Habitat Selection by Tundra Swans on Northern Alaska Breeding Grounds

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Abstract.—Habitat selection by the Tundra Swan (*Cygnus columbianus columbianus*) was evaluated on the Colville River Delta prior to oil field development (1982-1989). Tundra Swan territories comprised a lake, used for refuge and foraging, and terrestrial habitats and ponds near the lake's perimeter used for foraging and nesting. Tundra swan sightings from early and late summer aerial surveys were used to investigate habitat selection at the territory and within-territory scale. At the territory or lake scale, swan sightings/lake increased with lake size, and increased from discrete to tapped (i.e., connected to a river channel) to drained lakes within size categories. Overall, 49% of the variation in swan sightings/lake was explained by lake size and type, a size-*x*-type interaction term, and the proportion of lake perimeter comprised of Halophytic Ponds and Halophytic Wet Meadows. At the within-territory or within-lake scale, foraging swans significantly selected Halophytic Ponds, Halophytic Wet Meadows, and Fresh Ponds relative to Uplands; nesting swans significantly selected Halophytic Ponds and significantly avoided Fresh Wet Meadows relative to Uplands. Vegetation sampling indicated that sites used by Tundra Swans on river channels and tapped lakes were significantly more likely to have Sheathed Pondweed (*Potamogeton vaginatus*) than control sites. The three major components of Tundra Swan diet were *Carex* sedges, Sheathed Pondweed, and algae, together comprising 85% of identifiable plant fragments in feces. *Received 18 August 2003, accepted 30 December 2003.*

Key words.—Alaska, breeding grounds, *Cygnus columbianus*, diet, habitat selection, *Potamogeton*, Tundra Swan

Waterbirds 27(2): 224-233, 2004

The Eastern and Western Populations of Tundra Swans (*Cygnus columbianus columbianus*) breed across the tundra of northern Canada to Alaska and in western Alaska, respectively. Much of the range lies over extractable fossil fuel reserves, thus increasing the importance of understanding Tundra Swan habitat selection before the arctic landscape is altered by human activities (Stewart and Bernier 1989; Monda *et al.* 1994; Stickney *et al.* 2002). Past studies have provided a general description of Tundra Swan habitat use (McLaren and McLaren 1984; Wilk 1988; Stewart and Bernier 1989), and some have quantified habitat use relative to availability. For example, Tundra Swan density is typically correlated with the number of available wetlands (Lensink 1973; King and Hodges 1981; Spindler and Hall 1991), wetlands containing pondweed (*Potamogeton* spp.) are often used (Spindler and Hall 1991; Monda *et al.* 1994), and river channels are used in areas where they support beds of submerged vegetation, but not elsewhere (King and Hodges 1981; Spindler and Hall 1991; Monda *et al.* 1994). For nest sites, Tundra Swans typically use drier terrestrial habitats (Monda *et al.* 1994; Stickney *et al.* 2002).

This study evaluates Tundra Swan habitat selection on the Colville River Delta, the largest river delta along the north coast of Alaska, during years prior to oil field development (1982-1989). The conceptual approach is that of landscape ecology which recognizes that habitat selection occurs at a series of hierarchical scales of biological relevance to the organism, including landscape, territory or home range, and patch scales, and that the composition and juxtaposition of patches within territories are likely to influence habitat selection at the territory scale (Johnson 1980; Morris 1987; Wiens *et al.* 1987; Freemark *et al.* 1995).

On the Colville River Delta (Earnst 1992, 2002) and adjacent sections of the Arctic Coastal Plain (Stickney *et al.* 2002), Tundra Swan territories typically include a lake (i.e., a waterbody >1 ha) and adjacent habitats. The lake provides important refuge for cygnets during brood-rearing and for adults during the flightless stage of complete wing molt (Earnst 1994; Limpert and Earnst

1994); the lake and wetland habitats near its perimeter, such as ponds and wet meadows, are used for foraging and nesting (Earnst 1992, 2002). This study treats the lake as central to habitat selection and investigates selection at the i) territory scale in relation to lake size, type (discrete, tapped to river channels, or partially drained), and composition of lake perimeter habitat (ponds, wet meadows, or uplands), and ii) within-territory scale, i.e., among patches of lake perimeter habitat. In addition, the importance of Sheathed Pondweed (*Potamogeton vaginatus*) was investigated by comparing its availability at used and unused sites on lakes and river channels, and Tundra Swan diet was quantified using microhistological analysis of feces.

METHODS

Tundra Swan habitat selection was investigated using extensive and intensive aerial surveys, a land cover classification scheme based largely on aerial photography, and ground-based sampling of submerged vegetation.

