Local movements and habitat use of Tundra or Whistling Swans *Cygnus columbianus* in the Kobuk-Selawik Lowlands of northwest Alaska

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A radio telemetry study of Tundra or Whistling Swans in the Kobuk-Selawik Lowlands of northwest Alaska 1984-89 showed that late summer home range size differed according to breeding status. Family groups moved less than flocked non-breeders, with ranges averaging 139 ha and 1331 ha, respectively. Late summer movements of family groups usually centred on one to three wetlands, although some family groups and non-breeding pairs ranged over a dozen wetlands. Flocked non-breeders exhibited widespread late summer movements, departing to staging areas soon after regaining flight. Tundra Swans selected late summer home ranges that contained more water and wetlands, 41-47% by area, than available habitat which had only 19% water and wetlands. All flocked non-breeders made a staging movement, whereas 71% of territorial non-breeding pairs and 68% of family groups made such staging movements. Flocked non-breeders moved to staging areas earliest, departed latest, and staged for the longest duration, while family groups were the last to initiate staging and had the shortest staging duration. Family groups and territorial non-breeders that did not stage averaged earlier departure on migration than other swans. Family groups and flocked non-breeders moved an average of 30 and 49 km, respectively, from late summer home ranges to autumn staging areas. Brackish shorelines of river deltas in the study area provided an abundance of Potamogeton *tubers and remained clear of ice later than other wetlands. Delta tidelands are of major importance to the regional Tundra Swan population because they likely provide food critical to autumn migration.*

Tundra or Whistling Swans *Cygnus columbianus columbianus* nest across arctic Canada and Alaska, and south along the west coast of Alaska (King 1973, Bellrose 1980, U.S. Fish and Wildlife Service (USFWS) 1983). Although Tundra Swans in Canada and Alaska have been found to be sensitive to man-caused disturbances (Barry & Spencer 1976, Murphy *et al.* 1986), and their eggs have traditionally been taken by Native subsistence hunters, both eastern and western populations of Tundra Swans have increased (Bartonek *et al.* 1981). The Kotzebue Sound region, which includes all of the study area, had a 10-year average Tundra Swan breeding population estimated at 3330 in 1978-88 (USFWS unpubl. data). Although nearly pristine today, much of the Alaska Tundra Swan breeding and staging grounds are a mosaic of private and public lands under different management regimen which could complicate habitat conservation in the future. Prudent management of Tundra Swans dictates continued annual population inventory coupled with knowledge of habitat use. To better define Tundra Swan habitat protection needs in northwest Alaska we investigated habitat use, movements on late summer home range, movements from breeding to staging areas, and timing of staging and initial autumn migration.

Study area

We marked and monitored Tundra Swans on and near the 1,275,750 ha Selawik National Wildlife Refuge (NWR) (Fig. 1), which straddles the Arctic Circle (66°33'N) and is transitional between the forested interior of Alaska and the treeless tundra of Alaska's west and north coasts. Selawik NWR comprises most of the Kobuk-Selawik Lowlands (described by Wahraftig 1965). These lowlands are a basin of river deltas, floodplains, and extensive wetlands rimmed by low hills on the north, east, and south. Three large rivers, the Noatak, Kobuk, and Selawik form prominent deltas where they meet Hotham Inlet and Selawik Lake, which are brackish inland branches of Kotzebue Sound.

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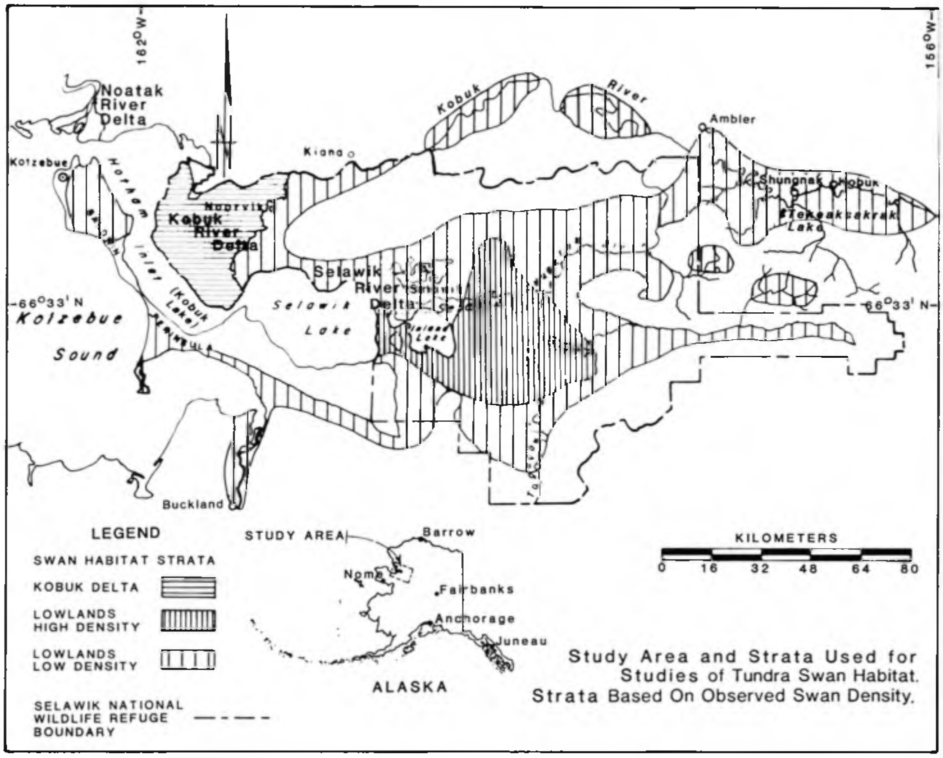


Figure 1. Stratification of Tundra Swan habitat in the Kobuk-Selawik Lowlands study area, based on observed swan density 1983-86.

Tidal influence reaches to 50 km inland via river channels because wind-driven storm tides may exceed 2 m, even though diurnal tides are minimal (<1 m, National Ocean Survey 1985). Expanses of tundra diminish and numbers of wetlands decrease with distance inland from the coast (from 162°W to 156°W). Geography, geology, climate, and vegetation of northwest Alaska were generally described by Selkregg (1976).

