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Distribution, Abundance, Population Structure and Productivity of Tundra Swans in Bristol Bay, Alaska

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ABSTRACT. Data on tundra swans (Cygnus columbianus columbianus) were obtained on the northern Alaska Peninsula from 1983 to 1987. Phenology was advanced 2-4 weeks of swan nesting areas in the Subarctic and Arctic, but a late spring retarded nesting by at least ten days. The highest densities of potential breeders (0.3-0.9 swans·km⁻²) occurred along the lowland coast and in broad drainage basins. Estimates of the breeding population ranged from 4000 to 4600 swans. Brood sizes in August ranged from 2.7 \pm 0.3 SE to 3.3 \pm 0.5 young. In summer, 51-66% of the adults and subadults were observed as potential breeders, and the remainder were in nonbreeding flocks. Between 31 and 40% of the observed pairs had nests or young. The population and production on the Alaska Peninsula may be less affected by weather than populations at higher latitudes.

Key words: aerial survey, Alaska Peninsula, Bristol Bay, Alaska, phenology, Cygnus columbianus, migration, productivity, tundra swan

RÉSUMÉ. On a relevé des données sur les cygnes siffleurs (*Cygnus columbianus columbianus*) dans le nord de la péninsule de l'Alaska, entre 1983 et 1987. Les conditions bioclimatiques étaient en avance de 2 à 4 semaines par rapport à celles des sites de nidification situés dans le sub-Arctique et l'Arctique, mais une année, le printemps tardif retarda d'au moins dix jours la nidification. Les densités les plus élevées de reproducteurs potentiels (de 0,3 à 0,9 cygnes·km⁻²) se retrouvaient le long des basses-terres côtières et dans les grands bassins hydrographiques. On estime que la population allait de 4000 à 4600 cygnes. La taille de la couvée au mois d'août allait de 2,7 ± 0,3 à 3,3 ± 0,5 petits. En été, on a observé que de 51 à 66% des adultes et des jeunes adultes étaient des reproducteurs potentiels, le reste étant dans des troupeaux non reproducteurs. Entre 31 et 40% des couples observés avaient un nid ou des petits. La population et la production sur la péninsule de l'Alaska sont peut-être moins affectées par le climat que les populations des latitudes plus élevées.

Mots clés: relevé aérien, péninsule de l'Alaska, Bristol Bay, Alaska, phénologie, Cygnus columbianus columbianus, migration, productivité, cygne siffleur

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INTRODUCTION

The breeding range of tundra swans (Cygnus columbianus columbianus) in North America extends from the eastern Canadian Arctic west and south to Bristol Bay, Alaska (Palmer, 1976; Bellrose, 1980). The only studies of the major nesting populations have been carried out on the Yukon Delta, Alaska (Lensink, 1973; Dau, 1981) and in the Keewatin District, N.W.T., Canada (McLaren and McLaren, 1984). There is a need for information on status, habitat requirements and production for all major nesting populations because of the different conditions to which each is subjected (Pacific Flyway Study Committee [PFSC], 1983; U.S. Fish and Wildlife Service, 1985).

Although the Bristol Bay population constitutes an estimated 18% of the Pacific Flyway population, data for this area are lacking (PFSC, 1983). The swans of Bristol Bay are of particular interest because habitat becomes suitable for nesting much earlier than in other major nesting areas. The earlier availability of nesting sites in Bristol Bay may result in a more stable annual production. Here information on distribution, abundance, population structure and productivity of swans in Bristol Bay is presented and compared with data on tundra swan populations in other areas.

STUDY AREA

The study area includes virtually all habitats of tundra swans on the northern two-thirds of the Alaska Peninsula (NAP), which adjoins the mainland of Alaska at about latitude 59°20′N, longitude 155°30′W and extends approximately 800 km southwest (Fig. 1). It is bounded by the Aleutian Mountain Range on the south and east, the Kvichak River on the north and Port

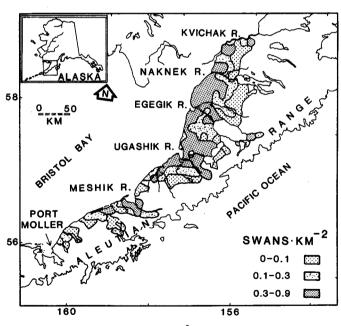


FIG. 1. Distribution and density (swans·km⁻²) of paired and single tundra swans on the northern Alaska Peninsula, 1983-87.

