SEASONAL AND ANNUAL SURVIVAL OF EMPEROR GEESE

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Abstract: Population levels of emperor geese (*Chen canagica*) in Alaska in 1993 were about half that estimated in the 1960s. Survival information is necessary for managers to decide how to best enhance recovery of this species to former levels. We calculated seasonal and annual estimates of emperor goose survival from resightings of neck-collared birds. Geese were neck collared in 1988–90 on their breeding grounds in the Yukon-Kuskokwim Delta, Alaska, and resighted each spring and fall, 1988–92, at staging areas on the Alaska Peninsula. Adult monthly survival rates during overwinter periods (1 Oct–30 Apr) were not different (P = 0.281) among years ($\hat{S}'$ = 0.940, SE = 0.009), whereas monthly rates of oversummer (1 May–30 Sep) survival showed annual variation (P = 0.048). However, we constrained oversummer survival to a single estimate of 0.980 (0.010). Monthly survival estimates for juveniles during their first overwinter period did not vary among years (P = 0.999) and was 0.710 (0.018). Subsequent monthly survival for juveniles was 0.943 (0.010), similar to that for adults. We developed an adjustment procedure to account for philopatric behavior of geese and this enabled us to use data for postbanding (1 Aug–30 Sep) periods. Survival estimates were low compared with those for other goose species, particularly for juveniles. We addressed collar loss and heterogeneity in resighting probabilities and felt their contribution to potential model bias was insignificant. Annual survival among adults ($\hat{S}'$ = 0.631, SE = 0.023) was not different (P = 0.709) from that observed during 1982–85 (Petersen 1992). The similarity in survival rates in these studies suggests that harvest regimes did not differ between the 2 periods. This suggests that continued subsistence harvest has contributed to persistent low population levels in emperor geese.

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Emperor geese have a relatively restricted distribution among geese (Owen 1980). Aside from small numbers occurring in eastern Russia, virtually all emperor geese breed on the Yukon-Kuskokwim Delta, Alaska (Eisenhauer and Kirkpatrick 1977). The delta also supports a large population of native people who harvest geese for subsistence (Klein 1966, Pamplin 1986, Raveling 1984). Emperor geese winter throughout the Aleutian Islands, a relatively high latitude and remote range compared with that for other North American geese.

This Yukon-Kuskokwim Delta population of emperor geese declined from the 1970s to the mid-1980s (Petersen and Gill 1982; R. J. King, U.S. Fish and Wildl. Serv., Fairbanks, Alas., unpubl. data). Spring aerial survey numbers have declined from 139,000 in 1964 to 42,000 in 1986 (U.S. Fish and Wildl. Serv. 1989). The emperor goose population has since increased only marginally, with a 1993 spring survey estimate of 52,000 (R. J. King, unpubl. data). An understanding of the factors affecting these changes is imperative to effectively manage the emperor goose population. Survival rates are an important factor affecting population change, yet little information exists concerning survival rates of emperor geese. Petersen (1992) estimated annual survival of adult females during 1982–86, a period of population decline. However, age and seasonal specificity in survival rates have not been examined. Our objective was to provide estimates of seasonal and annual survival for adult and juvenile emperor geese.

