Demography of Eastern Population Tundra Swans *Cygnus columbianus columbianus*

JONATHAN BART, ROLAND LIMPERT,
SUSAN EARNST, WILLIAM SLADEN,
JAMES HINES and THOMAS ROTHE

We present rates of productivity and survivorship during the first year of life for Eastern Population Tundra Swans based on several extensive data sets. Our main objective is to illustrate how such data can be used to construct a life table for populations that are inaccessible except by aerial survey on the breeding grounds or that migrate long distances and disperse over wide areas, and thus that are difficult to study via intensive long-term investigations. Our data were obtained from the northwestern third of the breeding range of Eastern Population Tundra Swans and throughout their wintering range during 1967-1989. An average of 77% of the sampled birds apparently held territories in the spring, 34% of them nested successfully, and the number of young per successful nest was 2.46. Survivorship during the first migration averaged 52% and during the first winter averaged 76%. We identify the additional information needed to construct a life table from these estimates and discuss problems encountered in using extensive survey data for these purposes.

Tundra Swans *Cygnus columbianus columbianus* breed throughout northern Canada and on the north and west coasts of Alaska (Fig. 1). Two populations are distinguished. The Eastern Population (EP) breeds north and east of Point Hope in Alaska (Limpert *et al.* 1991) and winters on the east coast of North America, mainly in Maryland and North Carolina. The Western Population (WP) breeds in western Alaska from Point Hope south to the Alaska Peninsula, and winters in the western United States, mainly in California.

We report on the demography of EP Tundra Swans on the breeding grounds and during their first year of life. Our general objective was to take the first steps towards constructing a life table for Tundra Swans. Specifically, we estimated production of young a few weeks after hatch and survival of young during their first migration and winter. We distinguished three components of productivity on the breeding grounds: probability of gaining a territory, proportion of territory holders that nested successfully (raised at least one cygnet to one month post hatch), and average number of young per successful nest. The product of these three factors is identically equal to the number of young per adult-plumaged bird present in the spring. We first present the estimates and then explain (see Discussion) how they can be used to construct the life table. Subsequent papers will provide the additional information re-

quired and present the life table and an assessment of its accuracy.

Methods

Data were obtained from long-term studies on the breeding and wintering grounds (Fig. 1). On the
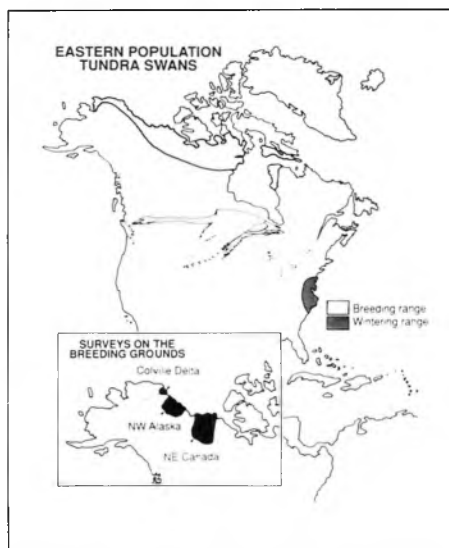

Fig. 1. Range of the Tundra Swan and location of study sites.

Table 1. Survey results from the breeding grounds of EP Tundra Swans.

	Study area			
	Colville Delta		NE Alaska	NW Canada
Average number of	1970-77[a]	1983-89[b]	1983-89[b]	1972-88[c]
Adults in spring	115	221	411	155
Territorial adults	—	167	335	111
Adults with young	32	52	117	—
Young	41	61	144	—

[a]one survey after hatch; number of adults after hatch assumed equal to number in early spring. [b]surveys during and one month after incubation. [c]surveys during incubation only. [d]birds in singles and pairs assumed to be territorial; birds in flocks assumed to be non-territorial.

breeding grounds, data were collected during aerial surveys in three locations: the Colville River Delta on the North Slope of Alaska, northeast Alaska from Prudhoe Bay to Canada within several km of the coast, and northwest Canada south and east of the Mackenzie River delta (primarily from US Fish and Wildlife Service Breeding Pair Survey stratum 14). Surveys were made in mid-June during incubation, in mid-August when the young were about 35-40 days old, or, in some years, at both times. Information on sample sizes and years of study is contained in Table 1. We assumed that birds recorded as singles or pairs held territories and that birds in flocks did not. Our field work on the Colville Delta during the past seven years indicates that this assumption is reasonably accurate, though we acknowledge that some pairs do not hold territories.