Aerial Surveys

Extensive surveys covered the entire delta; intensive surveys covered less area, but facilitated accurate plotting on aerial photographs and higher detection rates (S. L. Earnst, unpubl. data) because they were flown at lower elevation, slower air speed, and on more closely spaced survey lines. Sightings from extensive surveys within 150 m of a lake were assigned to the nearest lake during analysis and were used to investigate use of lakes in relation to lake size, type, and perimeter habitat. Families, pairs, singles, nests, and flocks were each counted as one sighting. The more accurately plotted sightings from intensive surveys were used to investigate swan use of habitat patches along lake perimeters (i.e., within 150 m). In the analysis of intensive surveys, use of habitats was considered separately for nests and foraging swans (i.e., all non-nest sightings).

Extensive aerial surveys. Fifteen surveys were flown by the Alaska Department of Fish and Game, one during each spring and autumn (approx. 20 June and 20 August, respectively), from spring 1982 to spring 1989. Surveys were flown at 1,500 m altitude and 160 km/h. Survey lines were 3.2 km apart and swans sighted 1.6 km on each side were plotted on a topographic map, thus providing complete coverage of the surveyed area. Extensive surveys were flown over the entire delta, an area bordered by the outermost channels of the Colville River (Nechelick and East Channels; Fig. 1) and the Beaufort Sea.

Intensive aerial surveys. A total of six intensive surveys were conducted, one during each spring and each fall (on same day as extensive surveys) from spring 1987 to autumn 1989. Survey lines were 0.8 km apart and were flown at 300 m altitude and 160 km/h; swans sighted 0.4 km on each side were plotted. Intensive surveys covered approximately 75% of the delta (Fig. 1).

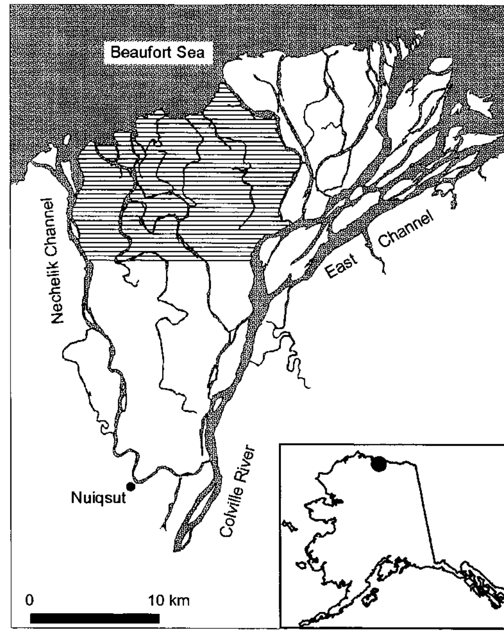

Figure 1. Map of the Colville River Delta showing the extensive study area, bordered by the Nechelik and East channels, and the intensive study area indicated by cross-hatching. The inset shows the location of the Colville River Delta in Alaska.

Classification of Lakes and Lake Perimeter Habitat

Lake size and type. Lake size was classified as small (1-5 ha), medium (5.1-30 ha), or large (>30 ha), and entered as a categorical variable in regression analyses. Lakes also were classified as tapped (connected to a river channel), discrete (not tapped), or drained. Drained lake basins were defined as those having >5% open water and substantial encroachment (≥30% of the basin) of wet meadow habitat (see below and Table 1). Lakes <1 ha in area were below the minimum mapping unit used in this study, and 27 lakes within 4 km of Nuiqsut village were excluded to avoid potential human-induced variation.

Land cover classification. The cover types of the delta were classified and mapped using aerial photography and ground-truthing prior to this study (described in Rothe *et al.* 1983), and the map was refined as necessary during our subsequent studies (1986-2000). In order to reduce the number of habitat classes and thus simplify analyses for this study, ecologically similar habitats along lake perimeters were combined, and rare habitats or those infrequently used by swans were combined. The major features of the resulting classification were the presence or absence of salt-tolerant (halophytic) terrestrial vegetation, the presence or absence of polygonal ponds, and the gradation from wet to dry habitat. Submerged aquatic vegetation was not included in the original or revised classification because its presence was difficult to ascertain with aerial photography.

The five categories of the revised classification were 1) Halophytic Ponds, those with rims dominated by salt-tolerant vegetation, 2) Fresh Ponds, those with rims dominated by non-halophytic vegetation, 3) Halophytic

Table 1. Description of the five cover types used in this study (I-V) and their major subtypes. Based on Rothe *et al.* 1983.