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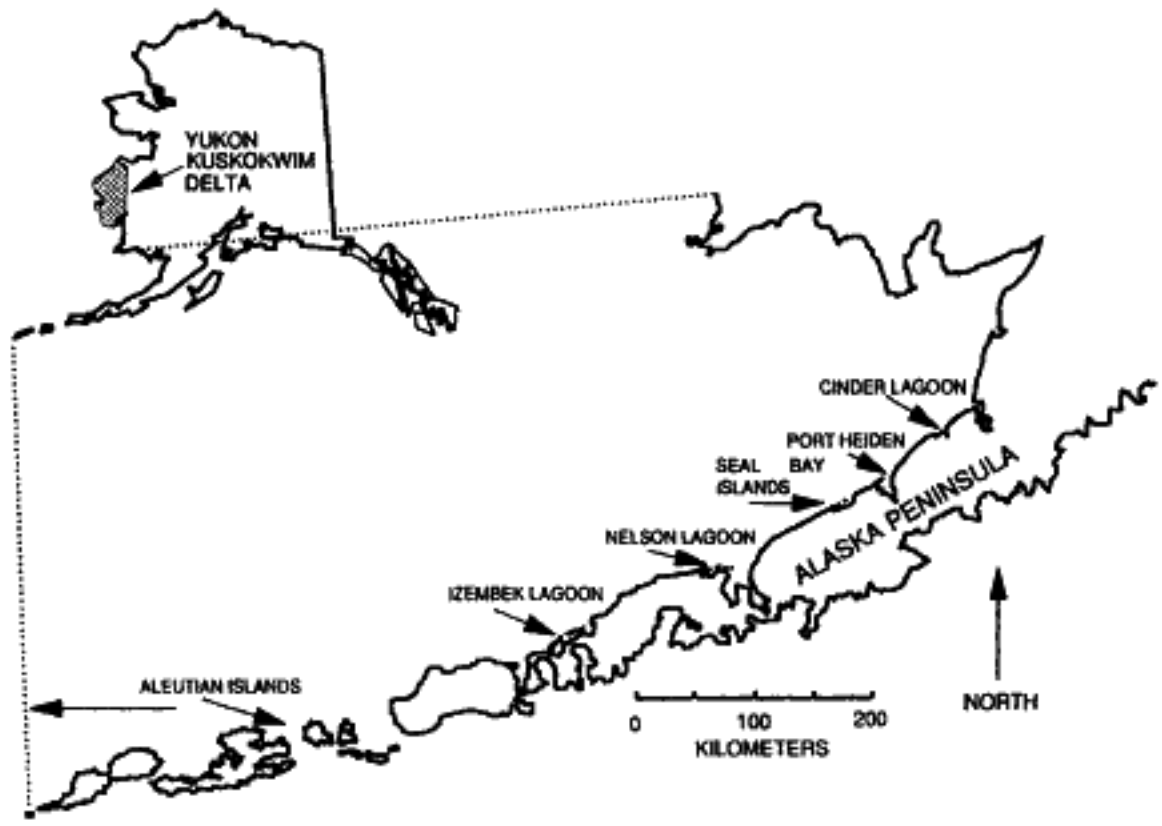

Fig. 1. Distribution of emperor geese during the breeding season on the Yukon-Kuskokwim Delta and during migration at staging areas on the Alaska Peninsula, 1988–92.

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METHODS

Banding and Resighting Effort

We captured adult (n = 1,115) and juvenile (n = 1,578) emperor geese with corral traps on the Yukon-Kuskokwim Delta (Fig. 1) during the flightless period in late July and early August 1988–90. We fitted geese with plastic neck collars and metal U.S. Fish and Wildlife Service leg bands. We used acrylic cement to bond the 2 ends of each collar. We determined sex by cloacal examination and age by plumage characteristics (Owen 1980).

We obtained resightings of banded geese on spring and fall staging grounds on the Alaska Peninsula (Fig. 1). All emperor geese were believed to use these areas during migration (Petersen and Gill 1982). The resighting period encompassed the majority, but not all, of the time geese were present at these staging areas. First and last dates of resighting were 17 April and 21 May (spring) and 9 September and 17 November (fall). Resighting effort initially began at Cinder Lagoon during fall 1988 and was expanded to Nelson Lagoon in spring 1989 and to Port Heiden Bay and Seal Islands in fall 1990 (Fig. 1). All resightings were obtained by 2–4 project personnel located at each staging area. On the basis of spring and fall aerial surveys, 84% of the emperor goose population was located in the 4 staging areas sampled (R. J. King, unpubl. data).

We opportunistically observed goose flocks at each staging area to maximize the number of unique individuals seen. Tide and weather considerations dictated specific sampling on a given day within staging areas, but we visited all accessible areas of goose concentration multiple times per season. We observed 44–711 individuals each season, totaling 2,147 observations.

Survival Rates

Definition of Sampling Periods.—Band-resight histories contained 3 banding periods (1988–90) and 8 resighting periods (fall 1988–spring 1992). This scenario allowed for survival estimation in 3 different seasons in each of 3 years, totaling 9 survival periods. On the basis of approximate midpoints of banding and resighting periods, survival periods pertained to the following: postbanding = 1 August–30 September, overwinter = 1 October–30 April, and

oversummer = 1 May–30 September. Because these seasonal periods were of different durations, we also calculated monthly survival estimates for each season to make estimates comparable among seasons.

