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Population structure and productivity of Whistling Swans on the Yukon Delta, Alaska

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Whistling Swans *Cygnus c. columbianus* are the most conspicuous of wildfowl of the Yukon-Kuskokwim Delta, the principal nesting grounds for swans wintering in western states. They are readily visible from low flying aircraft, and local pilots or their passengers frequently remark on their abundance, the occurrence of large flocks, or even of numbers of young in broods, or of eggs in nests.

The occurrence of a large population, and the ease with which swans are viewed from the air, permits detailed observations of many individuals with relatively small effort or cost. Because the various factors which may affect the welfare of Whistling Swans may affect other species similarly, much information on swans should be of significant value in understanding the ecology of species that are more difficult to study.

Methods

Most observations were obtained during routine flights over the Delta for several purposes, including hauling of freight and passengers from point to point, as well as systematic aerial census of wildfowl populations. Flights intended primarily for observing swans include only those conducted for censusing random plots in 1968 and 1971, and occasional flights in late fall to ensure adequate sampling of broods just prior to their migration. The observation and recording techniques used are described by King (1973).

Results are summarized for intervals of 10 days to provide reasonable sample sizes and still permit detection of changes in the structure of population units that may occur over the summer. The basic data are deposited in tabular form at the Wildfowl Trust, Slimbridge, being too extensive to publish with the present paper. The consistency of recording observations and the proportion of swans tallied in the flight path varied with the purpose and altitude of the flight, weather conditions, motivation and ability of observers and many other factors. Consistency has much improved in recent years of the study, as compared to years prior to 1967.

Results

Distribution and behaviour

First swans appear on the Yukon Delta in late April and most have arrived by mid-May. Pairs are soon dispersed widely across the tundra in all suitable habitats, with densities higher in areas near the coast between Nelson Island and Cape Romanzof, an area which, incidentally, is the most productive for several species of geese and ducks as well as swans. Non-territorial swans, presumably mostly subadults, gather in large flocks along coastal estuaries or occasionally on large inland lakes.

Nesting begins almost immediately in normal years, although late springs may delay nesting by 10 days or more. Hatching has begun as early as 20 June, or as late as 6 July—but, in either event, coincides with early growth of green vegetation and maximum activity of insects and other invertebrates.

During nesting incubation, paired swans are frequently separated from their mates and many enter our tally as singles. At hatching, the population structure changes abruptly—members of pairs are less commonly separated and the large non-breeding flocks break up into smaller flocks that begin dispersing over the Delta as they enter the moult.

Although we have not studied individual broods throughout the season, numerous observations suggest that many may remain with their parents near the nesting site (100–400 m) until fledging.

Nonbreeders remain in small flocks of three to fifteen individuals, but as flight is regained in late August they begin congregating in larger premigrant flocks along the coasts or in favourable foraging areas on large inland lakes. Pairs remain scattered until early September when those without broods join the larger flocks, causing a distortion in the apparent proportion of pairs with broods. By late September most swans have left the Delta but some, particularly those with late broods, may remain until freeze-up in October. The number which linger is clearly the direct result of spring conditions—a late spring retarding all events throughout the summer.

Table 1. Survival of cygnets as indicated by changes in size of broods expressed as percentage of the average clutch size for year

	Clutches		Survival (%)					
Year	No.	Average	June	July	Aug.	Sept.	Oct.	Winter
1963	47	4·32	–	(78·6)	(66·1)	66·4	59·1	–
1964	52	3·30	–	(78·5)	(72·1)	–	–	57·0
1965	44	4·34	–	(44·7)	(75·3)	61·5*	–	50·2
1966	21	4·14	–	(73·2)	(57·2)	60·6*	58·9	50·5
1967	42	4·95	(73·3)	(83·2)	60·2	61·4*	58·8	50·5
1968	59	4·80	(85·0)	77·3	75·8*	75·6*	–	53·5
1969	33	4·67	–	75·4	75·8*	75·1*	–	58·0
1970	20	4·45	–	(77·1)	77·5	75·0*	–	53·0
1971	36	3·34	–	(79·6)	78·1*	75·4*	86·5	–

Samples of less than fifty broods are bracketed; *, those with more than 200. The winter observations, in California and Utah during December or January, are summarized in various reports by J. J. Lynch.