Cover type	Primary vegetation
I. Fresh Wet Meadows	
A. wet sedge	*Carex aquatilis*, *Eriophorum* spp.
B. wet grass-sedge	*C. aquatilis*, *Arctophila fulva*
II. Fresh Ponds[a]	
A. moist-dry sedge-willow	*C. aquatilis*, *Salix* spp.
B. dry sedge-willow-forb	*C. aquatilis*, *Salix* spp., *C. bigelowii*, many forb spp.
III. Halophytic Wet Meadows	
A. wet sedge	*C. subspathacea*, *C. ursina*, *C. rariflora*, *Puccinellia phryganodes*
B. herb	sparsely vegetated; *Stellaria humifusa*, *Dupontia fischeri*, *C. rariflora*, *Cochlearia officinalis*, *C. ramenskii*, *Alopercurus alpinus*
IV. Halophytic Ponds[a]	
A. wet sedge	same as halophytic wet sedge meadows
B. mesic grass-sedge	*C. subspathacea*, *Puccinellia phryganodes*, *Dupontia fischeri*
C. herb	same as halophytic herb meadows
V. Uplands	
A. grass-sedge-willow	*C. aquatilis*, *Salix* spp.
B. halo. grass-sedge	*C. subspathacea*, *Puccinellia phryganodes*, *Dupontia fischeri*
C. sedge tussock	*Eriophorum vaginatum*, *Ericaceous* spp.
D. willow	*Salix* spp.
E. dune	*Dryas integrifolia*, *Saxifraga* spp., *Astragalus* spp., *Salix* spp., *C. aquatilis*, *C. bigelowii*, *Arctagrostis latifolia*, many other forb spp., *Poa* spp.; some sparsely vegetated
F. floodplains	Sparsely vegetated; *Arctophila fulva*, *C.aquatilis*, *Deschampsia caespitosa*, *Elymus arenarius*

[a]Primary vegetation refers to that on pond rims. Primary aquatic vegetation in Fresh Ponds included *C. aquatilis*, *Arctophila fulva*, *Hipparus vulgaris*, and *Ranunculus* spp., and in Halophytic Ponds included algae and *Hippuris vulgaris*.

Wet Meadows, 4) Fresh Wet Meadows, and 5) dry Uplands (Table 1). Pond habitat was representative of deep-center polygonal ponds with rims varying from 0.5-2 m in width and from a few cm to >1 m above the water's surface. Rims of Fresh Ponds were usually higher than those of Halophytic Ponds. Most Wet Meadows were characterized by moist to saturated soil, but some Fresh Wet Meadows consisted of emergent vegetation growing in water up to 1 m deep. Uplands were defined as areas without ponds and with dry soils supporting grasses, forbs, and willows; uplands were typically of higher elevation (approximate range of 2-10 m) than the four wetland types described above.

Pondweed Sampling on Channels and Lakes

River channels and lakes were sampled for Sheathed Pondweed in late July and August 1989. Used channel sites were points where swans had been plotted during the 14 extensive aerial surveys flown during 1982-1988. Pondweed data from used sites within 1.6 km of one another were averaged prior to analysis, resulting in a sample size of 43 used channel sites. Control sites were systematically placed at 1.6-km intervals along active river channels and not closer than 1.6 km to any used site; sequential control sites were placed along alternate shores. The 1.6-km interval spaced the desired number of control sites (N = 43) throughout available channels and facilitated statistical independence of sites. Control sites were placed near shores because water there is typically shallower, slower, and more conducive to pondweed growth. All active channels on the extensive study area were sampled except the Nechelik, or westernmost channel, which was not sampled due to logistical constraints and the proximity of Nuiqsut village.

Used tapped lake sites were those with more than one sighting in one quadrant of the lake during extensive aerial surveys, and control tapped lakes were those with no sightings on the lake proper. All used and control lakes within the extensive area were sampled except two used lakes that were inaccessible; thus, 21 used and 12 control lakes were sampled. For this analysis, tapped lakes also included any drained lake with an active connection to a river channel.

Used discrete lakes (N = 13) were those with more than one sighting on extensive aerial surveys or those on which swans were frequently observed from blinds during a companion study (Earnst 1992, 2002). Because swans were rarely observed on discrete lakes, we defined use more broadly for discrete than tapped lakes. This provided an adequate number of used discrete lakes for pondweed sampling, and the unequivocal nature of the results (i.e., no pondweed on any used discrete lakes; see Results) suggest that the outcome would have been similar with other arbitrary definitions of use.

Most sites were sampled from an inflatable boat; sites inaccessible by boat were sampled by wading. At each site, three 150-m transects were established parallel to and at 5, 10, and 15 m from the shore. Sheathed

Pondweed was sampled by scraping a rake along the substrate of the transect. Vegetation growing deeper than 1 m was considered inaccessible to swans and was not sampled. The rake head, which was attached to a 2-m handle, consisted of 14 nails driven into a wooden base 3-cm apart with heads protruding 8 cm. Each scrape covered 30 m of substrate; thus, five scrapes per transect and 15 scrapes per site were performed. The quantity of Sheathed Pondweed acquired during each scrape was scored on a scale from 1 to 6 based on ocular estimation, and the 15 scores were summed to obtain one score per site.

