

ANNUAL SURVIVAL RATES OF ADULT AND IMMATURE EASTERN POPULATION TUNDRA SWANS

JAMES D. NICHOLS, U.S. Fish and Wildlife Service, Patuxent Wildlife Research Center, Laurel, MD 20708

J. BART, Ohio Cooperative Fish and Wildlife Research Unit, U.S. Fish and Wildlife Service and Department of Zoology, Ohio State University, Columbus, OH 43210

ROLAND J. LIMPERS, Chesapeake Wildlife Heritage, P.O. Box 1745, Easton, MD 21601

WILLIAM J. L. SLADEN, Department of Immunology and Infectious Diseases, Johns Hopkins University, 615 N. Wolfe Street, Baltimore, MD 21205

JAMES E. HINES, U.S. Fish and Wildlife Service, Patuxent Wildlife Research Center, Laurel, MD 20708

Abstract: Tundra swans (*Cygnus columbianus*) of the eastern population were neckbanded in Maryland, North Carolina, and Alaska from 1966 through 1990. These swans were resighted and recaptured during autumn, winter, and spring, 1966–90. Although the original motivation for this study involved swan movements, we wanted to use the resulting data to test hypotheses about sources of variation in swan survival rates. Recaptures of legbanded and neckbanded swans permitted us to estimate neckband loss rates, which were found to vary with age and sex of swans, and number of years since initial application. Estimates of annual neckband retention rate ranged from about 0.50 for adult male swans ≥ 2 years after initial neckbanding to >0.96 for immature swans and adult females the first year following neckbanding. This variation in neckband loss rates prevented the simple correction of survival estimates to account for such loss. Consequently, we developed a series of multinomial models parameterized with survival, sighting, and neckband retention probabilities for use with the recapture and resighting data. Annual survival rate estimates for adult males and females were similar and very high (0.92). Estimates for immature males and immature females were 0.81 and 0.52, respectively. We recommend this model-based approach for the direct estimation of survival rates from capture-resighting data in the presence of neckband loss. We also recommend that future neckband study designs include regular recapture efforts for the purpose of estimating rates of neckband loss.

J. WILDL. MANAGE. 56(3):485–494

The eastern population of tundra swans breeds in northern North America from eastern Canada to Point Hope, Alaska and overwinters on the Atlantic Coast from New Jersey to North Carolina (Limpert et al. 1991). Mid-winter waterfowl surveys indicate increasing population size (Serie and Bartonek 1991a). Although this population is currently hunted in Alaska, North and South Dakota, New Jersey, North Carolina, and Virginia (Serie and Bartonek 1991b), little is known of survival rates, movements, or causes of mortality.

In a previous report, we estimated breeding frequency of the eastern population of tundra swans and survival of immature birds through the first winter (Bart et al. 1991b). One of our primary objectives here was to estimate annual survival rates for swans in this population using capture-recapture-resighting data obtained over the last 2 decades during studies of neckbanded birds by Sladen, Limpert, and others (e.g., Sladen 1973, Munro 1980).

Another primary objective was to test hypotheses about age- and sex-specific variation in annual survival of tundra swans. Annual survival rate estimates for other species of migra-

tory swans are high (approx 90%) for adult birds and lower for immature birds (Bart et al. 1991a). Geese and swans typically show similar survival rates for males and females (Johnson et al. 1992). We were interested to learn whether tundra swans showed these same survival patterns.

Neckband loss was substantial in this study (H. A. Allen, Johns Hopkins Univ., Baltimore, Md., unpubl. data), and loss rates were found to vary with time since banding. This precluded the straightforward application of capture-recapture models for open populations (Clobert et al. 1987, Hestbeck and Malecki 1989, Pollock et al. 1990). Thus, our secondary objective was to develop methods for estimating survival rates from capture-recapture-resighting data in the face of variable neckband loss rates.

We thank S. R. Baillie, J. B. Hestbeck, G. W. Pendleton, K. P. Burnham, and 1 anonymous referee for constructive reviews of the manuscript and C. M. Hagen for typing it.

METHODS

Marking and Resighting

From 1966 through 1990, 5,963 swans were captured and marked with both legbands and

neckbands in Maryland or North Carolina (Sladen 1973). Sex, age (first winter [imm.] vs. older [ad.]), and several morphological measures were recorded for each banded bird. We restricted our analyses of winter-banded birds to swans banded in January, February, and March.

Resightings were made in Maryland and North Carolina primarily during the winter between 1 October and 30 April. Most of the resightings were made by project personnel and volunteer observers working with project personnel. The remainder were reported by volunteer observers in the general public. For this analysis we used no more than 1 winter (1 Jan–31 Mar) resighting/bird/year. With resightings defined in this way, the data set contained a total of 7,033 resightings. Approximately 25% of the swans were never resighted, 25% were resighted in a single year, and the rest were resighted in 2–10 years. During 1971–74, 416 swans were neckbanded and legbanded in northern Alaska; 264 resightings were recorded for this sample during winter in Maryland and North Carolina.

Neckband Retention Rates

We were interested in using capture-resighting data to estimate survival rates of marked swans. However, if marks (neckbands) are lost over time, then resulting survival estimates will actually reflect the product of survival rate (the parameter of interest) and neckband retention rate (this can be thought of as a nuisance parameter). H. A. Allen (unpubl. data) estimated survival times of neckbands from our swan samples and concluded that unadjusted swan survival rate estimates based on resighting data would be severely biased. Thus, we were forced to consider neckband retention in our estimation work.