Review of land cover and wildlife habitat classifications for the region (Nodler *et al.* 1978, Craighead *et al.* 1988, U.S. Geological Survey (USGS) 1988, USFWS unpubl. data) resulted in designation of five habitat classes (plant nomenclature follows Hultén 1968). **Tussock-Lichen-Dwarf Shrub Tundra** occupies 41% of the area and is composed largely of the sedges *Eriophorum vaginatum* and *Carex Bigelowii* with abundant lichen cover and patches of low and dwarf shrubs such as *Betula nana* and *Ledum palustre decumbens*. **Wet-Moist Tundra** (19%) consists primarily of marshes and meadows of *Eriophorum angustifolium, Carex aquatilis, Arctophila fulva, Equisetum fluviatile* and *Calamagrostis canadensis*. **Water and Wetlands** (19%) include mostly shallow lakes and ponds with submergent growth consisting of *Potamogeton perfoliatus, P. pectinatus, P. vaginatus*, and *P. filiformis, Myriophyllum verticillatum, M. spicatum, Utricularia vulgaris*, and *Nuphar polysepalum*. Floating mats of *Menyanthes trifoliata, Calla palustris*, and *Sphagnum* spp. are extensive in numerous bog wetlands. Riparian and well-drained sites may include **Low-Medium Shrub Thickets** (13.5%) composed of *Alnus crispa, Salix arbusculoides, S. pulchra*, or **Tall Shrub-Deciduous Forests** (7.5%) of *S. alaxensis, Betula papyrifera, Populus tremuloides, P. balsamifera*, or *Picea glauca*.

Methods

Moulting adult or pre-fledging cygnet swans were captured on water while flightless during mid- to late summers 1984-89. A float-equipped Piper Super Cub airplane was taxied to within 2-3 m of each swan so that a person standing on one float could dip the bird out of the water with a long-handled fish landing net. Occasionally birds swam to land and were run down on foot.

Swans were transported to shore in a fabric holding jacket (Evans & Kear 1972).

Sex was determined using the criteria of Taber (1971) and USFWS & Canadian Wildlife Service (CWS) (1984). Age categories were differentiated as adult, subadult, and cygnet (Bellrose 1980). Breeding status groups were defined as family groups, non-breeding pairs, and flocked non-breeders (Lensink 1973). Except for a few cygnets too small to ring and collar, all birds captured were fitted with standard USFWS tarsus rings and blue plastic neck collars with white codes. Neck collars were as described by Sladen (1973), except size was 87 mm tall x 65 mm diameter and codes were 33 mm tall x 20 mm wide to facilitate reading at a distance. Codes were repeated three times around the circumference of the collar. Selected birds were fitted with a radio telemetry transmitter in a "backpack" harness configuration (Dwyer 1972) that was designed to fall off within a year. Radio-instrumented swans were monitored from initial capture until migration using an aircraft equipped with a telemetry receiver and directional antennas. We monitored movements and location an average of once per week except for two family groups near Kotzebue, which were monitored daily in 1989. All relocations were confirmed by visual sighting and plotted on 1:63,360 scale USGS topographic maps. Aerial transect surveys (King 1973, Wilk 1988) were conducted annually in June and August to esti-

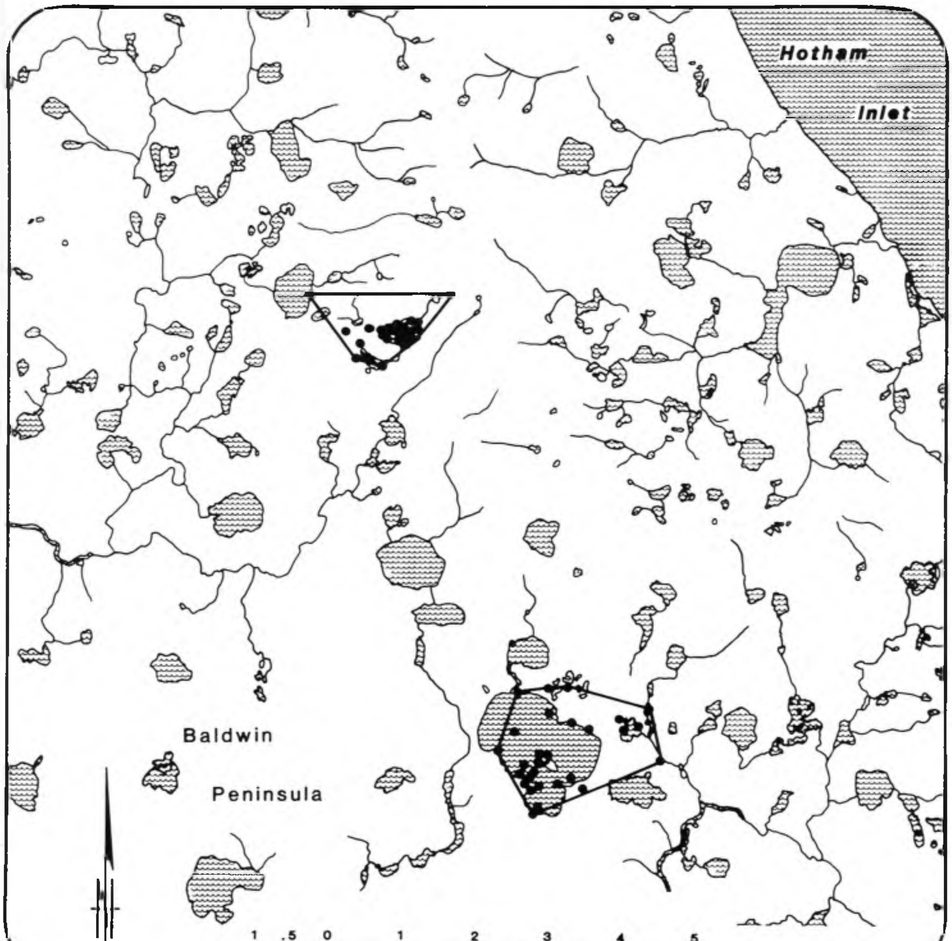


Figure 2. Late summer home ranges and movements of two radio-instrumented Tundra Swan family groups near Kotzebue, Alaska, based on daily aerial relocations, mid-August to late September 1989. Range areas were 98 ha for swan U136 (top) and 255 ha for swan U199 (bottom). On September 21 and 18, respectively, both family groups made their first fall staging movements to the shoreline of Hotham Inlet, in the northeast of the map. Five to eight days later both family groups moved another 20-50 km to the southeast for the remainder of their staging period.

mate nesting density and productivity, respectively (Fig. 1), and weekly along the coast in autumn to enumerate staging activities.

The area used by Tundra Swans from time of capture during their moult, usually mid-July to early August, until departure for staging or autumn migration, usually in mid-September, was defined as the late summer home range. Staging was defined as any premigratory movement to a swan gathering area. Late summer home ranges were determined by joining the outer-most locations recorded before any staging or migration movement (minimum area method, Mohr 1947). Areas of the resulting convex polygons were measured with a digital planimeter and checked by computer.