Diet

Fresh fecal samples were collected in 1987-1990 from 18 June-20 August. Most samples from adults were collected from known territories (N = 24 territories) during visits to determine the territorial pair's breeding status or success (Earnst 1992). More than one sample was collected on most territories (2 samples on nine territories, 3-4 samples on five territories, and 6 samples on two territories), but data from multiple samples within a territory were averaged prior to further analysis. Other adult fecal samples were collected while banding birds in non-breeding flocks at seven sites and in home ranges occupied by ten unmonitored pairs. Only one sample was collected from flocks or unmonitored pairs at sites <1 km from one another or within 150 m of the same lake. Thus, sites were considered independent for statistical analysis. Sites were stratified into halophytic and non-halophytic habitats and strata were treated as equal-sized in calculating overall mean percent discernible fragments. Treating strata as equal-sized reflected the approximately equal proportion of swan sightings in halophytic and in non-halophytic habitats (0.43 and 0.57, respectively) during intensive aerial surveys. Fecal samples from ten broods were collected opportunistically during visits to monitored territories. Cygnet and adult feces were readily distinguishable by size.

Samples were stored in alcohol and sent to the Composition Analysis Laboratory (Colorado State University, Fort Collins, Colorado) for microhistological analysis. To ensure a well-mixed sample of equal-sized fragments, samples were dried and ground to pass through a 1-mm mesh screen. For each sample, vegetation fragments were identified in 20 microscope fields at 125x magnification. Identification was based on, but not limited to, a set of reference slides prepared from probable food plants. Technicians were experienced with the analysis of goose and swan feces (see also Squires 1991). Fragments were identified to genus or species and the results were expressed as percent of discernable fragments.

The microhistological method does not take account of differences among plants in digestibility, nutrient content, or fragment size (Sparks and Malechek 1968). Therefore, caution is needed in interpreting percent of discernible fragments in feces as a strict quantitative estimate of the plant's importance in the diet. In this study, the microhistological method is used primarily to provide a qualitative list of diet components; previous lists have been based on behavioral observation (Monda *et al.* 1994) or small samples of gizzards (Spindler and Hall 1991). In addition, a second purpose of the fecal analyses is to compare diets among habitats. Using percent of discernible fragments is legitimate for this comparison unless digestibility varied among habitats.

Statistical Analysis

A stepwise general linear model was used to investigate the effect of lake size, lake type, and perimeter habitat on swan sightings/lake. A Kruskal-Wallis test, followed by pairwise Mann-Whitney tests, was used to compare sightings/km^2 among lake perimeter habitat types. In both analyses, the lake was the sampling unit. χ^2 tests with Yates' correction for continuity were used to compare proportion of used and unused sites having pondweed. Independent t-tests were used to compare pondweed density scores on used and unused sites and to compare mean percent of discernible plant fragments in feces among sites. SEs are reported with means unless noted otherwise.

RESULTS

Most Tundra Swan sightings (81%) during intensive and extensive aerial surveys were on or within 150 m of lakes, 19% were on or near river channels (includes some that were also near lakes), and 9% of sightings were >150 m from a lake or channel.

Selection of Lakes

Swan sightings/lake increased with lake size, and increased from discrete to tapped to drained lakes within size categories (Fig. 2). For example, among drained lakes, there were 2.2, 5.9, and 12.7 sightings/lake in small, medium, and large lakes, respectively; among large lakes, there were 4.3, 7.2, and 12.7 sightings/lake in discrete, tapped, and

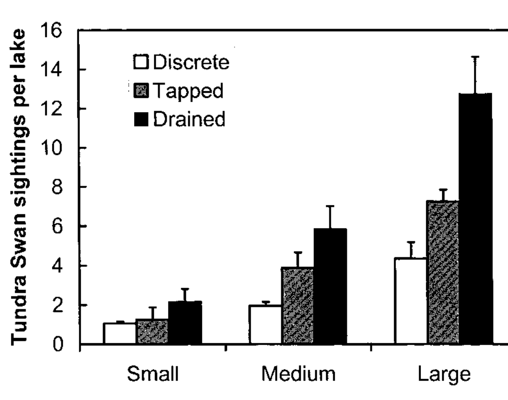

Figure 2. Mean number of sightings/lake by lake size and type during 15 aerial surveys of the Colville River Delta, Alaska. Lake size, type, and a size-x-type interaction were significant predictors of swan sightings/lake in a general linear model (see Table 2). Number of lakes in each category, from left to right, were: 254, 8, 12, 67, 16, 7, 26, 13, and 4.

drained lakes, respectively (Fig. 2). Lake size and type explained 31.9% ($P < 0.001$) and 8.6% ($P < 0.001$) of the variation in swan sightings/lake, respectively, in a stepwise general linear model (Table 2). The lake size-*x*-type interaction term was also significant ($P < 0.001$), explaining 5.3% of the variance, primarily because large drained lakes were used more than predicted by either size or type.