We estimated survival rates using Jolly-Seber mark-recapture models (Jolly 1965, Seber 1965, Lebreton et al. 1992) and computer programs RELEASE (Burnham et al. 1987) and SURVIV (White 1983). We classified geese as seen during a given season if they were located ≥1 time at any staging area anytime during this resighting period. We analyzed adults and juveniles separately (i.e., juveniles did not enter the adult cohort). U.S. Fish and Wildlife Service personnel banded an additional 1,335 geese on the Yukon-Kuskokwim Delta with neck collars during 1982–87. Capture protocol and neck collar materials were similar to 1988–90 banding efforts. We included these geese in survival analyses as adults if they were resighted on the Alaska Peninsula during fall 1988 or later (n = 56), in which case we treated their first resighting as their time of original banding.

Heterogeneity in Resighting Probabilities.— We did not expect to see some geese after banding because we did not monitor all staging areas. Because geese exhibit some philopatry to staging areas (Schmutz, unpubl. data), some geese may repeatedly use unmonitored areas and thus never be seen. We conducted simulations to estimate bias in survival rates caused by this interaction of goose philopatry with our resighting effort (Appendix A). To counter bias caused by heterogeneity in resighting probability, we investigated subsetting the data by treating an individual's first resighting as its time of original banding. This analysis strategy eliminated all those geese that consistently use unsurveyed areas, and effectively created philopatric subpopulations specific to each monitored staging area. Therefore, our simulations examined one dataset using all banding and resighting information (the Full dataset) and another dataset conditioned by first resighting (the Subset dataset). Simulations suggested that survival estimation using the Full dataset would result in a strong, negative bias in postbanding estimates and a weak, positive bias in some overwinter and oversummer estimates (Appendix A). However, estimation with the Subset dataset should result in unbiased estimates. Subsequent analyses of overwinter, oversummer, and annual survival used these data. Survival rates during postbanding periods were not estimable with Subset data. However, analyses of survival during postbanding periods, using the Full dataset, are described later.

Table 1. Series of models used to estimate survival rates (S) and resighting probabilities (p) using Subset data for emperor geese in Alaska, 1988–92. Subscripts indicate which factors are allowed to vary. For example, in Model 4, S varies by sex and season, but within sexes and seasons, S is constant across years. Resighting probability varies by year and season but is constant for sex. Model 7 is a special case of Model 3 where S is constrained across certain seasons and years.

Model no.	Model parameters
Adults	
1	$S_{sex \cdot year \cdot season}$, $p_{sex \cdot year \cdot season}$
2	$S_{sex \cdot year \cdot season}$, $p_{year \cdot season}$
3	$S_{year \cdot season}$, $p_{year \cdot season}$
4	$S_{sex \cdot season}$, $p_{year \cdot season}$
5	S_{season}, $p_{year \cdot season}$
6	S, $p_{year \cdot season}$
7[a]	$S_{year \cdot season\ (OS90=OS91,\ OW88=OW89=OW90)}$, $p_{year \cdot season}$
Juveniles	
8[b]	$S_{year \cdot season \cdot sex \cdot age}$, $p_{year \cdot season}$
9	$S_{year \cdot season \cdot age}$, $p_{year \cdot season}$
10	$S_{year \cdot season \cdot sex}$, $p_{year \cdot season}$
11	$S_{season \cdot age}$, $p_{year \cdot season}$
12	S_{season}, $p_{year \cdot season}$
13	S_{age}, $p_{year \cdot season}$
14	S, $p_{year \cdot season}$

[a] OS90 = oversummer survival in 1990; OS91 = oversummer survival in 1991; OW88 = overwinter survival in 1988–89; OW89 = overwinter survival in 1989–90; and OW90 = overwinter survival in 1990–91.

[b] Age was constrained to be invariant among oversummer periods but was allowed to vary between an individual's first overwinter period and all subsequent overwinter periods.

Seasonal Survival Rates from Subset Data.— Using Subset data, we constructed a series of models to define seasonal survival and resighting parameters across sexes, seasons, and years (Table 1). We analyzed juveniles and adults separately to simplify analyses and because few geese banded as juveniles were resighted at ≥2 years of age (the earliest suspected time of initial breeding). For analyses of juveniles, we included an age variable (Table 1). We defined 2 parameters for overwinter periods with respect to age: the first overwinter period after hatch and all other overwinter periods. We defined only 1 oversummer period with respect to age because of poor sample sizes. We tested for variation between sexes and ages and among seasons and years with likelihood-ratio tests between nested models (White 1983). We selected the most appropriate model by examining goodness-of-fit tests, likelihood-ratio tests, and Akaike's Information Criterion (AIC) (Burnham and Anderson 1992). After model selection, we

adjusted point estimates and their variances for collar loss (see below).