The majority of our information about neckband retention came from birds recaptured and examined for both legbands and neckbands during annual trapping efforts in winter. Such recapture information was available for 139 swans over the course of this study. We suspected that retention rates would not vary much by calendar year but that they might vary as a function of number of years since initial neckband application. For example, we suspected that the probability that a 2-year-old neckband would be retained for at least 1 more year was the same for 2-year-old neckbands present in 1972

and 1976, but that a 2-year-old and 5-year-old neckband present in 1972 might have different probabilities of being retained until 1973. We also suspected that retention rates might vary among age-sex classes of swans.

We developed models for use in investigating sources of variation in neckband retention rates. We let M_j denote the number of birds in a particular sex and age (at banding) class that were recaptured and examined for legbands and neckbands j years after banding. If C_j denotes the number of the M_j birds that have retained their neckbands, if neckband loss and recapture are independent events, and if neckband loss rates are the same for all birds in class j , then C_j simply follows a binomial distribution, conditional on M_j :

$$P(C_j|M_j) = \binom{M_j}{C_j} (\pi_j)^{C_j} (1 - \pi_j)^{M_j - C_j}, \quad (1)$$

where π_j represents the probability that a bird will retain its neckband for j years. If the individuals in each recapture sample (the M_j) are independent of each other and of individuals in the other samples (j) with respect to neckband loss, then we can write the joint probability function of the data as the product of the above conditional binomials for $j = 1, \dots, l$, where l is the largest number of years after banding for which a recapture sample is obtained:

$$P(\{C_j\}|\{M_j\}) = \prod_{j=1}^l \binom{M_j}{C_j} (\pi_j)^{C_j} (1 - \pi_j)^{M_j - C_j}. \quad (2)$$

If we allow neckband retention rates to vary by age-sex class, then we obtain a probability distribution (as in 2) for each class, and the joint distribution for all classes can be written as the product of the age- and sex-specific distributions.

If we let θ_k denote the probability that a bird alive and wearing a neckband at the beginning of the k th year after banding will retain its neckband until the end of the k th year after banding, given that it is alive at the end of the k th year, then we can write the π_j as follows:

$$\pi_j = \prod_{k=1}^j \theta_k. \quad (3)$$

The swan data included 4 age-sex classes and winter recapture samples for up to 10 years after banding. A fully-parameterized model for these data included a large number of parameters, θ_k ,

to be estimated. We were interested in reducing the number of neckband-retention parameters for 2 reasons. First, the data set was not very large, and we simply wanted to obtain the most parsimonious model that still fit the data reasonably. Second, if annual neckband retention rates do not vary with number of years after banding (i.e., if it is reasonable to use the model $\theta_k = \theta$ for all k), then post hoc adjustment of survival rate estimates to account for neckband loss is computationally simple (Arnason and Mills 1981, Pollock 1981).

We used a series of models to test hypotheses about sources of variation in neckband retention rates. Model 0 was the most general, having separate θ_k for each k , where k extended through the number of years elapsed since banding for the oldest recapture sample in each age-sex class (Appendix A). Under model 0, immature males were assumed to exhibit annual retention rates of adult males after 3 years (at this time immature males are believed to begin breeding behaviors that might influence retention rates, (J. Bart, unpubl. data), and immature females exhibited annual retention rates of adult females after 1 year (breeding behavior was not suspected to be an important determinant of retention rate in females).

Model 1 was similar to model 0 with the exception that annual retention rates for adult males and females were assumed to equal a single constant (i.e., no age- or sex-specificity) after 5 years. This assumption was necessary because of an absence of retention data after 5 years (recapture samples were very small, and no birds retained their collars in these old samples). Model 2 was similar to model 1, but annual retention rates were assumed to be equal for years 2, 3, and 4 after banding for adult males and for adult females. In addition, annual retention rates for immature males were assumed to be equal for years 1, 2, and 3 after banding. Model 3 was similar to model 2, except immature females the first year after banding were assumed to exhibit the same retention rate as immature males. Model 4 was similar to model 2, but with no separate parameters for first-year retention rates of adults. Adults were assumed to have constant, sex-specific retention rates for the first 4 years after banding. Finally, model 5 had only 2 parameters for all age-sex classes combined, 1 for the first 4 years after banding and 1 for all subsequent years. Models 1–5 are

thus obtained by placing various constraints on the parameters of model 0 (Appendix B). Models 0, 1, 2, 3, and 5 represent 1 sequence of nested models (i.e., each model with a larger number represents a "special case" of the models with smaller numbers, obtained by constraining parameters), and models 0, 1, 2, 4, and 5 represent another. Models 3 and 4 are not nested with respect to each other (i.e., one of these models cannot be obtained simply by constraining the parameters of the other).

We implemented the above models using program SURVIV (White 1983). For each model, we computed parameter estimates, goodness-of-fit test statistics, likelihood ratio statistics for tests between models within a nested sequence, and Akaike's Information Criterion (AIC; Akaike 1973). Because our models did not represent a single nested sequence, we based our selection of a neckband retention model primarily on the AIC values (Burnham and Anderson 1992, Lebreton et al. 1992).