Proportion of the lake perimeter in Halophytic Wet Meadow and Halophytic Pond habitat explained an additional 2.7% ($P < 0.001$) and 1.0% ($P < 0.006$) of the remaining variation, respectively (Table 2). Neither proportion of perimeter in Fresh Pond or Fresh Wet Meadow habitat explained a significant proportion of the remaining variance. Changing the order in which lake perimeter habitats were entered in the model did not change the proportion of variance explained by each. Overall, the model incorporating the five significant predictors explained 49.5% of the variation in swan sightings/lake (Table 2).

Selection of Lake Perimeter Habitat

Foraging habitat. Number of swan sightings/km^2 (not including nests) varied significantly among lake perimeter habitats (Table 3; Kruskal-Wallis $H_4 = 15.4$, $P < 0.004$). In particular, Halophytic Ponds, Fresh Ponds, and Halophytic Wet Meadows were significantly selected relative to Uplands (Table 3; based on Mann-Whitney tests). These three habitats accounted for 75% of all swan sightings, comprised only 56% of available lake perimeter, and had nearly four times as many sightings/km^2 as Uplands ($\bar{x} = 0.41 \pm 0.08$ vs. 0.11 ± 0.05, Mann-Whitney, $P < 0.001$).

Only Fresh Wet Meadows were not used significantly more than Uplands (Table 3). When Fresh Wet Meadow were divided into those containing Pendant Grass (*Arctophila fulva*) and those without, the tendency for Pendant Grass to have more sightings/km^2 was not significant and exhibited high variation ($\bar{x} = 0.58 \pm 0.28$, N = 53, and $\bar{x} = 0.08 \pm 0.04$, N = 118, respectively).

Swan distribution among the five habitat categories did not differ significantly between seasons or among years (Kolmogorov-Smirnov tests, all n.s.).

Nesting habitat. Number of nests/km^2 varied significantly among lake perimeter habitats (Table 3; Kruskal-Wallis $H_4 = 19.6$, $P < 0.001$). In particular, Halophytic Ponds and Fresh Ponds were significantly selected relative to Uplands and Fresh Wet Meadows, and Uplands were significantly selected relatively to Fresh Wet Meadows (Table 3).

Selection of Sites with Sheathed Pondweed

Swan use of aquatic sites on river channels and tapped lakes, but not discrete lakes, was related to availability of Sheathed Pondweed. Used sites on river channels were more likely to have pondweed ($\chi^2_2 = 12.6$, $P < 0.001$) and had higher pondweed density scores ($t_{84} = 2.42$, $P < 0.05$) than control sites (Fig. 3). Similarly, used tapped lake sites were more likely to have pondweed ($\chi^2_2 = 14.9$, $P < 0.001$) and had higher pondweed

Table 2. The effect of lake size (small, medium, or large), lake type (discrete, tapped, or drained), and perimeter habitats on swan sightings/lake. Swan sightings/lake increased with lake size (Fig. 2), from discrete to tapped to drained lake type (see Fig. 2), and with increasing proportion of perimeter in Halophytic Wet Meadow and Halophytic Pond habitat. General linear model based on 15 aerial surveys of the extensive study area during eight breeding seasons, N = 407 lakes, overall R^2 = 49.5%, P < 0.001. Only significant predictors are shown.

Independent variable	Variation explained (%)	$F_{10,396}$	P
Lake size	31.9	124.8	<0.001
Lake type	8.6	33.7	<0.001
Lake size-x-type interaction	5.3	10.5	<0.001
Proportion Halophytic Wet Meadow	2.7	21.0	<0.001
Proportion Halophytic Ponds	1.0	7.9	<0.006

Table 3. Number of sightings/km^2 (± SE) of foraging and nesting Tundra Swans varied significantly among lake perimeter habitats (Kruskal-Wallis H_4 = 15.4, P < 0.004, and H_4 = 19.6, P < 0.001, respectively). Based on a total of 87 swan sightings and 63 nest sightings on lake perimeters during six aerial surveys of the intensive study area (295 lakes).