Moller on the southwest. The northern boundary is beyond the boreal tree line but adjoins the broad, discontinuous ecotone of open spruce (*Picea glauca* and *P. mariana*) woodlands and tundra meadows. The area is crossed by the Naknek, Egegik, Ugashik and Meshik rivers and numerous smaller rivers and tributaries.

Alaska Peninsula/Becharof National Wildlife Refuges, U.S. Fish and Wildlife Service, P.O. Box 277, King Salmon, Alaska 99613-0277, U.S.A. Present address: Kanuti National Wildlife Refuge, 101 12th Street, Box 20, Fairbanks, Alaska 99701, U.S.A. ©The Arctic Institute of North America

Weather is highly variable, with a more extreme polar maritime climate in the north and a moderate Aleutian maritime climate in the south (Selkregg, 1976). The maritime influence and lower latitude of the NAP result in earlier thaws and later freezes than in the Subarctic and Arctic (Arctic = latitudes above the Arctic Circle, 66°33′N). The long-term average period of mean freezing daily temperatures is three weeks longer on the subarctic Yukon Delta (Bethel) and 13 weeks longer in the high Alaska Arctic (Barrow) than in King Salmon (Naknek River) of the NAP (Arctic Environmental Information and Data Center, 1986).

The lowland on the NAP is a gradually sloping plain mantled with glacial sediments, with volcanic deposits exposed in many areas (Pewe, 1983; Detterman, 1986). Habitats of wet and moist tundra are occupied by swans. Wet tundra includes grass and sedge meadows interspersed with ponds and marshes of moderate abundance and is generally confined to the coastal zones and lower river basins. Cottongrass (*Eriophorum* spp.) and *Sphagnum* spp. typify many meadows. Pond and marsh emergent flora include *Carex lyngbyaei*, horsetail (*Equisetum fluviatile*) and buckbean (*Menyanthes trifoliata*). Typical plants of the moist tundra, which extends to the upper drainages, include dwarf birch (*Betula nana*) and willow (*Salix arctica*), crowberry (*Empetrum nigrum*) and a variety of ericaceous shrubs.

METHODS

Numbers of migrant swans on the Naknek River were estimated from surveys by the author in small aircraft. Additional information (numbers of singles, pairs, flocks) came from ground (staging activities) surveys or during overflights for other purposes. Weather data were obtained from the National Oceanic and Atmospheric Administration station in King Salmon.

Aerial surveys of sampling plots in nesting areas were conducted systematically (1983-85) or randomly (1986-87) in late May or June and again in July or early August. Surveys were conducted at intervals of 3-24 calendar days and included replicate counts of several plots. The total number of days that surveys were conducted on plots ranged from 2 to 11 a month. Data on pairs, singles and flocks were also gathered during routine flights (point-to-point or meandering) in 1985-87 with methods described by King (1973) and Lensink (1973). The number of routine flights also ranged from 2 to 11 a month.

Aerial surveys in 1983 and 1984 were confined to the region between the Naknek River and Port Moller. In 1985 this area was surveyed in addition to the area between the Naknek and Kvichak rivers, establishing a study area covering an estimated 18 000 km² of potential swan habitat. In 1986 and 1987, plots between the Kvichak and Meshik rivers were surveyed. In 1983, 1984 and 1987, reconnaissance surveys of Pacific bays were also conducted. The proportion of the study area surveyed sequentially in June and July of each year was estimated at: 54 and 25% (1983); 87 and 57% (1984); 62 and 28% (1985); 18 and 13% (1986); and 7% during both surveys in 1987. The systematic coverage of relatively large areas by survey crews in 1983-85 and random coverage of smaller areas in 1986 and 1987 ensured that all potential habitats of swans were adequately represented each year.