Survival Rate Estimation

We wanted to use the observation histories of individual swans in conjunction with capture-recapture-resighting models to estimate annual survival rates. Our analysis of the swan recapture data using the collar retention models described above provided evidence that neckband retention rates were not constant and that they varied as a function of time since banding (see Results). In standard Jolly-Seber analyses, the number of animals released (in our study this number includes birds that are resighted) in any period includes both newly marked animals and animals marked in previous periods. Because time since marking varies among animals released at any period, if we estimate survival rates using only observation data, then we do not know how to adjust these estimates by estimated neckband retention rates to account for collar loss.

We are aware of 2 approaches to survival rate estimation that can be used in situations where tag retention rates vary as a function of years since marking. One approach involves using a cohort approach to Jolly-Seber analysis (Buckland 1980, Loery et al. 1987, Pollock et al. 1990), in which estimation is based only on animals marked at 1 sampling period (1 cohort). Under this approach, each estimate of annual survival rate is based on a group of birds, all of which

were banded exactly j years ago. Because of this homogeneity in time elapsed since banding for each sample, resulting survival estimates from observation data can be adjusted to account for neckband loss as follows:

$$\hat{\phi}_j^* = \hat{\phi}_j / \hat{\theta}_j \quad (4)$$

where $\hat{\phi}_j^*$ denotes the estimated probability of a bird alive at the beginning of the j th year after banding surviving the next year, $\hat{\phi}_j$ denotes the Jolly-Seber survival estimate based on reobservation data from a single cohort, and $\hat{\theta}_j$ denotes the estimated neckband retention probability defined above. When ϕ_j and θ_j are estimated independently, as they were in our case (ϕ_j was estimated from observation data and θ_j was estimated from recapture data), then $\text{var}(\hat{\phi}_j^*)$ can be estimated as:

$$\widehat{\text{var}}(\hat{\phi}_j^*) = (\hat{\phi}_j^*)^2 \left[\frac{\widehat{\text{var}}(\hat{\phi}_j)}{(\hat{\phi}_j)^2} + \frac{\widehat{\text{var}}(\hat{\theta}_j)}{(\hat{\theta}_j)^2} \right] \quad (5)$$

(e.g., Pollock 1981).

We used the above 2-step approach with the data set for tundra swans banded in Alaska. We first obtained survival estimates based on each of the 4 annual marked samples, 1971–74, of swans from Alaska. The relatively small sizes of these initial marked samples produced imprecise survival estimates, so we also used this approach with “composite” cohorts for each age-sex class. These composite cohorts were formed by combining all birds, regardless of the calendar year of banding, into 1 banded sample, and then looking at observation histories based only on years since banding. For these composite estimates we assumed that annual survival and sighting probabilities did not vary with calendar year, but only as a function of years since banding. Our results for the Maryland and North Carolina swans indicated that the assumption of constant survival was probably reasonable, but that the assumption of constant sighting probability likely was not met. However, the composite cohort approach provided our only means of obtaining estimates for the Alaska data, so we used this approach but treated the results with caution.

Resulting survival and associated variance estimates were then adjusted for collar loss using (4) and (5) above. Because the Alaskan birds were marked in July and resighted in subsequent winters, January–March, we needed an approximate 6-month neckband retention rate

estimate, rather than our annual estimates. We obtained 6-month estimates as $\sqrt{\hat{\theta}_j}$, with variance estimate (obtained using the delta method), $\widehat{\text{var}}(\hat{\theta}_j)/(4\hat{\theta}_j)$.

We developed a second approach to estimating survival rate in the presence of neckband loss using a single estimation model that included both recapture and reobservation data. Although this model was tailored to our specific situation of few recapture data, it is similar in some respects to a general model described by Kremers (1987). The recapture data were modeled as in equations (1), (2), and (3) using only collar retention parameters. Reobservation data were modeled as in the standard capture-recapture-resighting model of Pollock (1981), except that we included parameters not only for survival, ϕ_i for adults and ϕ_i' for first-year immatures (note that these denote the probability of surviving from the Jan–Mar sampling period in year i until the sampling period in year $i + 1$) and sighting probability, p_i (the probability of being sighted in sampling period i given that the bird was alive and present in the sampled area), but also for neckband retention probability, θ_j . Note that i corresponds to calendar year, whereas j corresponds to the number of years since banding.

Every survival probability in the new model was accompanied by the appropriate neckband retention rate. For example, the probability that an adult bird banded during the sampling period of calendar year i would be seen in the sampling periods of years $i + 1$ and $i + 2$ was modeled as $\phi_i \theta_{i+1} \phi_{i+1} \theta_{i+2} p_{i+2}$, with the subscripts of survival and sighting probability corresponding to calendar year, and the neckband retention subscripts denoting years elapsed since banding. Expected numbers of swans exhibiting different resighting histories under our general model are presented for the 3-year, 1-area case (Appendix C). For the work reported here, we actually used a 5-year, 2-area model.

The recapture and reobservation data were independent of each other, but the models for both types of data included the neckband retention parameters. Thus, we obtained a probability distribution for the combined recapture and reobservation data set as the product of the 2 separate probability distributions. Because this combined model was the product of binomial (recapture data) and multinomial (resighting data) distributions, we were again able to implement the model using program SURVIV

Table 1. Significance levels (*P*-values) for goodness-of-fit and likelihood ratio tests of the tag-retention models, eastern population tundra swans, 1966–90.