Habitat (N)[a]	% lake perimeter	% foraging sightings	Foraging sightings/km^2 [b]	% nests	Nests/km^2 [b]
Halophytic Ponds (64)	11	21	0.30 (0.10) A	17	0.44 (0.21) A
Fresh Ponds (183)	31	32	0.23 (0.06) A	41	0.27 (0.08) A
Halophytic Wet Meadows (139)	14	22	0.31 (0.09) AB	19	0.26 (0.11) AB
Fresh Wet Meadows (139)	9	10	0.23 (0.09) BC	0	0 (0) C
Uplands (246)	35	15	0.07 (0.03) C	22	0.13 (0.04) B

[a]N = number of lakes bordered by each habitat type. See Table 1 and Methods for definitions of habitats.
[b]Habitats sharing the same letter within this column did not differ significantly in sightings/km^2. Based on Mann-Whitney U-tests.

density scores (t_{31} = 4.61, P < 0.001) than control sites (Fig. 3). Pondweed was not found on any of the used discrete lakes (N = 13).

Diet

The three major components of Tundra Swan diet in both halophytic and non-halophytic habitats were *Carex* sedges, Sheathed Pondweed, and algae (Table 4). Together they comprised 85% of identifiable plant fragments in feces. Of secondary importance were grass seeds, Pendant Grass, crowfoot (*Ranunculus* spp.), and arthropods; each comprised 2% to 4% of all fragments. The relative contribution of most foods to the diet did not differ detectably in halophytic and non-halophytic habitat (Table 4). Only Pendant Grass differed, comprising less of the diet in halophytic habitats (t_{39} = 2.51, P < 0.05) where it was an uncommon vegetation type (Table 1).

Sheathed Pondweed was present in all four adult fecal samples collected from river channels and in 82% of those collected from tapped lakes, but in only 38% collected from discrete lakes. Similarly, Sheathed Pondweed comprised a higher proportion of plant fragments in feces collected along river channels (89%) and tapped lakes (53%) than along discrete lakes (4%, t_{28} = 7.39, P < 0.001, and t_{35} = 3.71, P < 0.001, respectively, Fig. 4).

In cygnet feces, discernible fragments were comprised of 52% Sheathed Pondweed, 32% *Carex* spp., 8.2% grass seed, 5.3% flowers and other forbs, and <1% each of al-

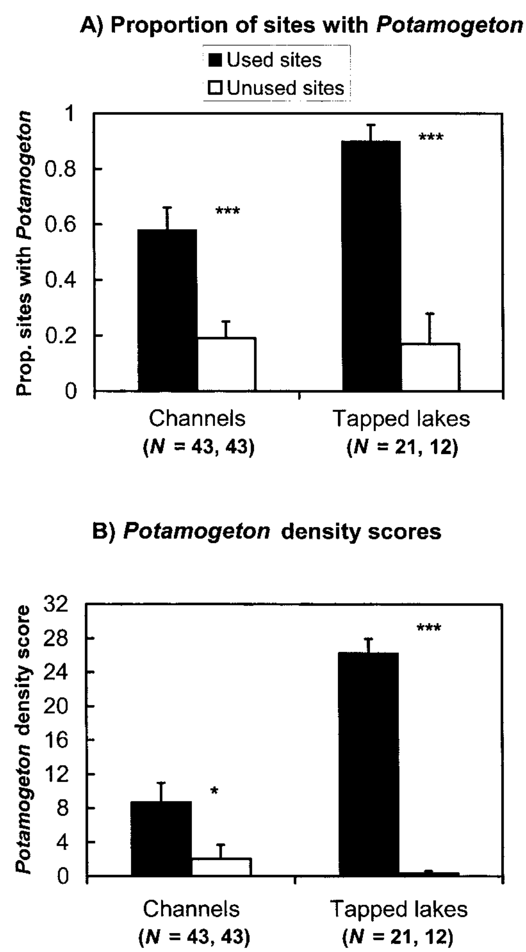

Figure 3. (A) Proportion of sites with Sheathed Pondweed and (B) pondweed density scores (see Methods) on sites used (black bar) and unused (white bar) by Tundra Swans. Error bars represent 1 SE; statistical comparisons based on χ^2 for proportions and t-tests for means, with asterisks denoting significance level (*P < 0.05, **P < 0.01, ***P < 0.001).

Table 4. Composition of Tundra Swan feces collected in halophytic and non-halophytic habitats.

