites in northwestern Minnesota, 1989-1991

Plant type	Nest sites			Random sites		
	N ^a	\bar{x} ^b	\pm SE	N	\bar{x}	\pm SE
Cattail	51	3.6	\pm 0.1	53	3.5	\pm 0.1
Bulrush	17	2.7	\pm 0.3	19	2.7	\pm 0.3
Phragmites	21	2.8	\pm 0.3	16	2.9	\pm 0.3
Sedge	36	2.7	\pm 0.2	39	3.2	\pm 0.2
Grass	7	1.7	\pm 0.3	8	2.2	\pm 0.3
Other	5	1.4	\pm 0.2	4	1.5	\pm 0.5

^a Number of nests or random sites at which the plant type occurred in one or more 0.25-m² quadrats.

^b Mean number of 0.25-m² quadrats containing the plant type at sites where the plant type was recorded.

Table 3

Total stems of each plant type in four 0.25-m² quadrats at 62 Greater Sandhill Crane nests and 62 random sites in northwestern Minnesota, 1989-1991

Plant type	Nest sites				Random sites				Mean paired differences ^b	
	N ^a	\bar{x}	\pm SE	Range	N	\bar{x}	\pm SE	Range	\bar{x}	\pm SE
Cattail	29	30.8	\pm 3.5	0-114	26	31.0	\pm 3.7	0-130	-0.1	\pm 1.1
Bulrush	7	13.6	\pm 4.4	0-170	6	17.5	\pm 5.0	0-163	-1.0	\pm 1.4
Phragmites	14	18.7	\pm 6.4	0-360	7	13.2	\pm 3.7	0-154	1.4	\pm 1.6
Sedge	10	21.7	\pm 4.6	0-195	22	61.6	\pm 13.3	0-535	-10.0	\pm 3.4
Grass	2	1.6	\pm 0.7	0-35	1	5.7	\pm 2.6	0-112	-1.0	\pm 0.6

^a Number of nest or random sites where the plant type had the highest stem count.

^b Computed as the mean of the 62 paired nest site - random site differences.

Table 4

Greater Sandhill Crane nest initiation dates and the percentage of nests depredated in
northwestern Minnesota, 1989-1991

	Nest initiation dates ^a		
	23-30 Apr	1-15 May	16-29 May
Total nests	22	23	8
% depredated	13.6	34.8	50.0

^a Date first egg was laid.

Table 5

Habitat characteristics at 39 hatched and 23 depredated Greater Sandhill Crane nests in
northwestern Minnesota, 1989-1991

Habitat characteristic	Nest fate			
	Hatched		Depredated	
	\bar{x}	\pm SE	\bar{x}	\pm SE
Mean water depth (cm)	12.4	\pm 1.4	7.1	\pm 1.2
Distance to upland (m)	74.0	\pm 10.4	39.5	\pm 9.9
Concealment score - low	45.3	\pm 3.6	65.1	\pm 4.7
Concealment score - mid	20.2	\pm 3.9	30.4	\pm 5.1
Concealment score - high	10.6	\pm 3.1	14.6	\pm 4.5
Cattail stems	28.0	\pm 4.0	35.5	\pm 6.8
Bulrush stems	14.1	\pm 5.6	12.6	\pm 7.3
Phragmites stems	17.7	\pm 9.6	20.5	\pm 6.4
Sedge stems	22.6	\pm 6.7	20.2	\pm 5.2
Grass stems	1.8	\pm 1.1	1.2	\pm 0.7