Each survey was flown along predetermined transects at an altitude of 150 m above ground level in a Cessna 180 with pilot and two observers or a Piper PA-18 Supercub with pilot and one observer. Indicated air speed was 175-210 km·h⁻¹ in the Cessna

and 160-180 km·h⁻¹ in the Piper. Observations to the front and 0.8 km each side of the aircraft were recorded directly onto 1:63 360 scale topographic maps. In some instances, broods or flocks were circled to enable accurate counts. Efficiency of observers in seeing swans along transects was unknown from 1983 to 1985 and 1987.

Flights were conducted to estimate numbers of swans missed in randomly selected 35 km² subplots within the same randomly selected plots for the scheduled survey in 1986. Each replicate was flown either immediately before or after (random selection) the regular survey over the same area. These were also flown along transects at a reduced ground speed and half the survey altitude and viewing distance as used in the scheduled survey. Swans were not disturbed by the lower passes and closure was assumed. This sampling effort was optimally allocated, with more plots surveyed in higher density plots and fewer in lower density plots.

Since single swans were considered only half of a breeding pair, and few singles were alone on territories, counts of breeding pairs of swans included total pairs plus half the total singles (Lensink, 1973; Dau, 1981). Although some two-year-old prebreeders establish territories but do not attempt to nest (T.W. Barry in Palmer, 1976; Scott, 1977), they could not be distinguished from adult pairs. The proportion of pairs with young included total nests and broods divided by the number of pairs of potential breeders (Lensink, 1973; Dau, 1981). These data were then pooled for each month. Swans in flocks were primarily nonbreeders, but some may have included unsuccessful breeders. Earliest hatching and laying dates were estimated from ages of the first observed broods. The peak of hatching was assumed to have occurred seven or more days later, based on observations of tundra swans on the southern Alaska Peninsula (J.E. Sarvis, unpubl. data). Brood sizes from Bristol Bay obtained in August 1969 using meandering searches are included.

The study area was stratified (three strata) based on the number of observed potential breeders km⁻² tallied inside 186 quadrants representing 1:63 360 maps divided into equal quarters. The area of potential swan habitat within each quadrant was estimated using a dot grid or planimeter, and each served as a sampling unit of unequal size. Potential habitats of swans included all wetland and adjacent terrestrial lowland and upland areas generally below 150 m elevation.

Estimates of populations of breeders in 1986 and flocked swans in all years were calculated using the ratio method for sampling units of unequal size without replacement for each stratum (Caughley, 1977). The strata estimates were then pooled to provide an overall number of breeding swans present. Sightability correction factors and expanded (corrected) estimates of potential breeders in 1986 were calculated from formulas provided by Gasaway et al. (1986). Thus, data on densities and abundance of the breeding population are corrected for sightability error.

RESULTS

Distribution and Abundance

Phenology and staging: Portions of the Naknek River were free of ice in March and snow cover on the lowlands was sparse in most years. The spring of 1985 was exceptionally late, with extensive snow cover lingering into early May in the central and southern study area. Temperatures in spring 1986 were also below normal. Other years were average or early.

Swans were among the earliest waterfowl to arrive and were first observed on or near the Naknek River between 14 and 29 March ($\bar{x} = 19$ March). By mid-April, hundreds of swans staged on the river; their distribution varied with the level of the tide, which affected feeding activity. Swans fed on pond weed (Potamogeton filiformis and P. praelongus) along shorelines and mud flats. By 20-24 April, 1965-2903 ($\bar{x} = 2567 \pm 209 \text{ SE}$) swans staged on the river at the peak of abundance. Swans arriving at that time nested almost immediately. In the late year (1985) however, more than 2500 swans remained on the river until at least 7 May, due to a later break-up of ponds. Nest initiation varied ten days between an early (1983) and late spring. The earliest hatching dates ranged from 3 to 13 June $(\bar{x} = 8 \text{ June})$, 40-50 days after the general peak of arrival. Between 300 and 600 nonbreeding swans remained near the Naknek River between late May and late June, but as human presence increased, the flock dispersed to undisturbed areas.

Potential breeders: Breeding swans were recorded in virtually all wetland habitats below 100 m elevation. One pair was seen at 183 m elevation. Most ponds above 100 m were lacustrine habitats with dominant limnetic zones, lacking islands and adequate emergent and shoreline vegetation necessary for feeding, nesting and cover. Swans were recorded in a few small areas of suitable habitat along the Pacific coast.