		Mean (± SE) percent of discernible fragments		
Species[a]	Percent of samples where present	All samples[b] (N = 41)	Halophytic (N = 25)	Non-halophytic (N = 16)
Carex sedges	73	38.9 (6.3)	39.6 (8.4)	38.3 (9.3)
Sheathed Pondweed	56	26.0 (6.1)	23.8 (8.0)	28.2 (9.3)
Algae	39	19.9 (4.7)	27.8 (7.4)	12.0 (5.8)
Grass seeds	37	4.2 (2.0)	4.3 (3.5)	4.2 (2.0)
Pendant Grass	24	3.2 (1.6)	0.1 (0.05)	6.2 (3.1)
Ranunculus spp.	19	2.0 (1.2)	0.3 (0.1)	3.7 (2.3)
Arthropods	32	2.0 (1.0)	0.8 (0.3)	3.2 (1.9)

[a]The following plants comprised ≤1% of discernible fragments: cottongrass (*Eriophorum* spp.), Tundra Grass (*Dupontia fischeri*), Alkali Grass (*Puccinellia phryganodes*), horsetail (*Equisetum* spp.), chickweed (*Stellaria* spp.).
[b]Means and SEs in this column were calculated by treating halophytic and nonhalophytic habitats as strata of equal size which reflects the nearly equal proportion of sightings in these habitats during intensive aerial surveys (43% and 57%, respectively).

gae, *Ranunculus* spp., arthropods, and grasses. When brood samples were compared to those from adults on the same territory, broods consumed significantly less submerged vegetation (Sheathed Pondweed, algae, and *Ranunculus* spp.) than adults ($\bar{x}$ = 52.5% and 82.2% of identifiable fragments, respectively, SE of difference = 12.0%, paired t-test, $t_9 = 2.46$, $P < 0.05$).

DISCUSSION

Selection of Lakes

Tundra Swan territories typically contain a lake, which is used for refuge and foraging, and adjacent habitats used for foraging and nesting (Earnst 1992, 2002; Stickney *et al.* 2002). Correspondingly, most swan sightings

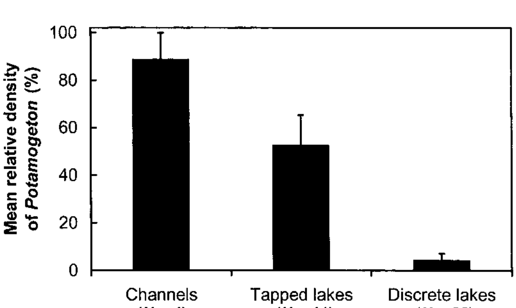

Figure 4. Mean percent of discernible fragments comprised by Sheathed Pondweed in Tundra Swan feces collected on different water body types. N = number of sites where fecal samples collected.

(this study) and nests (Stickney *et al.* 2002) are within 150 m of a lake. In this study, Tundra Swan sightings on or near lakes are shown to increase with lake size, and increase from discrete to tapped to drained lakes within size categories. Larger lakes likely provide superior refuge (especially for broods and molting adults) and may have more foraging and nesting sites on the lake proper and in adjacent habitats. The selection of tapped lakes relative to discrete lakes is consistent with the greater availability of Sheathed Pondweed on tapped lakes. In addition, many of the Delta's tapped lakes are inter-connected and thus provide superior protection for, and are heavily used by, molting flocks of Tundra Swans during their flightless period. The frequent use of drained lakes also may be related to the presence of Sheathed Pondweed (since many were also tapped), the large proportion of lake perimeter in wet meadow habitat (at least 30%, by definition), and a tendency for drained lake complexes to have convoluted shorelines (not quantified here). Stickney *et al.* (2002) also found that lakes closest to Tundra Swan nests were larger and had higher shoreline complexity than the average available lake.

The types of parameters used in this model, which explained 49% of the variation in swan sightings/lake, are available from existing land cover maps, digital hydrological layers, or satellite imagery for many large arctic regions, such as the National Petroleum Reserve-Alaska (e.g., USDI 1995). Thus, a similar approach may be useful in developing swan habitat models in large, remote areas where managers wish to minimize impacts of human activities on swan habitat (see also Stickney *et al.* 2002).

Selection of Lake Perimeter Habitat

The second scale of investigation, the within-territory investigation, indicated that foraging Tundra Swans selected Halophytic Wet Meadows, Halophytic Ponds, and Fresh Ponds relative to Uplands along lake perimeters. Fresh Wet Meadows, which included wet meadows dominated by Water Sedge (*Carex aquatilis*) and those dominated by Pendant Grass, were not selected relative to Uplands. Although other studies suggest that wetlands with Pendant Grass are heavily used by waterfowl (Bergman *et al.* 1977; Derksen *et al.* 1981), Pendant Grass wet meadows in this study were a) relatively rare, comprising 9% of lake perimeter habitat, b) highly variable in Tundra Swan use ($\overline{x}$ = 0.58 ± 2.04 [SD] sightings/km^2), and c) in patches smaller than the minimum mapping unit used here (1 ha) which might have resulted in some wet meadow sightings being recorded as on the lake proper.