Annual Survival Rates from Subset Data.—We calculated annual estimates with these same data. We restricted analyses of annual survival to adults for comparison with Petersen's (1992) data. Petersen (1992) conducted a neck-collar study of adult female emperor geese on the Yukon-Kuskokwim Delta during 1982–86. She marked females while they incubated nests and resighted them in subsequent breeding seasons. We incorporated her data into a SURVIV model (White 1983) to compare survival rates between the 2 studies with likelihood-ratio tests.

Seasonal Survival Rates from Full Data.—Estimation of postbanding survival was not possible with Subset data because the period from banding to fall was, by definition, excluded from these data. We therefore estimated survival for the 3 postbanding periods, using the Full dataset. Analysis with the Full dataset, however, would be expected to result in negative bias (Appendix A). Geese philopatric to unmonitored staging areas would appear in the data as having been banded and then disappearing during that first period after banding. To counter this bias, we developed an adjustment procedure that incorporated what proportion of the population occurred at unmonitored staging areas. By using different subsets of our resighting data with data on the population distribution of staging emperor geese, we developed a regression between estimated survival rates and what proportion of the population we sampled.

Aerial population surveys of emperor geese during spring and fall staging indicated a relatively consistent distribution among staging areas across years (R. J. King, unpubl. data). These surveys provided an independent assessment of the proportion of the population located in each staging area. For the 1990 banded cohort, all resightings occurred at 4 of these staging areas. By calculating survival estimates for this cohort, using data from all 4 sampled staging areas and also from subsets of these 4 areas, we obtained 15 different survival estimates for each period, each calculated from data where a different proportion of the total population was sampled (1 estimate, using all 4 staging areas; 4 estimates, using 3 staging areas; 6 estimates, using 2 staging areas; and 4 estimates when staging areas were analyzed alone). We calculated survival rates with RELEASE (Burnham et al. 1987) with no constraints on parameters. We then performed linear regressions for female and male adults between the proportion of the population sampled and the resultant survival estimate. We felt a similar analysis of juveniles would not be meaningful because we obtained too few resightings of juveniles during spring resighting periods. Each survival rate within each regression was weighted by the inverse of the estimated variance of that survival rate estimate. Using the predictive equation from significant ($P < 0.05$) regressions, we calculated a predicted value for $\hat{S}$, $\hat{S}_{predicted}$, given that 100% of the population was sampled. Variance of $\hat{S}_{predicted}$ was calculated, using the delta method (Seber 1982: 7), as

$$\hat{\text{var}}(\hat{S}_{predicted}) \approx \hat{\text{var}}(\hat{B}_0) + 2x\,\hat{\text{cov}}(\hat{B}_0,\hat{B}_1) + x^2\hat{\text{var}}(\hat{B}_1),$$

where $\hat{B}_0$ and $\hat{B}_1$ were estimates for the intercept and slope parameters, respectively, from the regression, and x was the proportion of the population sampled ($x = 1.0$). These estimates were then additionally adjusted for neck-collar loss (see below). With this analysis, we assumed that collared geese were distributed among staging areas similarly to the distribution of the entire population.

We did not apply regression analyses and adjustment procedures to 1988 and 1989 cohorts because fewer staging areas were sampled during these years. Instead of 15 possible survival rates as in the 1990 cohort, we could only derive 1 for the 1988 cohort and 3 for the 1989 cohort. Comparison of unadjusted estimates of postbanding survival among years would not be valid because of variable resighting effort. However, within-year comparisons between sexes should not be affected by among-year variation in resighting effort. Using the Full dataset, we compared postbanding survival between sexes with SURVIV (White 1983). We built only 2 models for this analysis: (1) a null model with its only constraint being that survival was equal between sexes during all 3 postbanding periods, and (2) an alternative model with no parameter constraints. We then tested the hypothesis of no sex differences in survival during postbanding periods with a likelihood-ratio test.