Size of clutches and broods

Sizes of clutches have varied from an average of 3·30 in 1964 to 4·95 in 1967 (Table 1). Modal size of clutches has varied from three to five. Average size of broods varies directly with size of clutches. Broods observed in the month following the hatch average only 75% of average clutch size. During the remainder of the summer, attrition to broods is relatively small, and at migration, broods still average between 60 and 75% of clutch size. Both the initial loss of cygnets and attrition to broods during the summer appear to be independent of clutch size.

A second sharp reduction in brood size is indicated by censuses of family groups in California and Utah, where broods observed in December average only a little more than 50% of clutch size (Lynch, 1972). Again, losses appear to be independent of original clutch or brood size.

Number of productive swans

When nesting is completed in late May or early June, the percentage of pairs observed with nests or broods becomes stable and remains relatively constant through August, suggesting that few pairs lose entire clutches or broods (Table 2). An apparent increase in the percentage of pairs with broods in September results from desertion of territories by idle pairs. The numbers of pairs with nests may vary considerably from year to year, and in the 9 years of our study, swans with broods in August ranged from 15·1 to 47·8% and averaged 31·4% of estimated total pairs.

Estimates of the proportion of productive swans in the population are somewhat more tenuous than our analysis of productive pairs, because of the difficulty in sampling the nonbreeding flocks which are not randomly distributed. During July and August, however, when flocks are smaller

Table 2. Percent of pairs with nest or brood

Year	May	June	July	Aug.	Sept.	Oct.
1963	–	–	35·4	(16·1)	52·1	(64·5)
1964	–	29·4	–	15·1	–	–
1965	–	(53·3)	(34·0)	36·6	(62·0)	–
1966	–	(25·4)	(39·5)	34·1	44·7	(60·0)
1967	16·8	47·0	(48·1)	30·1	46·3	(18·3)
1968	(19·5)	50·7	55·9	47·8	61·1	–
1969	(39·2)	48·3	51·6	45·4	71·7	–
1970	(25·4)	36·1	36·2	38·6	65·2	–
1971	–	27·9	24·3	19·2	23·5	(38·4)

Samples of less than 100 pairs are bracketed.

Table 3. Percent of adult or subadult swans identified as singles or pairs

Year	May	June	July	Aug.	Sept.	Oct.
1963	–	–	(57·2)	(22·1)	13·7*	(24·2)
1964	–	(85·6)	–	64·7	–	–
1965	–	(29·8)	(94·0)	(61·6)	(41·0)	–
1966	–	(59·5)	–	(25·8)	44·7	–
1967	(24·2)	56·3	–	(94·6)	49·4	–
1968	(23·9)	61·1	47·1	43·8*	39·2**	–
1969	(25·5)	50·8*	41·7*	52·6*	8·9**	–
1970	12·1	37·4**	62·6	(39·5)	16·2**	–
1971	–	39·1**	44·0	55·2*	44·4*	(13·2)

Samples of less than 1,000 swans are bracketed; *, those larger than 2,000; **, larger than 3,000.

and more dispersed than in other months, our samples seem adequately large, and between 40 and 60% of swans appear to be paired and on territories (Table 3). Occasional pairs are observed in nonbreeding flocks, but these are not considered as potential breeders. Although they may be adult swans, the companion birds may be together by chance, or they may be siblings, as most nonbreeders must be of yearling or other sub-adult age classes.

The proportion of swans occurring in flocks appears relatively stable and does not seem much affected by changes in the number of nesting pairs. We suspect that variation in productivity during preceding years changes the relative sizes of sub-adult age classes.