Generally, densities of swans in sampling plots were stable between and within years. The highest densities (0.3-0.9 swans·km⁻²) occurred primarily along the Bristol Bay coast and in broad drainage basins between the Naknek and Meshik rivers (Fig. 1), areas of little relief, wet meadow and an abundance of shallow lakes with littoral emergent vegetation. In 1986, the overall density of the nesting population varied between 0.22 and 0.26 swans·km⁻².

In 1986, sightability correction factors were determined and refined estimates of the breeding population were calculated (Table 1). The number of potential breeders observed was 31% (June) to 41% (July) higher in subplots that were resurveyed for sightability error. When this difference was adjusted for a bias associated with the small sample of subplots used to estimate the correction factor (Gasaway et al., 1986), the error was 38 and 54% in June and July respectively. Thus, estimates of the potential breeding population ranged between 2000 and 2300 pairs, with no significant changes occurring between 1983 and 1987.

Flocks: The largest flocks (i.e., 20-180 individuals) occurred in areas of high breeding pair densities, and none was recorded above 100 m elevation or along the Pacific coast. Mean densities of swans in flocks on plots ranged from 0.02 to 0.15 swans·km⁻². Flocks were largest in June ($\bar{x} = 15-22$ individuals), prior to molting, and in September and October, before migration ($\bar{x} = 15-24$ individuals). The largest flock seen on the tundra was estimated at 460 individuals (October 1986). In July and August average flock size was 5-11

TABLE 1. Observed sightability correction factors (SCF₀) and estimates of the potential breeding population of tundra swans on the northern Alaska Peninsula, 1986

Month	Sample plots (N)	Uncorrected estimate (± %SE)	SCF ₀ ± SE	Expanded estimate (± %SE)
June	25	2875 ± 8.9	1.38 ± 0.02	3954 ± 10.4
July	15	3016 ± 11.0	1.54 ± 0.17	4653 ± 15.8

swans, but over the summer flocks of 3-6 swans were most common. Flocks of >100 swans were recorded in all months except April and May, except for those staging on the Naknek River. Estimates of total swans in flocks ranged from $776 \pm 44\%$ SE (1986) to $1940 \pm 23\%$ (1985) in June, to $1515 \pm 40\%$ (1986) to $1844 \pm 16\%$ (1985) in July.

Population Structure and Productivity

The proportion of potential breeders observed in early spring varied (Table 2) in relation to ice conditions on ponds. In summer, fidelity of family groups and nonbreeding pairs provided a stable range of estimates from year to year (Table 2), and 31-40% of the pairs observed were with nests or young (Table 3). Accordingly, estimates of the proportion of productive swans ranged from 17 to 26%. Lone pairs were fewer in fall, as swans began joining into flocks before migration (Table 2).

The modal brood size in summer was 3 young, but ranged from 1 to 7. The number of young per brood was difficult to determine in June, when cygnets were small, but accurate data were obtained in 1987, when greater care was taken (Table 4). The smallest average brood sizes in July occurred in 1985 and 1987, years when temperatures were below normal during the hatch. However, broods in August 1985 were unexpectedly

TABLE 2. Adult and subadult swans (%) recorded as singles or pairs on the northern Alaska Peninsula

	Apr	May	June	July	Aug		Sept	Oct
1983			61	62		(61)		
1984			68¹	62^{2}	67^{3}	$(66)^4$		
1985			62^{1}	61		(62)		
1986	24^{3}	66^{3}	56^{2}	66	57^{3}	(58)	41^{3}	5 ²
1987	65^{3}	88^{3}	55^{3}	50	50^{3}	(51)	24^{3}	15^{3}

Samples larger than 3000 swans.

TABLE 3. Pairs (%) of tundra swans with nest or young on the northern Alaska Peninsula

	June	July	Aug	11121111111	Sept	Oct
1984	35	441	31	$(39)^2$		
1985	48	36	55^{3}	(40)		
1986	34	28	44 ³	(31)	24^{3}	57 ³
1987	37	41	25	(34)	38^{3}	34^{3}

Samples larger than 500 pairs.