Tag retention model	No. of parameters	AIC ^a	Goodness-of-fit tests ^b	Likelihood ratio tests ^c			
				2	3	4	5
1	13	52.803	0.72	0.83	0.84	0.07	0.02
2	7	43.597	0.86		0.42	<0.01	<0.01
3	6	42.244	0.87				<0.01
4	5	51.133	0.29				0.04
5	2	53.406	0.12				

^a Akaike's Information Criterion (Burnham and Anderson 1992, Lebreton et al. 1992). Smaller values of AIC indicate more appropriate models.

^b Small probabilities indicate poor fit of the model.

^c Small probabilities indicate that the less general model (identified at the top of the column, serves as the null hypothesis) should be rejected in favor of the more general model (identified in the far left column, serves as the alternative hypothesis). For example, $P = 0.07$ corresponds to the test of model 1 (alternative hypothesis) versus model 4 (null hypothesis).

(White 1983). We used a variety of constraints and produced over 20 different reduced-parameter models. These models were used to test hypotheses about sources of variation (e.g., area-, time-, and age- and sex-specificity) in survival, neckband retention and sighting probabilities, and to provide estimates of survival and sighting probabilities. Eight of these models proved especially useful in our analyses (Appendix D). We used this model-based approach with all capture-resighting data from samples on the wintering grounds (N.C. and Md.). SURVIV did not converge on estimates for the Alaskan data set, so we used the 2-step approach as described previously.

RESULTS

Neckband Retention Rates

Goodness-of-fit and likelihood ratio test statistics were computed for neckband retention models 1–5 (Table 1). Model 0 does not appear in Table 1 because it was too general for our data, and all parameters were not identifiable. Models 1–3 fit the data adequately, and likelihood ratio test results indicated that models 2 and 3 performed just as well as model 1. Goodness-of-fit statistics for models 4 and 5 both showed $P > 0.10$, but the likelihood ratio tests against model 1 provided evidence ($P < 0.10$) in favor of the more general model (Table 1). Similarly, likelihood ratio tests between model 2 (the more general model) versus 4 and 5, provided strong evidence ($P < 0.01$) in favor of the more general model. The value of AIC was lowest for model 3 (Table 1). Based on these results, we selected model 3 as the most parsimonious model for collar retention rates and based our estimates on this model (Table 2).

Estimates of adult retention rate for the first year after banding were higher than the estimates for subsequent years for both males and females (Table 2). The likelihood ratio test of model 2 versus model 4 indicated that these differences were significant ($P < 0.01$; Table 1). Neckband retention rate estimates were lower for adult males than for either immature males or adult females (Table 2).

Survival Rates

We used observation histories from the North Carolina (1973–77) and Maryland (1970–74) data sets in conjunction with the 8 models of Appendix D to estimate survival rates. Only for model 4' was it clear that the data did not fit the model (Table 3).

The model 0' versus 1' test indicated that the neckband retention parameterization of model 3 was adequate even in the presence of the additional data on neckband retention provided by the observation histories. The model 1' versus 2' test provided no evidence of temporal variation in survival within an age-sex class (Table 4). The model 2' versus 3' test provided no evidence of different survival rates for birds banded in North Carolina versus Maryland (Table 4).

The model 3' versus 4' test addressed the hypothesis of temporal variation in sighting probabilities. The null hypothesis was strongly rejected (Table 4), indicating that sighting probabilities did vary from year to year, and that year-specific parameters were needed to adequately model these probabilities.

The model 3' versus 5' test provided no evidence of sex-specific variation in survival probability within adults (Table 4). However, the test between models 5' and 6' did provide evi-

Table 2. Estimated annual rates of neckband retention based on tag-retention model 3, eastern population tundra swans, 1966–90.

Parameter ^a	Retention rate estimate	
	$\hat{\theta}$	SE ($\hat{\theta}$)
$\theta_{1,m}$ (ad male retention rate for the first yr after banding)	0.886	0.048
$\theta_{2,m} = \theta_{3,m} = \theta_{4,m} = \theta_{5,m}^*$ (annual retention rate for yr 2–4 after banding for ad male)	0.503	0.120
$\theta_{3,m} = \theta_{6,m} = \theta_{7,m} = \theta_{8,m} = \theta_{9,m} = \theta_{10,m} = \theta_{5,f} = \theta_{6,f} = \theta_{7,f} = \theta_{8,f} = \theta_{9,f} = \theta_{10,f}^*$ (annual retention rate for >4 yr after banding for ad male and female)	0.000 ^b	
$\theta'_{1,m} = \theta'_{2,m} = \theta'_{3,m} = \theta'_{1,f} = \theta'^*_{mf}$ (annual retention rate for the first yr after banding for male and female banded as imm and for yr 2–3 after banding for birds banded as imm male)	0.967	0.035
$\theta_{1,f}$ (ad female retention rate for the first yr after banding)	1.000	0.186
$\theta_{2,f} = \theta_{3,f} = \theta_{4,f} = \theta^*_{f}$ (annual retention rate for yr 2–4 after banding for birds banded as imm and ad female)	0.767	0.093

^a $\theta_{i,j}$ denotes the probability that a neckbanded bird of sex j (m = male, f = female) alive at the beginning of year $i - 1$, retains its neckband until the beginning of year i , given that the bird is still alive. Primes denote the parameters for birds banded as immature (in cases when these may differ from adult parameters) and asterisks denote parameters assumed to be constant for ≥ 2 years.