Habitat composition data were obtained from a satellite-derived digital land cover map (USGS 1988; see Talbot & Markon 1986 for methods). Each telemetry-derived swan home range polygon was digitally referenced onto the land cover map using a computerized geographic information system. The area of each habitat class within each home range polygon of instrumented swans was determined by counting the number of 0.62 ha picture elements (pixels) classified as a particular habitat within each home range polygon. Pixel counts were then converted to hectares. Composition of habitat in each of three swan density strata was determined in a similar manner. Estimates of each habitat class in home range polygons and habitat strata of varying sizes were standardized as a proportion of total area.

For habitat analyses we assumed that inclusion of a habitat class within a swan home range polygon represented "use" of that habitat in some degree, however, we recognized that the extent of use could vary from rarely used sites to critically needed feeding and shelter areas used daily. Selection for or against the five habitat classes by each swan was determined by taking the difference between the proportion of each habitat within its home range (habitat use) and the proportion of that habitat in the specific stratum where the swan occurred (habitat availability). Averaged over all swan ranges, a positive difference indicated selection for the given habitat and a negative difference indicated selection against the given habitat (Pietz & Tester 1982, Thomas & Taylor 1990). Statistical significance was determined using analysis of variance (ANOVA), Tukey multiple comparisons, and unpaired Student's t test (Zar 1984). Test results were considered significant if $P<0.05$.

Results

Forty-five Tundra Swans, including 34 adults and 11 cygnets, were radio-instrumented between 1984 and 1989. Resultant sample size was 37 for analysis of home range and staging movements and 29 for habitat analyses. Three swans died shortly after marking due to predation or capture trauma, two radios were shed, cygnet broods instrumented in 1984 contained some duplication within family groups, and some swans were captured in areas without satellite map coverage. The sample was evenly distributed on a geographic basis, with 15 in the western lowlands, 13 in the eastern lowlands, 11 in the Kobuk River delta, and six in peripheral areas. Ranges were determined for five

Table 1. Late summer home range and habitat use of Tundra Swans by breeding status, Kobuk-Selawik Lowlands, northwest Alaska, 1984-89. Figures are mean late summer home range size (top) and mean proportion of total habitat use (bottom). Parentheses indicate standard error.

	Breeding status			
	Family groups	Non-breeding pairs	Flocked non-breeders	ANOVA F-ratio
Mean late summer home range (ha)	139 (114)	362 (603)	1331 (1867)	6.126*
Range	16-511	18-1675	27-4412	
Radioed swans *n*	25	7	5	
Habitat type				
Water and Wetlands	0.494 (0.262)	0.365 (0.214)	0.410 (0.226)	0.637
Tussock-Lichen-Dwarf Shrub	0.238 (0.177)	0.296 (0.163)	0.343 (0.231)	0.714
Wet-Moist Tundra	0.123 (0.106)	0.168 (0.051)	0.112 (0.076)	0.546
Low-Medium Shrub	0.094 (0.081)	0.126 (0.126)	0.089 (0.072)	0.283
Tall Shrub-Deciduous Forest	0.048 (0.056)	0.044 (0.025)	0.049 (0.030)	0.015
n	19	5	5	

* Indicates significance at $P<0.05$.

flocked non-breeders, seven non-breeding pairs, and 25 family groups, which approximated the percent composition of the regional population. The flocked non-breeders we ringed and collared included about half subadult swans and half adult non-breeders or adult failed-breeders (n = 28).

Late summer movements and home range size

Most (18 of 25) family groups moved little in late summer and their activities were concentrated on one to three wetlands. Extent of movements, size and shape of late summer ranges, and focus of activities on wetlands as compared to non-wetlands, were generally similar among two family groups monitored daily (Fig. 2) and 22 other family groups which we monitored weekly. Ranges of the two daily-monitored family groups were estimated at 98 ha and 255 ha, as compared to the mean of 139 ha for all family groups (Table 1). Among family groups, some extremes in size and shape of ranges were observed, however (Fig. 3). In the highest density swan habitat, the Kobuk delta, two family groups occupied small (93 ha and 139 ha) contiguous ranges in different parts of the same 250 ha wetland. Yet 16 km away in similar high density habitat, the largest (511 ha) late summer range for a family group included 11 separate

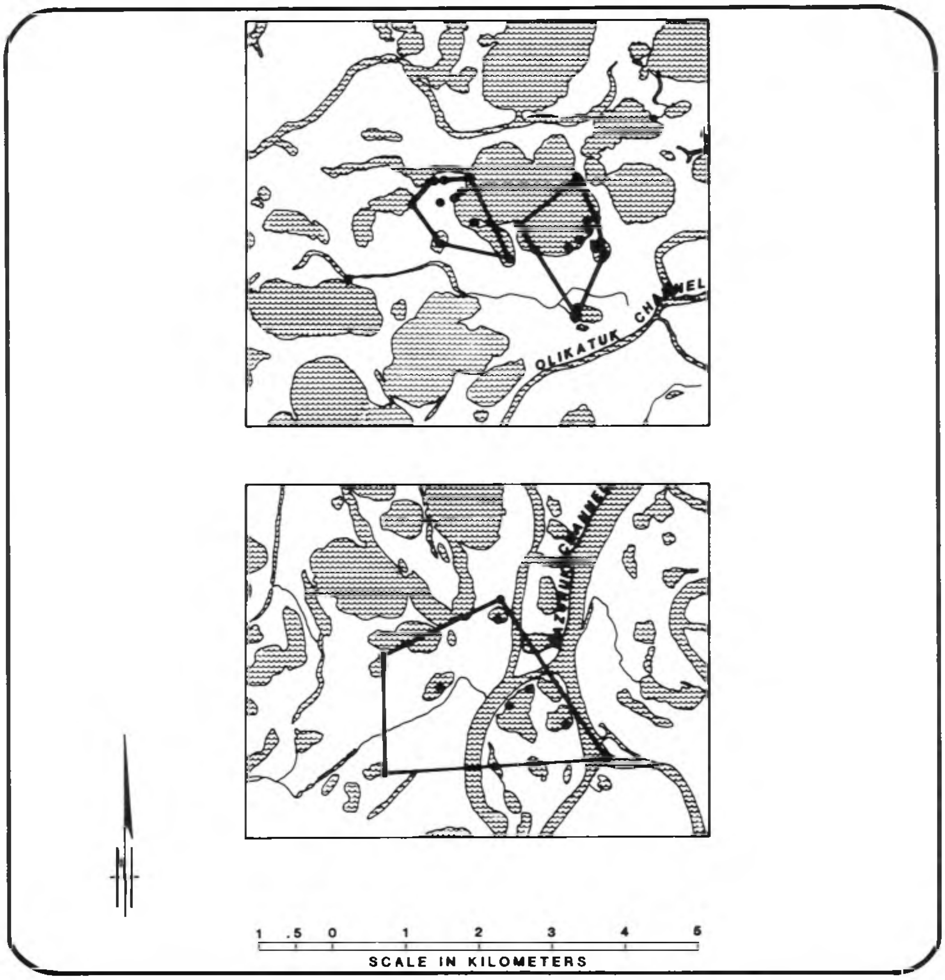


Figure 3. Late summer home ranges and movements of three radio-instrumented Tundra Swan family groups on the Kobuk River delta, Alaska, based on aerial relocations every 2-9 days, mid-August to early October 1984 and 1986. Areas of two contiguous territories in the central delta were 93 ha for swan U012 (top left) and 139 ha for swan U004 (top right). Only 16 km to the southeast the largest late summer home range area of any family group in the study was determined to be 511 ha for swan U158. All three family groups later staged on the western shoreline of the Kobuk River delta before migrating southeastward.

