TUNDRA SWAN HABITAT PREFERENCES DURING MIGRATION IN NORTH DAKOTA

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Abstract: I studied tundra swan (*Cygnus columbianus columbianus*) habitat preference in North Dakota during autumn migration, 1988–89. Many thousand tundra swans stop in the Prairie Pothole region during autumn migration, but swan resource use has not been quantified. I examined habitat preference in relation to an index of sago pondweed (*Potamogeton pectinatus*) presence, extent of open water, and wetland size. I compared habitat preference derived from counts of all swans to those derived from foraging swans only and cygnets only. Foraging swans preferred wetlands with sago pondweed ($P = 0.03$); the number of foraging swans per wetland was >4 times higher on wetlands with sago pondweed than on wetlands without sago. In contrast, nonforaging swans did not prefer wetlands with sago pondweed ($P = 0.85$) but preferred large wetlands ($P = 0.02$) and those with a high proportion of contiguous open water ($P < 0.01$). Thus, conclusions about habitat preference derived from counts of all swans, most of which were nonforaging, would not have revealed the importance of sago pondweed. Cygnets were more likely to be feeding than adults ($P = 0.03$) and occurred proportionately more often in smaller flocks ($P = 0.04$), but cygnets and adults had similar habitat preferences.

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Thousands of Eastern Population tundra swans stop in the Prairie Pothole Region of North Dakota en route from northern breeding grounds to the eastern U.S. coast (Bellrose 1980, Kantrud 1986). Understanding resource use of swans is of interest in North Dakota because swans forage solely in wetlands. In contrast, with a decrease in wetlands and an increase in agriculture, swans in many regions have shifted foraging, in part, to agricultural crops (McKelvey 1981, Munro 1981, Black and Rees 1984, Dirksen et al. 1991, Esselink and Beekman 1991). The need to identify and maintain adequate wetland resources for swans in the Prairie Pothole Region is underscored by the loss of wetlands throughout the Great Plains and the land-use conflicts that arise when swans turn to agricultural crops.

In this study, which was the first to address habitat preferences of tundra swans during migration, I had 2 principle goals. First, I identified tundra swan habitat preference in relation to an index of sago pondweed presence, extent of open water, and wetland size. The energy-rich (Kantrud 1990) tubers of sago pondweed are thought to be the primary food of tundra swans during autumn in North Dakota (Kantrud 1986, Swanson 1986). Second, I compared habitat preference derived from counts of all swans to those derived from foraging swans only and cygnets only. If nonforaging swans (which compose the majority of individuals at a given time) prefer different habitats than do foraging swans, then the aerial surveys typically used to assess waterfowl populations and use of habitat may not reveal the importance of foraging habitat.

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STUDY AREA

The study site was a 2,200-km² area in northeastern Kidder County, east-central North Dakota. The area's numerous wetlands were diverse in limnological features and plant communities. Dominant submersed plants included common watermilfoil (*Myriophyllum exalbescens*), common bladderwort (*Utricularia vulgaris*), coontail (*Ceratophyllum demersum*), claspingleaf pondweed (*P. richardsonii*), grassleaf pondweed (*P. pusillus*), and white watercrowfoot (*Ranunculus trichophyllus*) in wet-

lands with relatively fresh water (conductance <2,000 μmhos); sago pondweed, horned pondweed (*Zannichellia palustris*), and stoneworts (*Chara* spp.) in wetlands of intermediate salinity (2,000–15,000 μmhos); and saltwater widgeongrass (*Ruppia maritima*) in wetlands of high salinity (>15,000 μmhos; Stewart and Kantrud 1971). Bulrushes (*Scirpus* spp.) and cattails (*Typha* spp.) were the dominant emergent species in autumn. The study area and surrounding region were described by Stewart and Kantrud (1971), Cowardin et al. (1981), and Swanson et al. (1988).

METHODS

I collected data during peak autumn migration, 15 October–5 November 1988–89. An aerial survey was conducted over the entire study site in mid-October of each year. I defined wetlands as basins ≥0.08 km² that held water at the time of the aerial survey. Except for 5 wetlands that were inaccessible, I visited each wetland (n = 108) on the ground in at least 1 of the 2 years. I visited 83% in both years. During ground visits, which were made between 0900 and 1800, I scanned all swans and recorded the number of adults and cygnets and the proportion of each age group that was feeding. I observed swans from a vehicle with a window-mounted spotting scope and remained at the maximum distance (approx 200 m) from which ages and behaviors could be discerned. If swans appeared alert to my presence, I did not record proportion feeding. I averaged results from multiple visits (within and between years) to the same wetland so that each wetland entered the analysis once.