If we assume that approximately 50% of swans are paired and on territories, estimates of the proportion of productive adults range from about 9% of the total population in 1964 to 25% in 1968. This difference is proportionately much larger than differences in clutch size, hence it is a primary factor in determining annual productivity. As both clutch size and number of productive swans normally vary in the same direction, changes in productivity are larger than either. Thus, estimated production in 1964 was only 0·15 eggs per adult, but in 1968 was 0·62 eggs per adult.

Discussion

Climatic conditions in spring are invariably the most important of factors which affect the productivity of swans. Predators, disease, hunting, or other obvious factors do not cause significant annual variation in production. Hunting may have a controlling influence on the population if Klein's (1966) estimate of an illegal harvest of 5,000 swans on the Delta is correct. A late breakup of ice on rivers and ponds or lakes, caused by low temperatures in April or May, results in a reduction in both the size of clutches and the proportion of swans that nest (Table 4). Differences in survival of cygnets during the summer are comparatively small and seem also to be affected partly by spring conditions, as well as weather during summer months. However, our data is confusing and at present no

Table 4. Comparison of climatic factors and productivity

Year	Ice breakup		Mean temp. (°F at Bethel)				Average clutch	Pairs with broods (%)	Survival	
	Bethel	Chevak	April	May	June	July			Sept.	Winter
1963	5/19	–	19·4	40·6	47·1	54·2	4·32	33·7	66.4	–
1964	6/3	6/16	19·5	31·0	52·5	56·6	3·30	18·3*	72·1	5·0
1965	5/19	6/15	26·5	32·6	48·6	51·6	4·34	39·5	61·5	50·2
1966	5/23	6/15	23·0	33·2	51·8	53·2	4·14	31·5	60·6	50·5
1967	5/11	6/2	30·9	42·5	54·0	53·6	4·95	42·4*	61·4	50·5
1968	5/14	6/5	23·1	41·6	52·3	57·9	4·80	50·9**	75·6	53·5
1969	5/11	5/30	27·1	45·5	52·4	53·7	4·67	48·2**	75·1	58·0
1970	5/14	6/3	22·3	43·3	51·9	51·6	4·45	36·5**	75·0	53·0
1971	5/27	6/15	17·0	35·2	50·0	52·8	3·34	23·4**	75·4	–
Norm.	5/14	?	25·5	40·3	52·1	54·6				

The percentage of pairs with broods is derived from all observations June through August. *, Sample exceeding 500 pairs; **, and exceeding 1,000. Survival is calculated as percentage of average clutch size for year.

conclusion can be drawn. With the exception of 1964, a year when the reliability of our data is doubtful, survival of cygnets during migration was highest in years with early springs. Examination of many cygnets indicates that a few may not be fledged and others are only just fledging at the normal time for migration to begin. At this point in the cygnets' growth they are without fat reserves and muscle development is poor, and it is apparent that many cygnets are unable to survive the excessive demands of long, migration flights. It seems surprising that so many can.

The low productivity and the hazards to survival of cygnets on the Yukon Delta in years with late springs, suggests that swans nesting in more northern areas of Alaska, where shorter seasons are characteristic, are occupying habitat that is marginal for their survival. The relatively large population of swans on the Yukon Delta as compared to these areas (King, 1970), may be due entirely to the difference in length of the summer season.

Comparative data is limited to observations by Sladen (personal communication) in Bristol Bay in August 1969 and on the Arctic Slope in 1971. Swans from Bristol Bay are part of the western population while those from the Arctic Slope migrate to the Atlantic coast (Sladen 1973). In these years spring conditions in Bristol Bay were about normal and comparable to the Yukon Delta, but on the Arctic Slope they were unusually mild, although later than would be normal for the Yukon Delta. In Bristol Bay 31·4% of 156 pairs had broods averaging 3·57 cygnets. On the Arctic Slope 34·5% of 101·5 pairs had broods averaging 2·51 cygnets. Bristol Bay data was well within the normal range for that from the Yukon Delta. Although the season on the Arctic Slope was mild, the percentage of productive pairs were about normal for the Yukon Delta, and average brood size was similar to that observed there in late years.