wetlands and one large section of river channel. Late summer movements of territorial non-breeding pairs were more variable than family groups: one territorial non-breeding pair ranged over a 20 ha area that included a single wetland; another non-breeding pair ranged over a 506 ha area that encompassed six major (>10 ha) and a dozen minor (<10 ha) wetlands.

Flocked non-breeders exhibited widespread movement patterns and little tenacity to a specific home range. Late summer movements of three flocked non-breeders spread over large (397-4410 ha) areas prior to making staging movements. Two other flocked non-breeders on small (27-32 ha) late summer ranges showed limited movements that were followed by an immediate movement to a coastal staging area, with no observed return to each of their late summer ranges. These two birds apparently initiated their staging movement as soon as their moult was complete and were able to fly some distance to a staging area. Of five flocked non-breeders monitored, three remained with flocks until departure for staging; one ranged with flocks for at least 11 days, and then remained with another swan until departure for staging nearly a month after capture; and one other separated from the flock nine days after capture and departed for staging seven days later as a single.

Mean late summer home range size of flocked non-breeders was significantly greater than that of family groups (ANOVA, Tukey $P<0.004$, Table 1). Mean home range size of territorial non-breeding pairs was slightly larger than family groups. There was no significant difference in mean home range size between family groups and non-breeding pairs, which together were termed territorial swans. Among territorial swans, there were no significant differences in late summer home range size with respect to staging behaviour (stagers, 150 ha *v* non-stagers, 271 ha), or geographic location (coastal, 389 ha *v* inland, 289 ha) nor density stratum (Kobuk, 472 ha, Lowlands-high, 219 ha, and Lowlands-low, 480 ha). Mean late summer home range sizes for each stratum, combined with known nesting densities by stratum (Table 2), indicated that habitats on the study area were not saturated with swan ranges. About 36% of the Kobuk delta was occupied by late summer ranges of family groups, compared to 15% and 7% in the Lowlands-high density and Lowlands-low density, respectively.

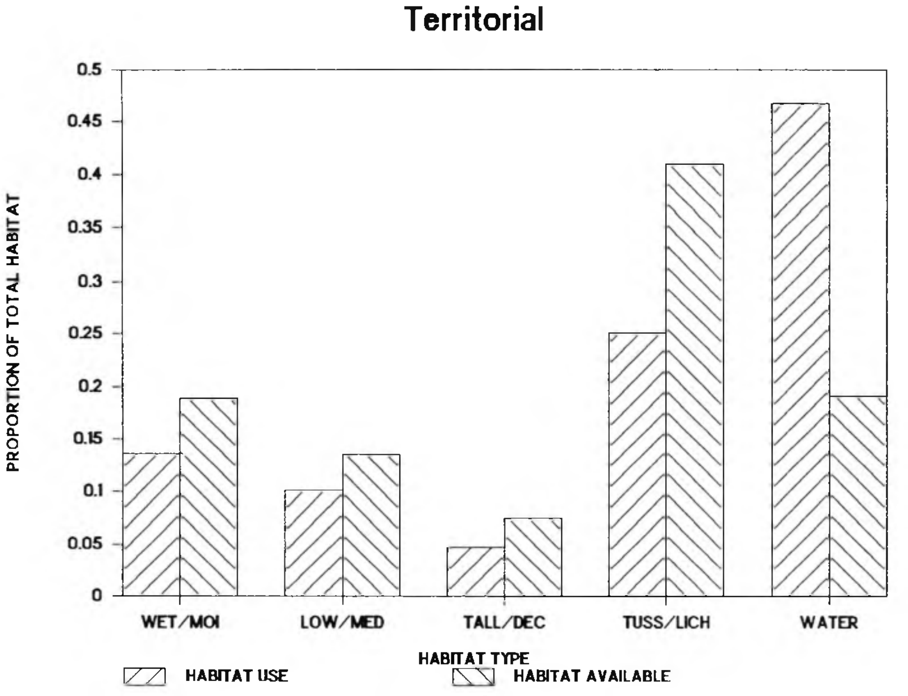
Habitat use and selection

Habitat use did not differ significantly among the three breeding status groups (Table 1). We analyzed habitat use and selection of the flocked non-breeders and territorial swans separately because their mean late summer home range sizes differed significantly. Territorial swans showed significant (ANOVA, Tukey $P<0.0005$) selection of water, while flocked non-breeders showed significant (ANOVA, Tukey $P<0.001$) selection of water and higher comparative use of Tussock-Lichen Tundra (Figs. 4 & 5). Water averaged 41% and 47% of the habitat used by 24 territorial swans and five flocked non-breeders, respectively, whereas water comprised only 19% of available habitat. Territorial and flocked non-breeders used Wet-Moist Tundra, Tall Shrub-Deciduous Forest, and Tussock-Lichen Tundra less than was expected based on availability.

Swan territories in inland portions of the study area contained significantly ($t = 1.832$, $P<0.05$) more Tussock-Lichen Tundra (32%) than territories near the coast (20%). Swans making a staging movement to the coast had significantly ($t = 1.812$, $P<0.05$) more Wet-Moist

Table 2. Mean annual nesting densities of Tundra Swans on the Kobuk-Selawik Lowlands in northwest Alaska compared to selected other sites in Alaska.