I indexed sago pondweed as present if a windrow of sago plants ≥5 cm wide was found along the downwind shore or absent if the windrow was <5 cm. The 5-cm threshold was derived from preliminary observations that wetlands typically had either small (much <5 cm) or large (≥5 cm) windrows and that wetlands with windrows <5 cm usually had no sago or a few dispersed plants (pers. obs.). I considered sago present for analytic purposes if it was classified as present in either of the 2 years. Although feeding waterfowl uproot sago plants, it is common for wetlands in North Dakota and elsewhere (pers. obs.) that are rarely used by waterfowl to have windrows of sago pondweed in autumn. Thus, most windrowed vegetation was probably senescent plants washed ashore by wind. I believe I correctly classified sago as present regardless of whether the wetland had been recently visited by waterfowl. I quantified only sago pondweed, because sago was the only tuber-producing species present and was known to be important to swans (Kantrud 1986, Swanson 1986, Beekman et al. 1991). Although swans also may have eaten other submersed vegetation, the foliage of most species is senescent by the time swans arrive.

During site visits, I visually categorized wetlands by the proportion of the wetland that was contiguous open surface water: closed wetlands had <95% open water with interspersed emergent vegetation, intermediate wetlands had <95% open water with emergent vegetation around the edges only (and thus had a higher proportion of contiguous open water than closed wetlands), and open wetlands had >95% open water. I selected these categories because they corresponded to cover types 2, 3, and 4, respectively, of Stewart and Kantrud (1971), and because wetlands could be reliably categorized visually. I categorized wetland size as small (0.08–0.26 km²), medium (0.261–1.30 km²), or large (>1.30 km²) according to a National Wetlands Inventory map.

I used simple and multiple linear regressions to test for a relationship between swans per wetland and sago presence, extent of open water, and wetland size. Sago pondweed presence was treated as an indicator variable. I recorded extent of open water and wetland size as categorical data but treated them as continuous variables in regression; performing regression on categorical rather than continuous data results in negligible loss of precision when ≥3 categories are used (Cochran 1983). Sample size varied among analyses because I did not determine habitat type, proportion of swans foraging, and age of swans for each wetland.

RESULTS

Sago pondweed occurred on 57% of the wetlands (n = 92). Small, medium, and large wetlands made up 28, 41, and 30% of the wetlands, respectively (n = 108). Wetlands composed of an intermediate proportion of contiguous open water were more common than closed or open wetlands (74 vs. 7 and 17%, respectively, n = 95).

Presence of sago pondweed was independent of open water category and wetland size (Table 1), but open water category and wetland size were not independent (χ^2 = 16.52, 4 df, P <

Table 1. Proportion of lakes, categorized by extent of contiguous open water and wetland size, on which sago pondweed was present in Kidder County, North Dakota, autumn 1988–89.

Variable Category	Proportion of lakes with sago pondweed[a]	Total no. of lakes
Open water (OW)		
Closed (<95% OW)	0.57	7
Intermediate	0.58	67
Open (>95% OW)	0.50	16
Wetland size		
Small (0.08–0.26 km²)	0.50	26
Medium (0.261–1.30 km²)	0.58	38
Large (>1.30 km²)	0.61	28

[a] Presence of sago pondweed was independent of open water (χ^2 = 0.36, $P > 0.5$) and wetland size (χ^2 = 0.68, $P > 0.5$).

0.005). Large wetlands were more likely to be open wetlands.

Total number of swans seen during aerial surveys (3,607 in 1988 and 4,186 in 1989) and use of habitat of foraging and nonforaging swans were similar between years (all *P*s >0.05). Also, there was no effect of year on proportion of young per flock (P = 0.91).

There was an average of 10 (SE = 3) foraging and 41 (SE = 10) nonforaging swans per wetland (range 0–159 and 0–569, respectively). Swans fed and roosted solely on wetlands. Nonforaging swans typically occurred in large flocks, 67% of all nonforaging swans observed were in 8 flocks, and most nonforaging swans were roosting (i.e., sitting or standing on shore; $\bar{x}$ proportion of nonforaging swans that were roosting = 0.95 ± 0.02, n = 19). Proportion of swans feeding and time of day were not correlated in either year (P = 0.63 and 0.79).

Foraging Swans

The number of foraging swans per wetland was >4 times higher on wetlands with sago pondweed than on wetlands without sago pondweed (P = 0.03; Fig. 1). Fourteen of the 17 wetlands that had >10 foraging swans present were sago wetlands, and sago wetlands supported most (86%) foraging swans observed.