^b Very small numbers of birds were recaptured in these neckband age categories and none had retained its neckband.

dence of sex-specific variation in survival among immature birds. The null hypothesis of no age-specific variation in survival within each sex was rejected strongly (model 3' vs. 7' test, Table 4). Based on these tests (Table 4) and AIC (Table 3), we concluded that model 5' provided the most parsimonious description of our data.

Table 3. Goodness-of-fit test significance levels (GOF P) and Akaike's Information Criterion (AIC) for the capture-recapture-resighting models, eastern population tundra swans, Maryland (1970–74) and North Carolina (1973–77).

Model	No. of parameters	GOF P	AIC ^a
0'	60	0.94	653.3
1'	50	0.93	643.0
2'	34	0.89	630.9
3'	30	0.86	629.6
4'	22	<0.01	805.1
5'	29	0.87	627.7
6'	28	0.78	634.1
7'	28	0.25	665.4

^a Smaller values of AIC indicate more appropriate models.

Table 4. Likelihood ratio tests between different capture-recapture-resighting models, eastern population tundra swans, Maryland (1970–74) and North Carolina (1973–77).

Models compared ^a		χ^2	df	P
More general	Less general			
0'	1'	9.7	10	0.46
1'	2'	19.8	16	0.23
2'	3'	6.7	4	0.15
3'	4'	191.6	8	<0.01
3'	5'	0.1	1	0.74
5'	6'	8.4	1	<0.01
3'	7'	39.8	2	<0.01

^a See Appendix D for descriptive model definitions.

The annual survival rate estimate for adult swans of both sexes was very high ($\hat{\phi} = 0.921$, $\widehat{SE}[\hat{\phi}] = 0.035$). The estimate for immature male swans was lower ($\hat{\phi} = 0.814$, $\widehat{SE}[\hat{\phi}] = 0.088$) and the estimate for immature females was lowest ($\hat{\phi} = 0.521$, $\widehat{SE}[\hat{\phi}] = 0.059$).

As indicated above, the Alaskan swan data did not permit estimation using the capture-recapture-resighting models. Thus, we estimated survival rates using the 2-step approach defined by equations (4) and (5) in conjunction with the combined cohort data from 1971–74. The best survival estimates resulting from this analysis corresponded to the 6-month period between banding in Alaska (Jul) and resighting on Maryland and North Carolina wintering grounds (Jan–Mar). These 6-month estimates were 0.655 ($SE = 0.164$) for adult males, 0.103 ($SE = 0.074$) for immature males, 0.886 ($SE = 0.143$) for adult females, and 0.081 ($SE = 0.037$) for immature females.

DISCUSSION

Survival rates have been estimated for several other species of swans (reviewed in Bart et al. 1991a), although in many cases the estimation methods have differed from ours and have typically been ad hoc in nature. Results for tundra swans from this study are similar to estimates for other migratory swan species. Bewick's (*Cygnus columbianus bewickii*), whooper (*C. cygnus*), and trumpeter (*C. buccinator*) swans are all migratory, and all had annual survival rate estimates near 90% after their third year. Survival rate estimates during the second year were about 50–75%; during the third year, survival rates were similar to adult rates. Compared

to migratory swans, non-migratory swans are reported to have lower adult survival rate estimates (about 80–85%), similar second year survival rate estimates (about 60–80%), and third year survival rate estimates similar to second-year estimates rather than to estimates for later years.

The finding of differences between survival rates of first-year versus older birds is common in studies of waterfowl banded during and immediately following the breeding season (Johnson et al. 1992). For birds banded during winter, however, most comparisons between young (approx 6 months old) and adults (≥ 18 months old) have provided little evidence of differences in annual survival rates, and even when evidence has been found, the estimated magnitude of differences has been relatively small (Johnson et al. 1992). Our evidence of substantial differences between annual survival rates of first-year versus older tundra swans is somewhat unusual in this respect. However, we might predict that the duration of age-specific differences in survival would be greater in longer-lived, slower-maturing birds, and our findings are consistent with this expectation.

The similarity of survival estimates for adult males and females is consistent with typical findings for geese and other swans (Johnson et al. 1992). However, the higher survival rates of immature male swans than immature females is not typical and is of interest. Even in species (e.g., most ducks) for which survival rates of adult males and females differ, survival rates of young males and females tend to be fairly similar (Johnson et al. 1992).