Site	Density (ha per nest)	Year(s)	Reference
Yukon-Kuskokwim delta			
Onumtuk	125	1972-79	Dau (1981)
Chevak	130-320	1968	Scott *et al.* (1972)
Kobuk-Selawik Lowlands			
Kobuk River delta	1297	1983-86	this study
Lowlands high density	1436	1985-86	this study
Lowlands low density	7283	1983-86	this study
Arctic Coastal Plain (North Slope)			
Arctic NWR coast	1667-2500	1983-85	Platte & Brackney (1987)
Colville River delta	1000-2000	1982-89	Campbell & Rothe (1990)
Lisburne oilfield	1875	1983-85	Murphy *et al.* (1986)
Kuparuk oilfield	5000	1988-90	Ritchie *et al.* (1990)



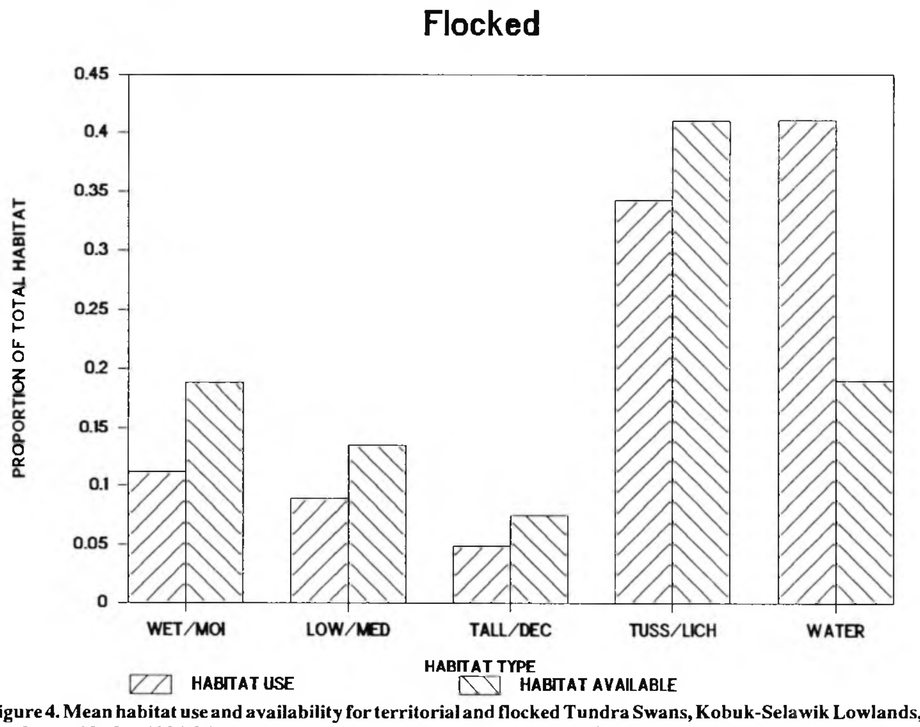
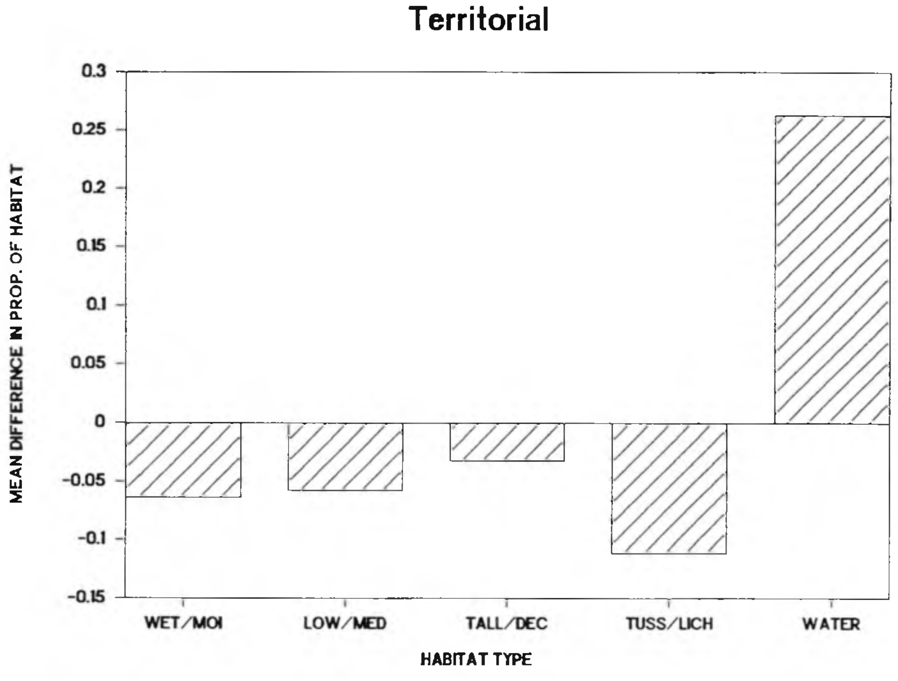


Figure 4. Mean habitat use and availability for territorial and flocked Tundra Swans, Kobuk-Selawik Lowlands, northwest Alaska, 1984-86. For each habitat, column on left is proportion of the given habitat averaged over all swan ranges (use); column on right is proportion of given habitat out of all habitat available. Abbreviations for habitats are: WET/MOI = Wet-Moist Tundra; LOW/MED = Low-Medium Shrub Thickets; TALL/DEC = Tall Shrub-Deciduous Forest; TUSS-LICH = Tussock-Lichen-Dwarf Shrub Tundra; WATER = Water and Wetlands.



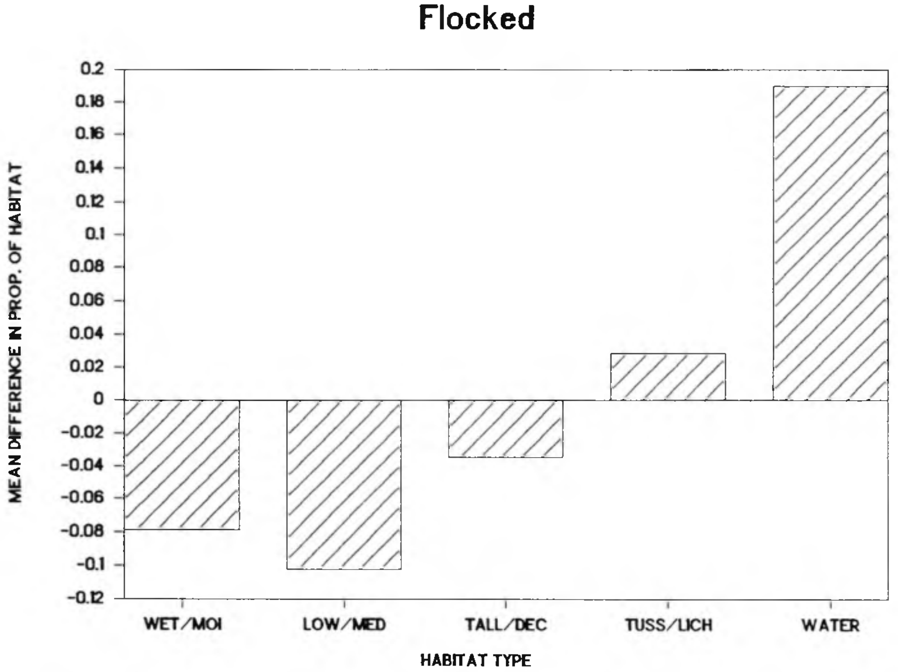


Figure 5. Habitat selection by territorial and flocked Tundra Swans, Kobuk-Selawik Lowlands, northwest Alaska, 1984-86. Vertical axis is mean difference between proportion of habitat included within the late summer home range and proportion of habitat available in the stratum. Positive values indicate selection for the habitat and negative values indicate selection against the habitat. For both territorial and flocked swans, selection of Water was significant (ANOVA, Tukey).