Neither the extent of contiguous open water nor wetland size was related to number of foraging swans per wetland (Fig. 1). Because of the nonlinear relationship between open water category and number of foraging swans, I also analyzed data with an analysis of variance (ANOVA); there were no differences in the

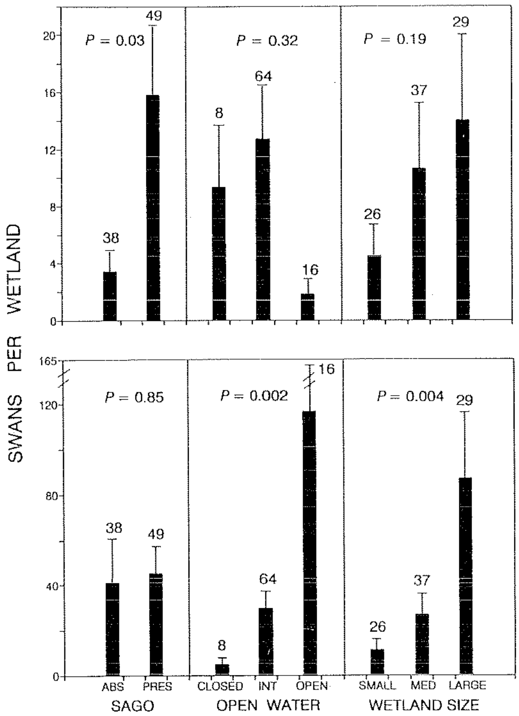

Fig. 1. Foraging (top) and nonforaging (bottom) tundra swans per wetland in habitats characterized by an index of sago pondweed presence, extent of open water, and size of wetland (small = 0.08–0.26 km², medium = 0.261–1.30 km², or large = >1.30 km²), in North Dakota, 1988–89. Bars are SEs. Sample sizes (no. of flocks) are given above bars. Statistical significance determined by linear regression. Abbreviations are as follows: ABS = absent, PRES = present, INT = intermediate, and MED = medium.

number of foraging swans among open water categories (P = 0.35).

The presence of sago pondweed was a significant predictor of foraging swans per wetland (partial R^2 = 0.053, P = 0.045) in multiple regression analysis, but proportion of contiguous open water and wetland size were not (partial R^2 = 0.018 and 0.017, P = 0.29 and 0.24, respectively). Interaction terms were added to the main effects individually and then removed. No interaction term was significant (sago by open water, P = 0.64; sago by size, P = 0.55; open water by size, P = 0.66).

Nonforaging Swans

The number of nonforaging swans per wetland did not differ between wetlands with and without sago pondweed (P = 0.85). Sago wetlands composed 56% of available wetlands and supported 59% of nonforaging swans. The number of nonforaging swans per wetland increased with an increasing extent of open water (P = 0.002) and with wetland size (P = 0.004; Fig. 1).

Similarly, in multiple regression analysis, extent of open water and wetland size were predictors of the number of nonforaging swans per wetland (partial R^2 = 0.086 and 0.065, P = 0.008 and 0.02, respectively). The interaction between open water and size was also significant (P = 0.04); nonforaging swans preferred large expanses of open water on large lakes and intermediate expanses of open water on small and medium lakes. Sago pondweed presence was not a predictor of number of nonforaging swans per wetland (partial R^2 = 0.003, P = 0.87) nor were the sago by open water and sago by size interactions (P = 0.21 and 0.41, respectively).

Most (81%) swans were not foraging at a given time, thus the distribution of the total number of swans per wetland (a mean of aerial and ground counts) across habitat types was similar to that of nonforaging swans per wetland. Total number of swans per wetland was not affected by the presence of sago pondweed (P = 0.42) and increased with proportion of contiguous open water (P = 0.007) and wetland size ($P < 0.001$).

Cygnets

Cygnets composed 8.3% (±0.9%) of swans. Patterns in the number of foraging cygnets per wetland across habitat types were similar to those of adults, and thus similar to those reported above for all foraging swans (i.e., adults + cygnets). Foraging cygnets were >3 times more common on sago pondweed wetlands than on nonsago wetlands ($\bar{x}$ = 1.44 ± 0.35 and 0.38 ± 0.16, respectively; P = 0.01). The number of foraging cygnets per wetland decreased with an increasing proportion of contiguous open water ($\bar{x}$ = 2.30, 1.00, 0.04 for the 3 open water categories; P = 0.007) and was not related to wetland size ($\bar{x}$ = 0.6, 1.1, 0.9 for the 3 size categories; P = 0.64).