Neck-Collar Loss.—We could not estimate rates of neck-collar loss in emperor geese because few geese ($n = 12$) were recaptured during banding drives. However, all 12 recaptures had retained their neck collars. Neck-collar loss was

Table 2. Model selection criteria (Akaike's Information Criterion [AIC], goodness-of-fit tests, and likelihood-ratio tests) for models of seasonal survival during overwinter and oversummer periods in adult and juvenile emperor geese in Alaska, 1988–92.

Model[a]	No. of parameters	AIC[b]	Goodness-of-fit test[c]	Likelihood-ratio tests that contrast model no. below with models listed in the far left column[d]					
Ad (model no.)				2	3	4	5	6	7
1	25	235.6	0.37	0.20	0.67	0.44	0.57	<0.01	0.78
2	19	232.1	0.28		0.99	0.69	0.83	<0.01	0.99
3	13	220.9	0.50				0.29	<0.01	0.76
4	11	221.7	0.39				0.89	<0.01	
5	9	217.9	0.46					<0.01	
6	8	238.0	0.02						
7	10	216.1	0.58				0.05	<0.01	
Juv (model no.)				9	10	11	12	13	14
8	23	214.0	0.46	0.78	0.34	0.35	<0.01	0.42	<0.01
9	15	202.8	0.56			0.09	<0.01	0.14	<0.01
10	13	205.1	0.42			0.36	<0.01	0.52	<0.01
11	10	202.3	0.42				<0.01	0.84	<0.01
12	9	267.7	<0.01						<0.01
13	9	200.4	0.45						<0.01
14	8	229.8	<0.01						

[a] Refers to models whose parameterizations are given in Table 1.
[b] Lowest AIC values indicate most appropriate model (Burnham and Anderson 1992).
[c] $P > 0.05$ indicates the model fits the data.
[d] Likelihood-ratio tests contrast a general model (far left column) with a reduced (fewer parameters) form of the same model. P-values are shown with probabilities <0.05 resulting in rejection of the reduced, or null, model in favor of the general, or alternative, model.

estimated for a sympatrically nesting population of cackling Canada geese (*Branta canadensis minima*). Similar collar materials and application procedures were used for both species. Sixty-nine cackling Canada geese were recaptured 1–9 years after original banding, and 5 losses were recorded (C. R. Ely, Natl. Biol. Survey, Anchorage, Alas., unpubl. data). We calculated annual collar retention rate, $\hat{\theta}$, and its variance with SURVIV (White 1983). The estimated rate of annual collar retention was 0.981 (SE = 0.019). Because survival periods of interest were <1 year, we assumed collar loss was constant throughout a year and adjusted for shorter periods with $\hat{\theta}' = \hat{\theta}^{(m/12)}$, where m = the number of months in the relevant survival period, and $\hat{\theta}'$ was the retention rate for the relevant survival period. Variance of $\hat{\theta}'$ was derived with the delta method (Seber 1982:7) and was computed as

$$\hat{\text{var}}(\hat{\theta}') \approx \hat{\text{var}}(\hat{\theta})m^2\hat{\theta}^{(m/6-2)}/144.$$

Following Pollock (1981) and Nichols et al. (1992), we then calculated adjusted survival rates as $\hat{S}' = \hat{S}/\hat{\theta}'$, where $\hat{S}$ was the Jolly-Seber estimate of survival, and $\hat{S}'$ was the Jolly-Seber estimate adjusted for collar loss. Variance of this adjusted estimate was

$$\hat{\text{var}}(\hat{S}') \approx (\hat{S}')^2(\hat{\text{var}}[\hat{S}]/[\hat{S}]^2 + \hat{\text{var}}[\hat{\theta}']/[\hat{\theta}']^2).$$

RESULTS

Overwinter and Oversummer Survival

Model Selection.—Resighting probabilities did not differ between adult males and adult females (Model 1 vs. 2, Table 2), and thus were constrained to be equal in later analyses. Resighting parameters could not be further reduced because of variable resighting effort. Survival rates between adult males and adult females did not differ (Model 2 vs. 3, Table 2). Overall, there was no detectable variation in survival among years within seasons (Model 3 vs. 5). However, examination of point estimates under Model 3 led to the hypothesis that survival during oversummer 1989 did not differ from survival during oversummer 1990–91. Because this test (Model 5 vs. 7, Table 2) was an unplanned comparison, we used a more stringent α level. Therefore, we interpreted the resultant $P = 0.05$ as a failure to detect annual variation in oversummer survival. We here relied on the likelihood-ratio test for inference, rather than the AIC, which was lowest for the year-specific model. Model 5 (Table 1) was therefore used to describe data for adults. This model fit the observed data (Table 2).