Table 3. Timing, duration, and distance of first movement to autumn staging areas in relation to breeding status of radio-instrumented Tundra Swans, Kobuk-Selawik Lowlands, northwest Alaska, 1984-89. Parentheses indicate standard error.

Breeding status	*n*	% making staging movement	Mean distance first staging movement (km)	Mean date arrival staging area	Mean date migration departure	Mean duration staging (days)
Flocked non-br.	5	100	49 (13)	31 Aug	3 Oct	35 (5)
Non-br. pairs	7	71	38 (16)	20 Sept	28 Sept	14 (7)
Family groups	25	68				
Stagers	17		30 (21)	22 Sept	3 Oct	11 (6)
Non-stagers	8				23 Sept	

Tundra (16%) in their territories than did swans which did not make a staging movement (9%). There were no other significant differences in composition of habitat used by inland v coastal or staging *v* non-staging territorial swans.

Autumn staging

Twenty-nine of 37 radio-instrumented swans flew to staging areas in northwest Alaska prior to autumn migration. All flocked non-breeders made a staging movement, whereas 71% of non-breeding pairs, and 68% of family groups made staging movements (Table 3). Flocked non-breeders arrived on staging areas earliest and departed on migration latest, thus had the longest staging duration, while family groups were last to arrive on staging areas and had the shortest staging duration (ANOVA, Tukey $P<0.001$). Among stagers, non-breeding pairs arrived on staging grounds about the same date as family groups but emigrated earlier (Table 3). Eight of 25 family groups that did not stage averaged the earliest departure on migration. Staging family groups traveled an average of 30 km on their first detected staging movement while flocked non-breeders moved an average of 49 km. Non-breeding pairs were intermediate in distance of first detected staging movement.

Four coastal staging areas (east shore Baldwin Peninsula, and the shorelines of the Noatak, Kobuk, and Selawik River deltas, Fig. 6) had peak counts of 7300, 6000, 1600, and 5600 Tundra Swans in aerial surveys during the autumns of 1984-1987, respectively. For staging, radio-instrumented swans most frequently used the river delta or tidal shoreline closest to their summering area, and the swans most likely to stage were those summering nearest the coast. All instrumented swans summering on the Baldwin Peninsula, Kobuk delta, Noatak Lowlands, and Squirrel River staged, whereas 67% of swans from the western Selawik Lowlands staged, and only 37% of swans from the eastern Selawik Lowlands staged. An additional inland staging area, Tekeaksakrak Lake, attracted 50-100 swans, including one radio-instrumented family from the eastern portion of the study area. Swans often used more than one staging area before autumn migration (Fig. 6). Four swans made intermediate stops on their flight west to staging areas, and eight swans made such intermediate stops on their eastbound migration. Four swans made round-trips to a staging area lasting 3-13 days but spent most of the autumn staging period on their late summer home ranges.

Spatial segregation by groups of differing breeding status was partially evidenced in the radio-instrumented sample - only family groups used the Kobuk delta, while all breeding status groups used the other deltas (Table 4). Aerial surveys flown at 7-14 day intervals in the au-

Table 4. Primary autumn staging area in relation to breeding status of radio-instrumented Tundra Swans, Kobuk-Selawik Lowlands, northwest Alaska, 1984-89.

	Breeding status		
Staging area	Family groups	Non-breeding pairs	Flocked non-breeders
Noatak delta	2	2	4
Kobuk delta	9		
Selawik delta	5	3	1
Tekeaksakrak Lake	1		
Non-stagers	8	2	
Total	25	7	5