Productivity appraisals reported by Lynch (1972) for the swans wintering on the Atlantic coast indicate consistently poorer nesting success than western swans, averaging only 11·8% cygnets in wintering populations as compared to 20·6% cygnets for western swans. The number of cygnets in family groups also differs, averaging 2·02 for the Atlantic population and 2·33 for the western. These data confirm our observation on the Delta that the length of the summer season is critical to production among Whistling Swans.

Weather conditions of early spring affect productivity of other wildfowl in Alaska as well as that of Whistling Swans. The deleterious effect of late springs was conclusively demonstrated for ducks of several species during my studies on the Yukon Flats between 1961 and 1964, but on the Yukon Delta our data for most species is too meagre to permit adequate comparison with that of swans. Studies now in progress should meet the necessary data requirements if continued for a sufficient period.

Because of the dominating effect of spring conditions, we can predict production by swans with reasonable accuracy before the first egg is laid. Subsequent observations during the summer essentially confirm and increase the accuracy of earlier predictions. We are satisfied that we can also predict trends in productivity for other species, but cannot at present estimate accurately the magnitude of change that may occur—even after the fact.

Productivity of geese on the Yukon Delta (Black Brant *Branta bernicla orientalis*, Cackling Geese *Branta canadensis minima*, Emperor Geese *Anser canagicus* and White-fronted Geese *Anser albifrons frontalis*) appears generally to be much more stable than that of swans. Perhaps adaptation of these species to changing conditions may not have to be nearly as great as for swans which require a significantly longer period of time between nesting and fledging of young. Among ducks, productivity of late nesting species such as Scaup *Aythya marila* and *A. affinis* seem less affected by late springs than that of earlier nesting dabbling ducks, particularly Mallard *Anas platyrhynchos* and Pintail *Anas acuta*, our earliest migrants and nesters.

Maximum changes in productivity that we have noted for any species occurs among Snow Geese *Anser caerulescens*, which we can observe only during their migration. Bands that we have recovered indicate that the population passing through the Delta nests primarily on Wrangel Island in the Soviet Arctic, and its productivity as indicated by percentage of immatures in the population has ranged from near 0 to 54%. As Wrangel Island has a much shorter season than the Yukon Delta, productivity of Snow Geese there may be analogous to that of swans in northern Alaska.

Acknowledgments

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1963. In addition, King (1973) has contributed observations made during annual surveys of breeding populations on the Delta and elsewhere in Alaska. All members of the refuge staff, particularly Jerry Hout, and several visitors to the Wildlife Range have participated as observers.

Summary

Observations of Whistling Swans from low flying aircraft on the Yukon Delta, Alaska, provide records which permit analysis of annual variations in productivity. Climatic conditions of early spring are the most important factor affecting production, a late spring resulting in a reduced number of nests and reduced clutch size. The percentage of territorial pairs with broods has varied from about 15 to 50%. The average number of cygnets in broods at time of fledging has varied from 2·52 to 3·63.

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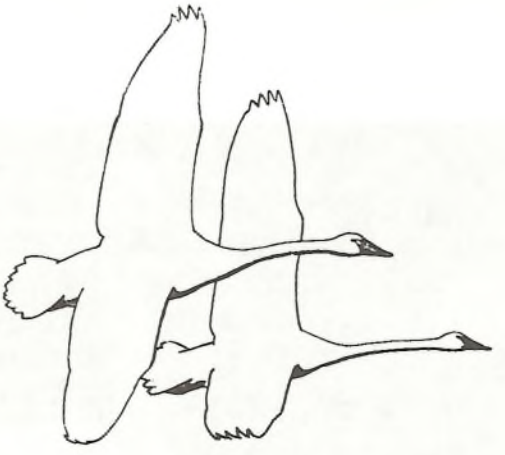

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Plate I. Above: Trumpeter Swans *Cygnus c. buccinator* and (below) Whooper Swans *Cygnus c. cygnus* were breeding freely at Slimbridge in 1972.

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