Survivorship during the first winter was determined from counts in which observers reported the number of adults and young in flocks widely distributed across the wintering ground throughout the period 1967-1988. During this period, 1,401 flocks containing 206,330 swans were surveyed. Survivorship during migration was determined primarily by comparing the ratio, number of young/number of adults, at the end of the breeding season and at the start of the wintering period (defined as December 15 to March 15). Additional information about mortality during migration was obtained from counts of flocks in North Dakota in 1969.

We expressed production as young per adult-plumaged bird (e.g. birds more than one year old at the time of the survey) in this paper. In a future report we will estimate age at first breeding and survivorship to that age, and we will use these estimates to convert the present results to young per breeding age adult. Although we occasionally refer to "adults" in this paper, we always mean adult-plumaged birds and are thus including some birds two years old. We did not correct any of the survival rates (obtained from young:adult counts) for mortality of adults. An-

nual adult mortality appears to be approximately 5% (Bart *et al.* in prep.), so this correction would have made very little difference in the estimated survival rates of young, and the correction would have been difficult to make because we do not know when during the year the adults die.

Rates were compared using t tests or Fisher's exact test. In calculating standard errors, we treated annual means as the primary units in a multiple-stage sample (Cochran 1977). Thus, the standard error was calculated using the customary formula for simple random sampling with annual means as the observations.

Results

Success on the breeding grounds

Approximately three-quarters of the adult-plumaged birds gained a territory, one-third of these produced at least one cygnet, and the average number of cygnets per successful adult (not pair) was 1.23 (Table 2). The number of young produced per adult-plumaged bird in spring was 0.33. There was little variation between the three study areas in the long-term averages for any of these factors.

Substantial year-to-year variability occurred in each of the factors we investigated (Table 2). In each study area, the coefficients of variation (SD/mean) were smallest for young per successful adult and probability of gaining a territory and greatest for proportion of birds nesting successfully and overall productivity (young per adult in spring).

Migration and first winter

The ratio, number of young/number of adults, fell from 0.33 on the breeding grounds in mid-August to 0.17 in mid-December, suggesting a 52% survivorship of young during their first migration (Table 3). The period

Table 2. Factors influencing production of young EP Tundra Swans. Coefficients of variation[a] for each rate are shown in parentheses.

Study area	Year	P(gaining a territory)	P(raising 1+ young to 1 month	No. young/ successful adult	No. young/ adult in sping
Colville	1970-77	—	—	1.28 (unk.)	0.36 (0.34)
	1983-89	0.78 (0.15)	0.32 (0.39)	1.13 (0.10)	0.29 (0.49)
NE Alaska	1983-89	0.82 (0.13)	0.35 (0.47)	1.23 (0.08)	0.35 (0.55)
NW Canada	1972-88	0.72 (0.23)	—	—	—
Averages	(and ave cv)	0.77 (0.18)	0.34 (0.43)	1.21 (0.09)	0.33 (0.46)

[a]standard deviation of the estimate divided by the estimate.

here referred to as migration begins well before cygnets leave the breeding grounds. There is thus no way at present to know what fraction of the mortality occurs as the birds are staging for migration. Large portions of the breeding range have not been surveyed, so the young:adult ratio at the start of migration (0.33) may not be representative of the entire population. On the other hand, the similarity of all the productivity figures from surveys on the breeding grounds (Table 2) provides some reassurance that the population-wide values may not be too far from the average values obtained in this study.

Data from the single location and year surveyed during migration suggest that mortality may occur throughout migration (Table 3), but surveys from several migration stopovers in each of several years are needed before any conclusions will be possible about the timing of mortality during migration.