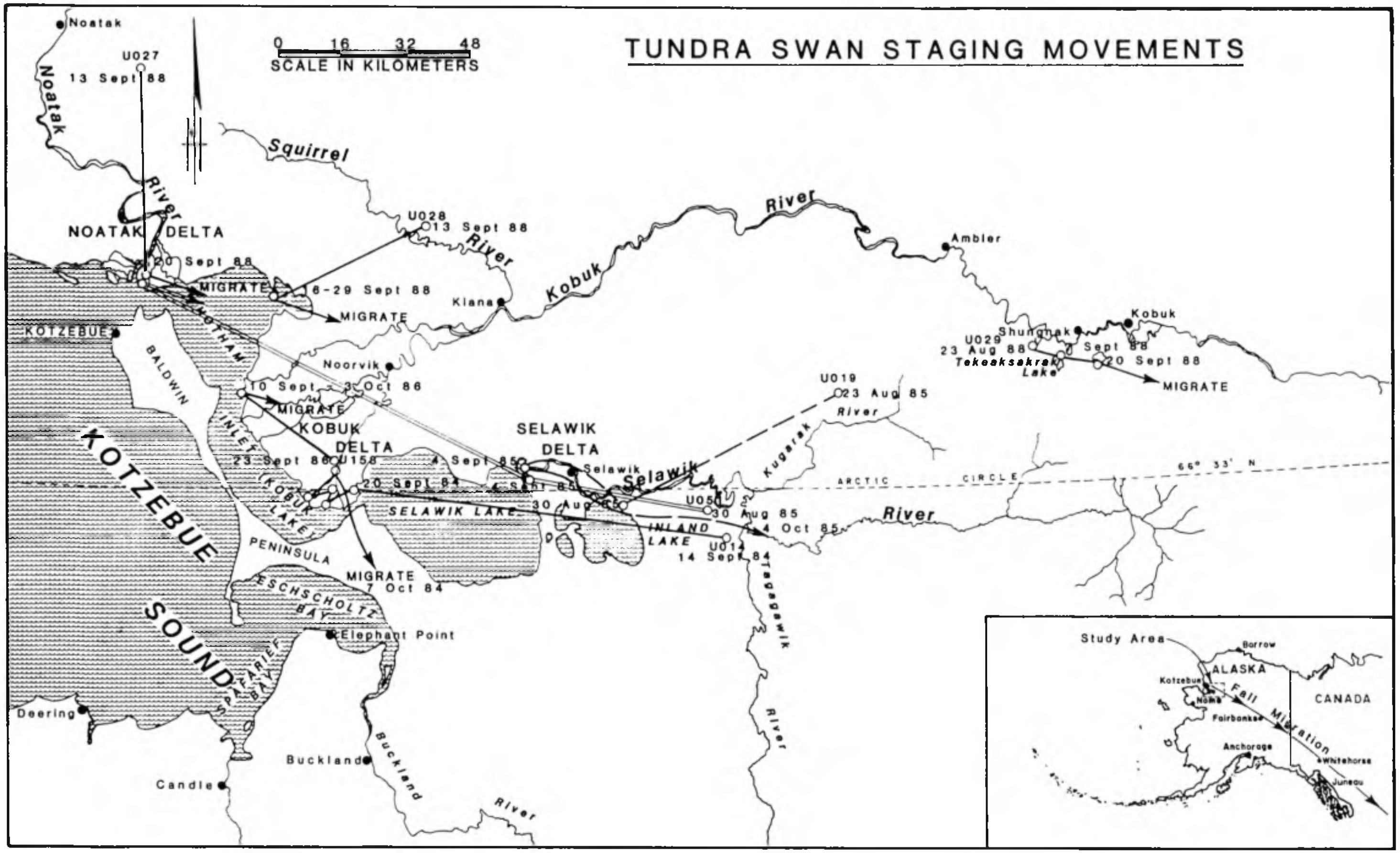


Figure 6. Movements of five Tundra Swan family groups (solid lines), one non-breeding pair (double line), and one flocked non-breeder (dashed line), from summering areas to fall staging areas, Kobuk-Selawik Lowlands, northwest Alaska, 1984-88.

Table 5. Timing, duration, and distance of first movement of 25 radio-instrumented Tundra Swans in relation to primary autumn staging area, Kobuk-Selawik Lowlands, northwest Alaska, 1984-89. Parentheses indicate standard error.

Staging area	*n*	Mean distance from summering area (km)	Mean date arrival staging (km)	Mean date migration departure	Mean duration staging (days)
Noatak delta	8	45 (9)	11 Sept	4 Oct	23 (14)
Selawik delta	9	36 (17)	16 Sept	28 Sept	17 (10)
Kobuk delta	9	23 (27)	26 Sept	6 Oct	11 (8)

tumns of 1984-87 qualitatively showed a preponderance of flocked non-breeders on the Noatak delta in late August and early September and a majority of family groups on the Kobuk delta mid- to late September. These patterns were corroborated by differential timing of use periods among the deltas. The Noatak delta averaged significantly (ANOVA, Tukey $P<0.04$) earlier arrival of stagers, compared to the Selawik and Kobuk deltas (Table 5). The Noatak delta also held stagers for the longest period while the Kobuk delta had the shortest period and averaged the latest mean departure.

Tundra Swans used river delta shorelines to stage in autumn because the brackish waters and current at river mouths provided the latest unfrozen waters combined with high availability of edible vegetation. The submerged brackish water mudflats of the deltas contained abundant growth of *Potamogeton pectinatus*, *P. vaginatus*, *P. filiformis*, and *P. perfoliatus*. These species produced overwintering tubers (turions of corms) 6-12 mm long by the end of the growing season in late August. Gizzards of ten Tundra Swans taken in September on the western Noatak delta were full of *Potamogeton* sp. corms and contained lesser amounts of foliage of *Potamogeton* sp. and new growth of *Carex* spp., *Puccinellia* sp., and *Arctophila fulva* (W.R. Uhl unpubl. data). Two mid-June specimens from the same area had gizzards full of new growth of *Puccinellia* sp. and *Arctophila fulva* but no *Potamogeton*, which is not available in spring and early summer.

Mortality

The 25 family groups in the 1984-89 sample collectively had 57 Class IIc (Bellrose 1980) cygnets when captured and were known to have left the study area on migration with 40 cygnets, a 30% loss. We suspected that capturing both adults increased chances of total brood loss (two of four *v* one of three broods lost when both adults *v* single adult were captured in 1985, respectively). To prevent such loss, after 1985 only one member of each breeding pair was captured and marked, which resulted in no known brood loss. Two radio-instrumented subadult swans died within two weeks of capture and both carcasses were scavenged before discovery. The lighter ($\bar{x}$ = 6.4 kg) subadults may not have been able to carry the radio package as easily as adults ($\bar{x}$ = 7.2 kg). All of five family groups with known brood sizes before and during autumn migration kept their broods into migration. Of the 45 radio-instrumented swans, six were found dead along the fall migration route within a year after marking. An additional one hunting mortality was documented among the combined radio and neck collar sample of 104 swans. Efforts to monitor radio-instrumented swans returning to the study area the year after capture were unsuccessful due to shed radio harnesses, failed batteries or radios, and mortality. On the Selawik Lowlands, sightings were made of two collared birds that had been radio-instrumented in previous years, and sightings were made of three additional birds that had not been radio-instrumented. Swans that had been captured were extremely wary of aircraft and people on the nesting ground, therefore successful attempts to read collar codes were rare.

Discussion

Late summer movements and home range size

Size of Tundra Swan late summer home range within the study area differed significantly according to breeding status but not staging behaviour, habitat stratum, or geographic area. Intuitively, home range size would be expected to vary according to food requirements and behaviour as related to habitat quality and breeding status, respectively. Wide-ranging movements of flocked non-breeders were expected because the flocks consisted of at least half subadults that had not yet established territories. Lack of preferred food in areas not already defended by territorial swans, premigratory restlessness, or lack of familiarity with the surroundings could have contributed to these movements. In contrast, family groups would be expected to have the smallest home ranges because they defend territories and flightless cygnets, and are presumed to be familiar with their ranges (Scott *et al.* 1972, Scott 1977, Hawkins 1986). Also, poorer mobility of cygnets, together with the time that they need to spend feeding to ensure rapid growth, is also likely to influence size of home range for breeders in comparison with non-breeders. Early moult and attainment of flight by non-breeders as compared to breeders, as observed in this study and elsewhere (Scott *et al.* 1972, W.R. Uhl unpubl. data), would allow the non-breeders greater freedom to move about in the same period that breeders were restricted by flightlessness.