Nesting habitat selection was similar to that for foraging in that Halophytic Ponds and Fresh Ponds were significantly selected compared to Uplands. However, for nesting, neither wet meadow habitat was selected over Uplands. Tundra Swan nest mounds, which are used repeatedly among years, are up to 0.5 m in height, built of dried vegetation, and often placed on a substrate elevated above the surrounding tundra (Monda *et al.* 1994). Polygonal pond rims provide a dry, elevated substrate and are relatively isolated within a matrix of water-filled pond basins. Similarly, islands are preferred nesting sites on the Yukon-Kuskokwim Delta (Lensink 1973) where islands are relatively more common, and ponds relatively less common, than on the Colville River Delta. Stickney *et al.* (2002) also found that up to 55% of Tundra Swan nests on the coastal plain east of the Colville River Delta were on polygonal rims and on the driest substrates.

Selection of Sites with Sheathed Pondweed

Several species of swans are known to rely on the vegetation and energy-rich tubers of *Potamogeton* spp. during breeding, staging, and migration (Sherwood 1960; Wilk 1988; Beekman *et al.* 1991; Spindler and Hall 1991; Squires 1991; Earnst 1994; Grant *et al.* 1994; Monda *et al.* 1994; Nolet and Drent 1998). In this study, Sheathed Pondweed was an important component of Tundra Swan diet and habitat selection. Sheathed Pondweed was present on most used, but few unused, tapped lake sites and was common in feces collected near tapped lakes.

Because tapped lakes are connected to river channels, the water depth, salinity, and substrate of tapped lakes is conducive to pondweed growth, but control tapped lakes typically lacked the shallow, protected bays that aid its growth (pondweed ecology reviewed in Kantrud 1990). Discrete lakes, which swans used less than other lake types and in which pondweed was not discovered, had no influx of channel water and probably had salinity lower than optimal for pondweed growth.

On river channels, Sheathed Pondweed usually occurred in relatively shallow water (≤1 m) protected from waves and currents. Sheathed Pondweed was present on most channel sites used by swans, on few unused sites, and comprised most of the vegetation in fecal samples collected on riverbanks. Pondweed may be particularly important in early spring and late autumn at sites where channels provide some of the only ice-free habitat (e.g., the mouth of the Miluveach River on the Colville River Delta; see also Wilk 1988; Spindler and Hall 1991).

Diet

Carex sedges, which also are important to tundra-breeding geese (Sedinger and Raveling 1986), were a common component of Tundra Swan feces from halophytic cover types, where Hoppner Sedge (*C. subspathe-*

cea) and Bear Sedge (*C. ursina*) were common, and non-halophytic cover types, where Water Sedge was common (Table 1). Grasses were not major components of feces, despite the abundance of Alkali Grass (*Puccinellia phryganodes*), Tundra Grass (*Dupontia fischerii*), and Pendant Grass (Table 1). The infrequency of Pendant Grass in feces is consistent with the view that it may be valuable to waterfowl as protective cover for broods or as a substrate for invertebrate prey (Bergman *et al.* 1977), but not necessarily as a food source (Bart and Earnst 1991). Tundra Swans were rarely observed foraging on Pendant Grass during time budgets on the Colville River Delta (S. L. Earnst, unpubl. data; but see Monda *et al.* 1994).

Submerged plants, particularly Sheathed Pondweed, algae, and *Ranunculus* spp., were important components in the diet of adult Tundra Swans, but less important in the diet of cygnets. This is consistent with cygnets' difficulty in obtaining submerged vegetation, especially when young, and their more frequent use of terrestrial foraging modes and habitats (Monda *et al.* 1994; Earnst 2002).

Because fecal samples were not collected during early spring, our analysis underestimates the importance of plants eaten soon after swan arrival on the breeding grounds, such as Sheathed Pondweed and horsetail (*Equisetum* spp.) (see also Rothe et al. 1983), when foraging is restricted to ice-free river banks and shallow sloughs. In particular, although horsetail is relatively uncommon on our study area, it may be an important source of protein early in the breeding season, as it is for several northern-breeding geese and swans (Thomas and Prevett 1982; Ohtonen and Huhtala 1991; Grant *et al.* 1994; Einarsson and Rees 2002; Knudsen *et al.* 2002).

ACKNOWLEDGMENTS

Funding for field work was provided by USGS Northern Prairie Wildlife Research Center, a National Wildlife Federation Environmental Conservation Research Award, and a National Science Foundation Graduate Fellowship. The Alaska Department of Fish and Game funded and conducted the extensive aerial surveys. James Helmericks served as pilot-observer in all aerial surveys and the Helmericks family provided logistic support and hospitality. R. Field, J. Nickles, and K. Wohl of U.S. Fish and Wildlife Service, Region 7, generously loaned field equipment. Thanks to J. Bart for advice throughout the study. This manuscript was improved by the constructive criticism of J. Coulson and an anonymous reviewer.

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