The young/adult ratio continued to decline throughout the first winter, falling from 0.17 to 0.13, indicating a survivorship for this period of 0.76 (Fig. 2). We found no evidence that either the young:adult ratio or the survivorship of young varied between the two principal wintering areas, Maryland and North Carolina. Sample sizes within years were too small to study annual variation in survival rates during migration or winter.

Discussion

The results of this study agree fairly closely with those from other studies of the EP of
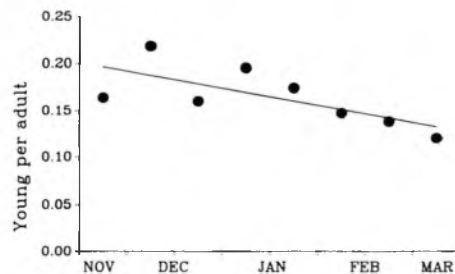

Fig. 2. Survival of young EP Tundra Swans during their first winter (Dec. 15 to Mar. 15). The young:adult ratio fell from 0.13 to 0.17 indicating a survivorship of 76%. The negative slope is just significant (p = 0.05).

Tundra Swans (Table 4). Where results can be compared, they are similar in our study and in others except for young per adult at shortly after hatch. The one other study reporting this figure had data from only one year. More information on clutch size is desirable as the two available studies (Rothe *et al.* 1982, Brackney *et al.* 1984) produced quite different estimates and were each based on a single year of data.

Similarity of estimates within years, between areas

We prepared several scatterplots to examine how similar the components of breeding success were within years between the Colville and northeast Alaska. In the plots, results from the Colville were on one axis and results from northeast Alaska were on the other axis. Each dot represented the value for a given rate (ie.

Table 3. Survival of young EP Tundra Swans during their first fall migration[a].

Stage	Young/adult start of stage	P(surviving the stage)	Sample size (no. of years)
First half of migration	0.33	0.79	11
Second half of migration	0.26	0.67	1
Start of winter period	0.17	-	16

[a]survivorship throughout migration: 0.17/0.33 = 0.52

Table 4. Tundra Swan productivity and survivorship estimates.

Stage	Eastern Population		Western Population
	This study	other studies	
Proportion of adult-plumaged birds gaining a territory	0.77	-	0.50 , 0.56
Average clutch size	-	3.5[d], 2.6[e]	4.3[b], 4.3[c]
Proportion of territorial birds that raise 1+ young to 1 month	0.34	-	0.34 , 0.35
No. young per successful adult	2.46	2.1 - 2.5	3.0[b], 2.9
Young/adult one month after hatch	0.33	0.16 (1 yr)	0.41
Young/adult at end of first migration	0.17	0.18	0.54
Young/adult at end of first winter	0.13		

[a]King (1970), [b]Lensink (1973), [c]Dau (1981), [d]Rothe *et al.* (1982), [e]Brackney *et al.* (1984), [f]McLaren & McLaren (1984), [g]Conant & Cain (1987), [h]Serie & Bartonek 1991.

proportion of birds gaining a territory) in one year.

The proportion of birds gaining a territory in the Colville Delta, and in northeast Alaska, showed a strong correlation ($r^2 = 0.92$). In contrast, the comparable correlation for the proportions of territorial birds raising at least one young was much lower ($r^2 = 0.42$), and there was virtually no relationship between young per successful adult in a given year on the Colville Delta and in northeast Alaska ($r^2 = 0.11$).

We assume that variation in the proportion of birds holding territories is due to variation in the number of birds in flocks since the number of occupied territories remains relatively constant (pers. obs.). This analysis thus suggests that variation in the proportion of birds gaining a territory may operate at a much larger geographic scale than factors affecting nesting success. This would seem reasonable - though to our knowledge the pattern has not been reported before - if nesting success is strongly affected by local conditions such as flooding and number of predators in the immediate area, whereas the abundance of flocks (and thus proportion of birds gaining a territory) is determined primarily by events occurring during the previous winter and spring migration.