Our 6-month survival rate estimates for the small sample of immature birds banded in Alaska were 10% for males and 8% for females. We have little faith in these estimates because of the small samples and the use of a composite cohort approach when 1 of the underlying assumptions (constant sighting probabilities over time) likely was not met. Estimates of these rates can also be obtained from the estimate of Bart et al. (1991b) that approximately 13% of the tundra swan eggs survive from laying until the start of their fourth year. Survival during these 4 years may be expressed as the product of (1) survival from laying until July (when the immature birds were banded in Alas.), (2) 6-month survival from July to January, (3) survival during the second year, and (4) survival during the third year. The first rate is probably not above

80% (Bart et al. 1991b); the third and fourth rates are probably not above 80 and 95%, respectively. This approach suggests that the 6-month survival rate of immature swans banded in July is probably not less than 21%; whereas our empirical estimate was about 9%. Possible explanations for the discrepancy between these 2 estimates include a combination of sampling error and biases in the various estimates (in fact the estimate for immature male swans in Alas. does not differ significantly from 21%); Alaska birds have lower survival rates than the average for the population; 1971–74 (when the birds were banded) was a period of unusually poor survival for immature swans; capture of the immatures decreased their survival rate (by separating them from their parents); and neckbands reduced survival of the immature swans. We doubt that these possibilities, which are not mutually exclusive, can be rigorously investigated with the existing data set.

RESEARCH IMPLICATIONS

We presented 2 methods for estimating survival in the presence of neckband loss rates that change with number of years since banding. The first method involved a 2-step approach in which the product of survival and neckband retention probabilities was estimated using a cohort-based Jolly-Seber approach (Buckland 1980, 1982; Loery et al. 1987; Pollock et al. 1990). This product estimate then was divided by an independent estimate of neckband retention rate in order to estimate survival. The second approach involved the development of a single model that used both recapture and resighting data. This model was parameterized with sighting probabilities, survival rates and neckband retention rates, and these parameters all were estimated directly. We prefer this latter approach because it provides direct estimates of survival using data from all banded cohorts in a single model, rather than using a 2-step approach involving data from 1 cohort at a time. This use of more data in the more direct, single-model approach should result in more precise estimates. Other benefits associated with this approach include direct estimation of sampling variances and covariances and the ability to test alternative models. We believe that this and similar (Kremers 1987, 1988) model-based approaches to estimating survival in the presence of neckband loss may be useful in other analyses of neckband resighting data.

We suspect that our survival estimates for immature swans banded in Alaska are biased low. We suggest that other researchers on the breeding grounds who plan to mark immature swans with neckbands try to evaluate possible effects of capture and/or neckbands on swan survival.

Finally, we emphasize the importance of recapture data to neckband observation studies. Without recapture data (or data from some other method of resampling double-banded birds), it would not be possible to obtain estimates of the parameter of interest (survival rate) that are not confounded by neckband loss. Thus, it is very important that neckband study designs include regular recapture efforts for the purpose of estimating rates of neckband loss. In most neckband studies of which we are aware, recaptures occur as a by-product of efforts to catch and mark new birds. Because the precision of survival estimates is a function of both resighting and recapture data, it is important that designs of future neckband observation studies explicitly consider sample size in terms of both resighting and recapture data (Hestbeck et al. 1990).

LITERATURE CITED

- AKAIKE, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 267–281 in B. N. Petran and F. Csaki, eds. International symposium on information theory, Second ed. Akademiai Kiad., Budapest, Hungary.
- ARNASON, A. N., AND K. H. MILLS. 1981. Bias and loss of precision due to tag loss in Jolly-Seber estimates for mark-recapture experiments. *Can. J. Fish. Aquatic Sci.* 38:1077–1095.
- BART, J., S. EARNST, AND P. J. BACON. 1991a. Comparative demography of the swans: a review. Pages 15–21 in J. Sears and P. J. Bacon, eds. Proceedings of the third IWRB international swan symposium, Oxford 1989. *Wildfowl-Suppl.* 1.
- , R. LIMPERT, S. EARNST, W. SLADEN, J. HINES, AND T. ROTHE. 1991b. Demography of eastern population tundra swans, *Cygnus columbianus columbianus*. Pages 178–184 in J. Sears and P. J. Bacon, eds. Proceedings of the third IWRB international swan symposium, Oxford 1989. *Wildfowl-Suppl.* 1.
- BUCKLAND, S. T. 1980. A modified analysis of the Jolly-Seber capture-recapture model. *Biometrics* 36:419–435.
- . 1982. A mark-recapture survival analysis. *J. Anim. Ecol.* 51:833–837.
- BURNHAM, K. P., AND D. R. ANDERSON. 1992. Data-based selection of an appropriate biological model: the key to modern data analysis. In D. R. McCullough and R. H. Barrett, eds. *Wildlife 2001: populations*. Elsevier Scientific Publ. Co., Amsterdam.
- CLOBERT, J., J.-D. LEBRETON, AND D. ALLAINE. 1987. A general approach to survival rate estimation by recaptures or resightings of marked birds. *Ardea* 75:133–142.
- HESTBECK, J. B., AND R. A. MALECKI. 1989. Estimated survival rates of Canada Geese within the Atlantic Flyway. *J. Wildl. Manage.* 53:91–96.
- , D. H. RUSCH, AND R. A. MALECKI. 1990. Estimating population parameters for geese from band-recovery and mark-recapture data. *Trans. North Am. Wildl. and Nat. Resour. Conf.* 55:350–373.
- JOHNSON, D. H., J. D. NICHOLS, AND M. D. SCHWARTZ. 1992. Population dynamics of breeding waterfowl. In press in B. D. J. Batt and M. G. Anderson, eds. *The ecology and management of breeding waterfowl*. Univ. Minnesota Press, Minneapolis.
- KREMERS, W. K. 1987. Estimation of survival rates in the presence of tag loss: the binomial and hypergeometric model. Universität Dortmund (Germany), Fachbereich Statistik, Forschungsbericht Nr. 87/6. 20pp.
- . 1988. Estimation of survival rates from a mark-recapture study with tag loss. *Biometrics* 44:117–130.
- LEBRETON, J.-D., K. P. BURNHAM, J. CLOBERT, AND D. R. ANDERSON. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol. Monogr.* 62:67–118.
- LIMPERT, R. J., W. J. L. SLADEN, AND H. A. ALLEN. 1991. Winter distribution of tundra swans, *Cygnus columbianus columbianus*, breeding in Alaska and western Canadian Arctic. Pages 78–83 in J. Sears and P. J. Bacon, eds. Proceedings of the third IWRB international swan symposium, Oxford 1989. *Wildfowl-Suppl.* 1.
- LOERY, G., K. H. POLLOCK, J. D. NICHOLS, AND J. E. HINES. 1987. Age-specificity of avian survival rates: an analysis of capture-recapture data for a black-capped chickadee population, 1958–1983. *Ecology* 68:1038–1044.
- MUNRO, R. E. 1980. Traditional return of *Cygnus columbianus columbianus* to wintering areas in Maryland's Chesapeake Bay. Pages 81–98 in G.V.T. Matthews and M. Smart, eds. Proceedings of the second IWRB international swan symposium, Sapporo, Japan 1980. Slimbridge, England.
- POLLOCK, K. H. 1981. Capture-recapture models allowing for age-dependent survival and capture rates. *Biometrics* 37:521–529.
- , J. D. NICHOLS, C. BROWNIE, AND J. E. HINES. 1990. Statistical inference for capture-recapture experiments. *Wildl. Monogr.* 107. 97pp.
- SERIE, J. R., AND J. C. BARTONEK. 1991a. Population status and productivity of tundra swans, *Cygnus columbianus columbianus*, in North America. Pages 172–177 in J. Sears and P. J. Bacon, eds. Proceedings of the third IWRB international swan symposium, Oxford 1989. *Wildfowl-Suppl.* 1.
- . 1991b. Harvest management of tundra swans, *Cygnus columbianus*, in North America. Pages 359–367 in J. Sears and P. J. Bacon, eds.