We observed higher variability in late summer home range size among family groups than expected (CV = 0.82, Table 1), which suggested variability in the quality of swan habitat. In a habitat of variable quality, family groups residing in the most desirable areas with abundant food would not have to range as far as those in less desirable areas. We estimated that, depending on habitat, 7-36% of the Kobuk-Selawik Lowlands (by area) was occupied by the late summer ranges of Tundra Swan family groups. Some sites, however, in both high and low breeding density areas could have been saturated with contiguous ranges of family groups. In the high density Kobuk delta area we documented two contiguous radio-monitored ranges on the same lake (Fig. 3). In the Lowland-low density portion of the study area a 451 ha lake held three family groups including one radio-instrumented family group with a 66 ha range. This lake had abundant *Potamogeton* sp. that apparently permitted the radioed family group to remain on the lake without having to feed or stage at other wetlands. On the Yukon delta, Lensink (1973) suggested that family groups made limited movements 100-400 m from the nest until fledging, but Dau (1981) noted that families seeking more favourable habitats moved "considerable distances". Dau (unpubl. data) also noted that territories were larger in open wetlands than in wetlands mixed with uplands where swan pairs were more visually separated. Territory size and nesting density differed spatially across the Kobuk-Selawik Lowlands, as did nesting density in several sites across Alaska (Table 2). These data suggested widely differing qualities of Tundra Swan habitats, with the highest densities, occurring south of the arctic circle.

Habitat use and selection

A satellite land cover mapping resolution of 0.62 ha determined that water area was a primary factor in swan habitat selection, regardless of breeding status or geographic area within the study area. Several Alaska studies (King 1973, Lensink 1973, Platte & Brackney 1987, Wilk 1988) noted high density of Tundra Swans in habitats with a high proportion of water area compared to uplands. King & Hodges (1981) found a correlation between swan densities and length of lake shoreline as well as number of lakes and number of small islands per unit area. At Izembek NWR, on the western Alaska Peninsula, lakes with outlets large enough to sustain a salmon run were fertile, supported good stands of *Potamogeton perfoliatus*, *P. filiformis*, and *Sparganium hyperboreum*, and were preferred by Tundra Swans for breeding, moulting, and brood-rearing (J.E. Sarvis unpubl. data). Use of *Potamogeton* by Tundra Swans during staging and migration has been well documented (Sherwood 1960, Scott *et al.* 1972, Wilk 1988, this study), however, little information is available about the combination of wetland morphologic, edaphic, and chemical factors which foster its abundant growth in certain high density breeding areas. The dwarf shrubs, *Vaccinium uliginosum* and *Empetrum nigrum*, common in the Tussock-Lichen Dwarf Shrub Tundra, frequently produced large crops of berries that were eaten in quantity by Tundra Swans (W.R. Uhl & M.A. Spindler unpubl. data). We suspected that a predominance of these berry-producing species associated with the Tussock-Lichen-Dwarf Shrub Tundra could explain why some areas summered and produced more Tundra Swans than others. Unfortunately, the satellite land cover mapping method did not have sufficient accuracy to discern tundras with abundant berry-producing shrubs nor could it distinguish fertile wetlands with abundant *Potamogeton* sp. from those with scant submergent growth.

Autumn staging

Timing, duration, and extent of participation in staging by the population of Tundra Swans in the Kobuk-Selawik Lowlands was primarily related to breeding status and proximity of their late summer home range to the coast. Differential timing of staging movements by flocked non-breeders and non-breeding pairs of Tundra Swans was observed on the Yukon River delta (Lensink 1973), but there has been no such documentation for family groups. Differences in moulting locations according to breeding status of waterfowl (Salomonsen 1968), swans (Scott *et al.* 1972) and *Cygnus olor* (Mathiasson 1980) have been attributed to the need to relieve pressure on local food supplies that would increase survivability of offspring. Early staging and geographical segregation of flocked non-breeders observed in the present study could have been for similar reasons. Why 68% of family groups in this study made a similar fall staging movement was less easily explained, because there was no significant difference in late summer home range size between territorial stagers and non-stagers. Stagers did average smaller ranges than non-stagers, suggesting that even though staging swans may have had smaller, higher quality territories than non-stagers, they may have staged to gain access to other areas of high quality forage. Late summer ranges of territorial stagers had significantly more Wet-Moist Tundra than non-stagers, indicating that lack of the berry-producing shrubs in the habitat could have contributed to the swans need to make a staging movement. Also, staging may have occurred for reasons unrelated to habitat, e.g. social, or to provide flight exercise for cygnets.

Inland portions of the study area froze earlier than coastal portions and we expected more family groups from inland areas to stage than family groups near the coast. Instead, the inland family groups simply migrated: 80% of the inland (east half) family groups migrated directly without a staging movement, whereas only 15% of the coastal (west half) family groups migrated directly. This could have been because energetic advantages of coastal staging would diminish for swans breeding far inland due to the greater distance to the staging areas. Also, phenology inland was advanced compared to coastal areas (Selgregg 1976), which may have allowed a comparatively longer breeding season inland, in part negating the need for coastal staging. Premigratory nutritional needs of the non-breeding pairs that did not stage could have been met prior to freeze-up in mid-September because they would not have had to expend energy in brood rearing, and hence could migrate directly. Several of the Selawik Lowlands swans that migrated directly without staging stopped 480 km southeast of the study area at Minto Flats, a major swan stopover near Fairbanks. Energetics of staging and migration have not been studied in Tundra Swans, but the necessity of staging behaviour in relation to long distance migration in Snow Geese *Chen caerulescens* has been documented (Wypkema & Ankney 1979, Brackney *et al.* 1987).

Legislative efforts in 1980 to protect remote arctic and subarctic wildlife habitats in Alaska, including waterfowl breeding areas, resulted in the establishment of nine new national wildlife refuges and enlargement of several existing refuges. A complex land ownership pattern, including significant private inholdings, resulted from settlement of aboriginal land claims, and many coastal staging areas were not legislatively protected. Dependence of the Kobuk-Selawik Tundra Swans on river deltas on and off conservation areas demonstrates the importance of cooperatively managing and conserving the significant staging and migration stopovers which may be as important to the welfare of swans as are the breeding and wintering areas. Along with the Tundra Swans, significant numbers of ducks and geese also use the estuarine deltas of the region and would no doubt also benefit from their conservation.

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(Photos by senior author unless noted otherwise)

Photo 1. A Tundra Swan cygnet, approximately 60 days since hatching, is fitted with a plastic neck collar and backpack telemetry radio harness, Kobuk River delta, Alaska, September 1984.

Photo 2. Plastic neck collars were affixed to all Tundra Swans captured during local movements study, Kobuk-Selawik lowlands, Alaska, August 1985.

Photo 3. A flock of staging Tundra Swans at the mouth of Riley Channel, Kobuk River delta, Alaska, September 1987. Peak numbers observed in staging flocks along the delta shorelines in northwest Alaska were 7200 in 1984, 5900 in 1985, 1600 in 1986, and 5600 in 1987. (Photo by Dennis Witmer).

Photo 4. Culmen length was one of several morphometric measurements taken while Tundra Swans were marked for the local movements study, Kobuk-Selawik Lowlands, northwest Alaska, 1984-1989.