Comparisons between Eastern and Western Populations

The proportion of birds recorded on territories was higher in the EP than in the WP. EP birds laid smaller clutches, but about the same fraction produced at least one young out of the nest. From these facts one would expect the number of young per successful nest and the young:adult ratio in the winter to be higher in the WP, and this was indicated by the survey results (Table 4). The young:adult ratio reported in winter for

WP birds was much higher than the ratio for EP birds.

The differences between EP and WP birds might be due to the higher latitude at which EP birds breed or to their longer migration routes. These two hypotheses could be tested by comparing Eastern and Western Population birds in western Alaska near their contact zone (Limpert *et al.*, 1991).

Use of the estimates to construct a life table

We now discuss briefly what additional information is required to construct a life table for Tundra Swans and how this information can be obtained. Two forms of a life table might be distinguished. The first is a simplistic model which assumes that all birds begin breeding at a given age and that throughout their lives, they have the same rate of fecundity and their offspring have the same probability of surviving to breeding age. Though not fully realistic, such a model would provide many useful insights about swan biology and management. It could, for example, help answer the question "How much can an adult swan afford to give up in personal survivorship to increase the survivorship of its offspring at any given stage?" Such a model could also be useful in predicting whether the population could sustain a given level of hunting pressure. Mertz (1971) and Nichols *et al.* (1980) provide additional examples of how such models can be used in solving both applied and theoretical problems.

The second type of life table would give the average number of young produced by females of each age class and the proportion of these young that survive to age of first breeding. Such a model would provide a much more detailed picture of lifetime reproductive strategies and success and would be useful in addressing many

questions in applied and theoretical behavioral ecology (e.g. Clutton-Brock 1988, Newton 1989).

Conceptually, the simplest way to construct either type of life table is to follow numerous individuals from birth to death recording all their nesting attempts and the fate (survivorship to independence) of their young. This approach has been used successfully on non-migratory swans breeding in areas accessible to researchers (e.g. Bacon and Andersen-Harild 1989). For swans that migrate a long distance, it is far more difficult to obtain comprehensive information. It has sometimes been possible to study adult survival and young:adult ratios in the winter (e.g. Scott 1988), but for many populations there is currently little information on natality or early survival of offspring and information from the migration or wintering grounds may come from only a few small areas. Thus if estimates - even first approximations - of the needed rates can be obtained from extensive surveys, they may fill a gap in our knowledge of swans that will not soon be filled in any other way.

The first type of life table could be constructed from the data in Table 4 if we knew whether all territorial birds are of breeding age (as seems plausible), whether any breeding-age birds do not hold territories, and what fraction of territorial birds attempt to nest. To take a simple case, suppose that all breeding-age birds were territorial, no birds younger than breeding age held territories, and that 80% of the territorial birds laid clutches (which averaged 3.0 eggs - see Table 4). Natality, the average number of eggs laid per breeding-age pair, would thus be $0.80 \times 3.0 = 2.4$. To estimate the survival rate from laying until two weeks after hatch, we would use the fact that out of each 100 pairs, an average of 34 nested successfully and produced 2.46 young per successful nest, so $34 \times 2.46 = 84$ young were produced (per 100 pairs). Only 80 of the 100 nested, producing 240 eggs, so the survivorship is $84/240 = 0.35$. Survivorship rates to older ages could be calculated in a similar way. Thus, it appears possible to piece together the data required to obtain a simple life table from a combination of extensive surveys backed up by occasional intensive field studies to obtain information such as detection rates on aerial surveys, proportion of territorial birds that nest, and average clutch size. Development of the second type of life table would be more complex, and would require that individually recognizable birds be present on the breeding grounds, but might proceed using essentially similar methods.

Age-specific survival rates of adult-plumaged birds are probably necessary for determining whether most territorial birds are of breeding age and most birds in flocks are younger than breeding age. If the fraction of birds estimated to be pre-breeding age is approximately equal to the fraction of birds in flocks, then a reasonable first assumption might be that most breeding age birds hold territories and few younger birds do. If true, this finding would simplify construction of the life table. The proportion of territorial birds that lay clutches may require intensive field studies, though repeated aerial surveys might also provide the needed information (but see below).