Proceedings of the third IWRB international swan symposium, Oxford 1989. Wildfowl-Suppl 1.
 SLADEN, W. J. L. 1973. A continental study of whistling swans using neck collars. Wildfowl 24:8-14.
 WHITE, G. C. 1983. Numerical estimation of sur-

vival rates from band-recovery and biotelemetry data. J. Wildl. Manage. 47:716-728.

Received 29 April 1991.
 Accepted 12 February 1992.
 Associate Editor: Morrison.

APPENDIX A. Age-, sex-, and year-specific neckband retention parameters under the most general tag-retention model, model 0 (22 parameters).

Years after banding (k)	Males		Females	
	Adult	Immature	Adult	Immature
1	$\Theta_{1,m}^b$	$\Theta'_{1,m}$	$\Theta_{1,f}$	$\Theta'_{1,f}$
2	$\Theta_{2,m}$	$\Theta'_{2,m}$	$\Theta_{2,f}$	$\Theta'_{2,f}$
3	$\Theta_{3,m}$	$\Theta'_{3,m}$	$\Theta_{3,f}$	$\Theta'_{3,f}$
4	$\Theta_{4,m}$	$\Theta_{4,m}$	$\Theta_{4,f}$	$\Theta_{4,f}$
5	$\Theta_{5,m}$	$\Theta_{5,m}$	$\Theta_{5,f}$	$\Theta_{5,f}$
6	$\Theta_{6,m}$	$\Theta_{6,m}$	$\Theta_{6,f}$	$\Theta_{6,f}$
7	$\Theta_{7,m}$	$\Theta_{7,m}$	$\Theta_{7,f}$	$\Theta_{7,f}$
8	$\Theta_{8,m}$	$\Theta_{8,m}$	$\Theta_{8,f}$	$\Theta_{8,f}$
9	$\Theta_{9,m}$	$\Theta_{9,m}$		
10	$\Theta_{10,m}$	$\Theta_{10,m}$		

^a Age at banding. A prime denotes a bird banded as immature (during its first winter), but the prime notation is only used in cases where tag retention is modeled with different parameters for immature and adult birds.

^b $\Theta_{k,s}$ denotes the annual tag retention rate for the kth year after banding for a bird of sex s (m = male, f = female).

APPENDIX B. Constraints on the parameters of model 0 (Appendix A) that define the more restrictive tag-retention models.