TABLE 4. Brood sizes $(\overline{x} \pm SE)$ of tundra swans on the northern Alaska Peninsula

	June	July	Aug	Sept	Oct
1984		3.4 ± 0.1^{1}	3.2 ± 0.2		
1985		3.0 ± 0.1^{1}	3.3 ± 0.5^2		2.5 ± 0.3^{2}
1986		3.6 ± 0.1	2.7 ± 0.3^{2}	2.8 ± 0.3^{2}	
1987	3.3 ± 0.4^2	3.0 ± 0.1^{1}	3.1 ± 0.3	2.9 ± 0.3	3.1 ± 0.7^2

Samples larger than 100 broods.

²Samples larger than 2000.

³Samples of less than 1000.

⁴Weighted mean combining June, July and August in parentheses.

²Weighted mean combining June, July and August in parentheses.

³Samples less than 100.

²Samples less than 25.

larger than in July (Table 4). In August 1969, broods tallied in Bristol Bay by W.J.L. Sladen averaged 3.6 ± 0.1 (n = 157; C.J. Lensink, unpubl. data) young in an early year. Based on observations in sampling plots, young constituted 24-28% of the population in July.

Surveys in 1987 revealed that 18% of the broods recorded along transects were of unknown size. This value provides a crude estimate of the proportion of broods seen on plots that may have been inaccurately tallied, especially in 1984 and 1985 when sizes of some broods may have been imperfectly estimated.

DISCUSSION

Phenology of tundra swans in Bristol Bay is the earliest reported of the major tundra swan populations (Wilk, 1987). Major movement of swans to the Naknek River area clearly preceded reported first arrivals of swans to nesting areas of the Yukon Delta by at least two weeks ($\bar{x} = 27$ April at Bethel $[n = 5 \text{ yr}]; \overline{x} = 5 \text{ May at Old Chevak } [n = 10 \text{ yr}];$ Lensink, unpubl. data), and four weeks or more in the Arctic (first week of May at Selawik NWR [Kotzebue], Alaska [M.A. Spindler, pers. comm. 1988]); after mid-May in arctic Canada and Alaska (McLaren and McLaren, 1984; Hawkins, 1986a; U.S. Fish and Wildlife Service, 1986). Similarly, first hatching dates were earliest in Bristol Bay and later in subarctic (20 June-6 July; Lensink, 1973) and arctic Alaska (late June to early July; A.W. Brackney, Arctic NWR, and M.A. Spindler, Selawik, NWR, pers. comm. 1988) and arctic Canada (early July; McLaren and McLaren, 1984).

Densities of potential breeders on the NAP were comparable to those reported for some populations in other parts of Alaska (0.45-0.64 swans·km⁻², Arctic NWR, 1981-85 [Platte and Brackney, 1986]; 0.22-0.34 swans·km⁻², Kotzebue Sound, 1983-87 [B. Conant, unpubl. data]; 0.47-0.60 swans·km⁻², Yukon Delta [inland], 1983-87 [Conant]) but lower than those from the Yukon Delta coast (3.70 swans·km⁻², 1986 [Lensink, unpubl. data]) and arctic Canada (1.35-2.52 swans·km⁻² [known breeders only], Mackenzie Delta, 1983-86 [T.W. Barry, unpubl. data]; 0.85 swans·km⁻², Keewatin, N.W.T., 1975-76 [McLaren and McLaren, 1984]).

The relatively larger flocks observed along the lowland coast and major rivers of the NAP in June constituted a significant proportion of the population of nonbreeders but were smaller than the aggregations of 1800-4000 reported on the vast Mackenzie and Yukon deltas (Palmer, 1976; Lensink, pers. comm. 1986), where summering populations range from 20 000 to 40 000 swans (Bellrose, 1980). On Selawik NWR, Spindler (pers. comm. 1988) observed that flocks of >10 swans in spring were rare.