Among flocks containing cygnets and adults, 36% of cygnets were feeding while a lower percentage (30%) of adults were feeding (paired t-test, n = 49, P = 0.03). If cygnets forage more often than adults, the proportion of young per flock might be higher in habitats favored by foraging swans (although, note that an analysis of proportions is restricted to wetlands with flocks). However, the proportion of young per flock was not related to sago presence (P = 0.70), open water (P = 0.18), or wetland size (P = 0.64). Flock size was the only variable related to proportion of young per flock (Fig. 2); smaller flocks had proportionately more young than did larger flocks.

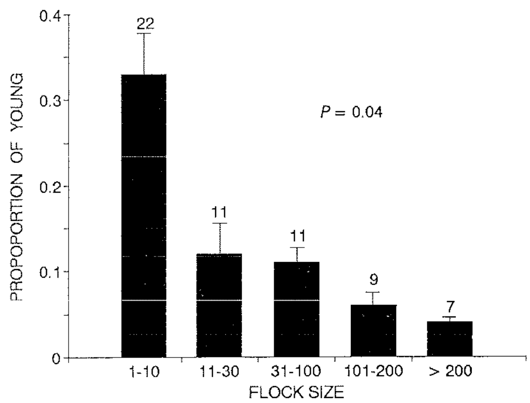

Fig. 2. Proportion of young tundra swans in 5 flock-size categories on a migratory stopover in North Dakota, 1988–89. Means and SEs were weighted by flock size. Sample sizes (no. of flocks) are given above bars. The regression was performed on the original data rather than means per flock size category.

DISCUSSION

Foraging swans strongly preferred wetlands with sago pondweed. Measures more refined than sago pondweed presence or absence, such as tuber density, tuber patchiness, and the distribution of available tuber sizes and depths, might have revealed more complex preferences. Bewick's swans (*C. c. bewickii*), for example, did not return to a sago pondweed patch after tuber density dropped below a threshold value, and they preferred large tubers to small tubers, even though large tubers were buried deeper (Beekman et al. 1991). Such complexity may have accounted for the low explanatory power of sago pondweed presence in this study (sago explained 5% of the variation in number of foraging swans/wetland). Other unmeasured factors, such as presence of hunters and distance to nearest roosting site, probably also accounted for variation in the number of foraging swans per wetland.

Nonforaging swans did not prefer wetlands with sago pondweed. Nonforaging swans, which typically roosted in large flocks on unvegetated mud bars, preferred large and open wetlands, possibly because of the greater availability of suitable roosting sites. Large wetlands have more shoreline than do smaller wetlands, and open wetlands have more unvegetated shoreline than do closed wetlands. A regression model incorporating mud bar availability, proportion of contiguous open water, and wetland size would elucidate whether the latter 2 variables had explanatory power alone or were correlates of mud bar availability.

A negative relationship between flock size and proportion of cygnets may be common in swans (tundra swans on the wintering grounds: Bart et al. 1991; whooper swans [*C. cygnus*]: J. M. Black, Int. Waterfowl and Wetlands Res. Bur., Slimbridge, U.K., unpubl. data) and other species in which family members travel as a unit (sandhill cranes [*Grus canadensis*]: Tacha and Vohs 1984; R. C. Drewein, Univ. Idaho, Moscow, unpubl. data). Possible explanations for this pattern include (1) families are dominant over nonparents (Scott 1980, Earnst and Bart 1991) and exclude nonparents from small flocks, (2) families are more likely to be feeding than nonparents (Earnst and Bart 1991) and settle preferentially in smaller flocks to avoid foraging competition, or (3) flocks of ≥1 family and nonparents move and settle independently of one another, and, on average, flocks of families have fewer birds than flocks of nonparents. To distinguish among alternatives, one needs an approach, such as the stable group-size model (Giraldeau 1988), that considers the costs and benefits of joining or not joining a flock of a given size. This would require that field workers first quantify benefits to families and nonfamilies of foraging and roosting in large and small flocks. To understand the relationship between flock size, proportion of young, and use of habitat, it also would be valuable to know whether adult plumaged young from previous seasons associated with families and whether family and nonfamily groups segregated within wetlands.

MANAGEMENT IMPLICATIONS

Conclusions about habitat preference derived from counts of all swans, most of which were nonforaging, would not have revealed the importance of sago pondweed. However, foraging swans were >4 times as common on wetlands containing sago pondweed than on wetlands without pondweed. Recording the behavior and number of birds using a habitat is useful to wetland managers because it helps identify the habitat's function (Van Horne 1983, Hobbs and Hanley 1990). Scan sampling of behavior (Altmann 1974) can be done quickly and therefore can be incorporated easily into population surveys.

The tendency for proportion of young to decrease with flock size has implications for estimating the proportion of young in the population. Flocks must be selected at random or the sample must be stratified by flock size to adequately estimate proportion of young in the population. If small flocks are oversampled, the proportion of young will be overestimated.

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