In summary, we believe that extensive surveys can be used to assemble life table data for species where following marked individuals throughout their lives is impractical or when interest centres on the entire population rather than one small segment of it. For dispersed breeders that migrate long distances, this approach seems to offer special opportunities for investigating management or theoretical issues which require demographic information.

Assessment of the survey data

This study has provided an opportunity for indepth review of the strengths and weaknesses of data collected during routine, usually government-sponsored, survey activities. We briefly review problems we have encountered. We acknowledge, however, that in most cases the surveys were designed to provide only indices to the various rates rather than estimates of the rates' actual values.

Two problems have been especially troublesome during this analysis. The breeding grounds surveys estimate numbers of nests, but in cases where broods were counted during a second aerial survey, they often outnumbered nests, indicating that many nests had apparently been missed on the earlier surveys (study areas were too large for immigration of broods to have been a significant factor). In the studies we reviewed, this problem prevented us from estimating nesting success or proportion of birds attempting to nest.

As noted above, the purpose of many of these surveys is to provide an annual index of nesting rates, and the data may be adequate for this purpose. Nonetheless, their value would be enhanced if more intensive surveys could be conducted (perhaps over selected portions of the survey area) or if detection rates could be estimated by observers working on the ground.

The second problem concerns the proportion

Table 5. Variation in the ratio, number of young:number of adults, with flock size and habitat. Flocks were counted during winter in Maryland.

Flock size		Habitat		
		Terrestrial	Aquatic	Either habitat
1 - 20	Ratio	0.42	0.34	0.35
	N flocks	7	317	324
21 - 100	Ratio	0.35	0.18	0.20
	N flocks	32	515	550
> 100	Ratio	0.20	0.14	0.16
	N flocks	72	124	198
All flocks	Ratio	0.21	0.16	—
	N flocks	111	969	—

of young in flocks during migration or winter. Counts during migration must be distributed throughout the migration period as there are pronounced differences in when adults with and without young pass through an area. In addition, we have found that the young:adult ratio varies substantially with habitat and flock size (Earnst in prep.). For example, in North Dakota during migration the young:adult ratio (in 1988) varied consistently with flock size from 0.41 (flock size < 10) to 0.05 (flock size > 200). Among the flocks counted in Maryland in winter, analysed in this study, the proportion of young varied from about 40% in small flocks on land to 14% in large flocks on water (Table 5).

At present, we have no formal sampling scheme for collecting these data, either in the program on which we report here, or in the U.S.

Fish and Wildlife Service mid-winter inventory (which includes ground counts to estimate age ratios). We also do not know how the proportion of birds on land or in small flocks varies between years. A change either in which flocks were surveyed or in the proportions of birds occurring in different habitats or flock sizes could cause a substantial difference in reported age ratios, even if no real difference occurred. Problems of this sort may explain some of the variation in age ratios evident in Serie & Bartonek 1991 and acknowledged by these authors. The best way to avoid this potential bias might be to view land and water birds as comprising two strata, estimate stratum sizes by an aerial survey, and then visit flocks in each habitat following a well-defined sampling plan which specified areas to be checked for flocks.

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Jonathan Bart, Ohio Cooperative Research Unit, USFWS, and Department of Zoology, The Ohio State University, 1735 Neil Avenue, Columbus, Ohio, 43210, USA.
Roland Limpert, Chesapeake Wildlife Heritage, P.O. Box 1745, Easton, Maryland, 21601, USA.
Susan Earnst, Ohio Cooperative Research Unit, USFWS, and Department of Zoology, The Ohio State University, 1735 Neil Avenue, Columbus, Ohio, 43210, USA.
William J. Sladen, Department of Immunology and Infectious Diseases, Johns Hopkins University, 615 N. Wolfe St., Baltimore, Maryland, 21205, USA.
James W. Hines, Patuxent Wildlife Research Center, Patuxent, Maryland, 20708, USA.
Thomas C. Rothe, Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, AK, 99518, USA.