A late spring in Bristol Bay did not have a significant effect on the nesting distribution or proportion of pairs with young, although on the Yukon Delta and in the Canadian Arctic the proportion of pairs that nested was reduced (Lensink, 1973; Dau, 1981; McLaren and McLaren, 1984). The proportions of potential breeders (range = 40-60%, n = 9 yr; Lensink, 1973), pairs with nests or broods ($\bar{x} = 34\%$, range = 13-51%, n = 17 yr; Lensink, 1973; Dau, 1981) and productive swans (9-25%; Lensink, 1973) on the Yukon Delta and Bristol Bay ($\bar{x} = 36\%$) appear to be similar but less variable in Bristol Bay (Tables 2 and 3).

Geographic variability, however, may influence the timing of nesting in Bristol Bay, as local phenology varies within the study area. Marginal nesting conditions over portions of the study area in the late spring may have caused some swans to delay nesting. As a consequence, a less synchronous hatch might have occurred. Data from the southern peninsula verified that no peak hatch of swans occurred on the Alaska Peninsula in the late season (J.E. Sarvis, unpubl. data). The larger-than-expected mean brood size in August 1985 may be explained in part by an asynchronous hatch (Table 4).

Brood sizes in August in Bristol Bay averaged larger than those on the Yukon Delta (1.7-3.6, n = 17 yr; Lensink, 1973; Dau, 1981), Selawik NWR (2.7-3.1, n = 3 yr [includes early Sept]; M.A. Spindler, unpubl. data), the Alaska Arctic Slope (Arctic NWR; 2.2-2.7, n = 4 yr; Platte and Brackney, 1986), and arctic Canada (1.6-2.5, n = 2 yr; McLaren and McLaren, 1984). Indeed, in all areas average size of broods appears to be correlated with the time of nesting. Thus clutch and broods are largest in Bristol Bay and smallest in the Alaskan and Canadian Arctic (assuming that relative brood size is an indicator of and varies directly with clutch size [Lensink, 1973:22; Haapanen et al., 1973:35]).

Brown bears (*Ursus arctos*) may be an important predator affecting productivity of swans on the Alaska Peninsula (J.E. Sarvis, unpubl. data). Gray wolves (Canis lupus), wolverines (Gulo gulo), gulls (Larus glaucescens and L. canus) and jaegers (Stercorarius parasiticus and S. longicaudus) also may be important (pers. obs.). In arctic Alaska, arctic foxes (Alopex lagopus) were the most important predators of swans on the Colville River delta (Hawkins, 1986b). Presently, man probably has little impact on swans on the NAP. Subsistence harvest is small (Fall and Morris, 1987), as the area is sparsely populated and more ducks and geese are taken as they stage in larger numbers than swans during migration. The greatest threat to this swan population by man may be disturbance during spring staging on the Naknek River by recreational and commercial fishing boats and aircraft using a nearby airport. Further, developments along the river such as construction of motels and housing tend to displace the birds from their traditional feeding areas.

There were problems with the basic survey procedure adopted in this study. First, the number of potential breeders observed in 1986 (and most likely all years) was higher in subplots of moderate to high swan densities (i.e., ≥0.1 swans·km⁻²) that were resurveyed (from a lower altitude and viewing distance) for sightability error (Table 1). This error could be alleviated in future surveys by flying smaller plots (≤25 km²) using meandering searches or more closely spaced transects (≤ 0.8 km apart). Second, an unknown number of brood sizes in 1984 and 1985 may have been underestimated. In August 1984, brood sizes observed on the north side of Bristol Bay averaged 2.8 ± 0.3 cygnets (n = 15) and 2.6 ± 0.3 (n = 15) and 3.2 ± 0.4 (n = 18) in July and August 1987 respectively (Togiak NWR, unpubl. data). These means were the same as or smaller than those reported in this study (Table 4), suggesting a negligible error, if any, in the data.

In conclusion, the annual variation in the population and production of tundra swans on the NAP and Bristol Bay may be less affected by weather than populations at higher latitudes. Even in late springs, swans clearly have a seasonal advantage over their northern conspecifics. Indeed, a later season may not significantly change the number of swans that nest or significantly alter the proportion of swans observed with young, and it favors the survival of young where the length of season does not limit their development before migration. However, a late season did affect the timing of nesting. Overall, production of

broods appears to be most stable in Bristol Bay and least stable in arctic nesting areas.

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