Model	Constraints
1	Model 0 constraints; $\Theta_{5,m} = \Theta_{6,m} = \Theta_{7,m} = \Theta_{8,m} = \Theta_{9,m} = \Theta_{10,m} = \Theta_{3,f} = \Theta_{6,f} = \Theta_{7,f} = \Theta_{8,f}$
2	Model 1 constraints; $\Theta_{2,m} = \Theta_{3,m} = \Theta_{4,m}$; $\Theta_{2,f} = \Theta_{3,f} = \Theta_{4,f}$; $\Theta'_{1,m} = \Theta'_{2,m} = \Theta'_{3,m}$
3	Model 2 constraints; $\Theta'_{1,f} = \Theta'_{1,m} = \Theta'_{2,m} = \Theta'_{3,m}$
4	Model 2 constraints; $\Theta_{1,m} = \Theta_{2,m} = \Theta_{3,m} = \Theta_{4,m}$; $\Theta_{1,f} = \Theta_{2,f} = \Theta_{3,f} = \Theta_{4,f}$
5	Model 3 and 4 constraints; $\Theta_{1,m} = \Theta_{2,m} = \Theta_{3,m} = \Theta_{4,m} = \Theta'_{1,m} = \Theta'_{2,m} = \Theta'_{3,m} = \Theta_{1,f} = \Theta_{2,f} = \Theta_{3,f} = \Theta_{4,f} = \Theta'_{1,f}$

APPENDIX C. Expected numbers of resightings under a general 2-age model with tag loss.

Number of swans released ^a	Number of swans with specified capture/sighting history for periods i, i + 1, i + 2 ^b	Expected number of sightings ^c
R_i	X_{111}	$R_i \phi_i \Theta_i p_{i+1} \phi_{i+1} \Theta_2 p_{i+2}$
	X_{110}	$R_i \phi_i \Theta_i p_{i+1} (1 - \phi_{i+1} \Theta_2 p_{i+2})$
	X_{101}	$R_i \phi_i \Theta_i (1 - p_{i+1}) \phi_{i+1} \Theta_2 p_{i+2}$
	X_{100}	$R_i [1 - \phi_i \Theta_i + \phi_i \Theta_i (1 - p_{i+1}) (1 - \phi_{i+1} \Theta_2 p_{i+2})]$
R_{i+1}	X_{011}	$R_{i+1} \phi_{i+1} \Theta_{i+1} p_{i+2}$
	X_{010}	$R_{i+1} (1 - \phi_{i+1} \Theta_{i+1} p_{i+2})$
R'_i	X'_{111}	$R'_i \phi'_i \Theta'_i p_{i+1} \phi_{i+1} \Theta_2 p_{i+2}$
	X'_{110}	$R'_i \phi'_i \Theta'_i p_{i+1} (1 - \phi_{i+1} \Theta_2 p_{i+2})$
	X'_{101}	$R'_i \phi'_i \Theta'_i (1 - p_{i+1}) \phi_{i+1} \Theta_2 p_{i+2}$
	X'_{100}	$R'_i [1 - \phi'_i \Theta'_i + \phi'_i \Theta'_i (1 - p_{i+1}) (1 - \phi_{i+1} \Theta_2 p_{i+2})]$
R'_{i+1}	X'_{011}	$R'_{i+1} \phi'_{i+1} \Theta'_{i+1} p_{i+2}$
	X'_{010}	$R'_{i+1} (1 - \phi'_{i+1} \Theta'_{i+1} p_{i+2})$

^a R_i = the number of adult swans banded and released in the winter of year i; R'_i = the number of immature swans banded and released in the winter of year i.

^b $X_{i+1,i+2}$ = the number of swans with the capture history specified by the subscripts. Subscripts for the 3 sampling periods are either "0" indicating no capture or sighting or "1" indicating initial capture (the first "1") or sighting (subsequent "1's"). For example, X_{101} denotes a swan first captured in period i, not seen in period i+1, but sighted in period i+2. Prime denotes a capture history for birds initially captured and banded as immature.

^c ϕ_j = probability of surviving from period i to i+1. Θ_j = probability that a swan with a neckband j-1 years after banding will retain the neckband until year j after banding; p_i = probability that a neckbanded swan alive and in the sampled area in period i is sighted.

APPENDIX D. Descriptive summary of combined capture-recapture-resighting models used to estimate survival rates.

Model	Tag retention rates ^a	Survival rates	Sighting probabilities
0'	No constraints (as in Model 0) except θ_{ks} , the same for the N.C. and Md. data sets ^b	No constraints (as in Pollock 1981) ^c	No constraints (as in Pollock 1981) ^c
1'	Model 3 constraints; same θ_{ks} for N.C. and Md.	No constraints	No constraints
2'	Model 3 constraints; same θ_{ks} for N.C. and Md.	Survival within each age-sex class constant over time	No constraints
3'	Model 3 constraints; same θ_{ks} for N.C. and Md.	Survival within each age-sex class constant over time and area	No constraints
4'	Model 3 constraints; same θ_{ks} for N.C. and Md.	Survival within each age-sex class constant over time and area	Sighting probability within each sex constant over time
5'	Model 3 constraints; same θ_{ks} for N.C. and Md.	Survival constant over time and area. M and f survival rates are equal within ad but not within imm	No constraints
6'	Model 3 constraints; same θ_{ks} for N.C. and Md.	Survival constant over time and area. M and f survival rates are equal within ad and within imm	No constraints
7'	Model 3 constraints; same θ_{ks} for N.C. and Md.	Survival constant over time and area. Imm and ad survival rates are equal within m and within f	No constraints

^a Model numbers in this column relate to the collar retention models described in the text.^b N.C. data are for birds banded and observed during 1973-77; Md. data are for birds banded and observed during 1970-74.^c Time-, age-, sex-, and area-specific survival and sighting probabilities.