We did not detect differences among sexes (Model 8 vs. 9, Table 2) or years (Model 9 vs. 11, Table 2) for survival rates in juveniles. How-

Table 3. Estimates of seasonal and monthly survival for adult and juvenile emperor geese in Alaska, 1988–91. Overwinter (1 Oct–30 Apr) and oversummer (1 May–30 Sep) estimates were derived from the Subset dataset, which was conditioned by first resighting.

Period	Seasonal survival		Monthly survival	
	$\hat{S}$	SE	$\hat{S}$	SE
Adults[a]				
Overwinter 1988–90	0.663	0.024	0.940	0.009
Oversummer 1989–91	0.898	0.032	0.980	0.010
Juveniles[b]				
First overwinter	0.104	0.018	0.710	0.018
Subsequent overwinter	0.708	0.045	0.943	0.010
Oversummer	0.707[c]	0.045	0.943	0.010

[a] Estimates from Model 5 of Table 1.
[b] Estimates from Model 13 of Table 1.
[c] Although constrained in Model 13 to be equal to estimates for subsequent overwinter estimates, this estimate is slightly different because different period durations resulted in slightly different collar loss adjustments.

ever, survival in the first overwinter period after hatch was lower than in subsequent overwinter periods (Model 11 vs. 12, Table 2). Subsequent overwinter and oversummer periods did not differ from each other (Model 11 vs. 13, Table 2). Data for juveniles best fit Model 13 (Tables 1 and 2). Results of model selection for adults and juveniles were identical for seasonal and monthly parameterizations of survival.

Point Estimates.—We report survival estimates for adults, using Model 5, and for juveniles, using Model 13 (Tables 1 and 3). Monthly survival among all seasons and age classes was ≥0.940, except for juveniles during their first overwinter period (0.710) (Table 3).

Annual Survival

Three annual survival parameters, fall 1988–91, were estimable. From our seasonal analysis, we detected no differences in survival between sexes (Model 2 vs. 3, Table 2), so we pooled sexes to estimate annual survival rates. We detected no annual variation in survival ($P = 0.775$). We estimated annual survival of geese during this study to be 0.619 (SE = 0.019). Three annual estimates, spring 1982–85, were estimable from Petersen's (1992) data. We detected no overall annual variation in survival ($P = 0.304$); however, large variances may have precluded detection. From Petersen's (1992) data, we estimated annual survival of geese during 1982–85 to be 0.601 (SE = 0.056), which is similar to the 0.587 estimated by Petersen (1992) via a Kaplan-Meier analysis procedure (Pollock et al. 1989). Annual survival of geese during this study (1988–91) and Petersen's (1992) study (1982–85) did not differ ($P = 0.709$). Using program SURVIV, we investigated the power of this test to detect differences between the 2 studies, given they really existed. If the true difference in survival rate was only 0.619 − 0.601 = 0.018, then we had only a 7% chance of detecting the difference (for $\alpha = 0.05$). However, if true survival had changed by 0.10, then we had a 63% chance of detection, and if survival had changed by 0.20, then we had a >99% chance of detection. After adjustment for collar loss, annual survival of adults for this study was 0.631 (SE = 0.023).

Postbanding Survival

Regressions between estimated survival rates and the proportion of the population sampled were significant for female and male adults during postbanding periods (Table 4). Similar regression analyses during overwinter ($r^2 = 0.14$, $P = 0.16$) and oversummer ($r^2 < 0.014$, $P = 0.96$) periods were not significant for adult females, indicating survival estimates for these periods were insensitive to what proportion of the population we sampled. These nonsignificant regressions corroborated results of our simulations of resighting effort (Appendices A and B). Estimated survival of adult females was less than that for adult males across all 3 postbanding periods ($P = 0.001$). The model for survival differences between sexes fit the data ($P = 0.077$).

DISCUSSION

Estimated seasonal and annual survival rates for emperor geese are low relative to some other goose populations (e.g., Owen and Black 1989*a*).

Table 4. Bias adjustment of postbanding survival of emperor geese banded in 1990 on the Yukon-Kuskokwim Delta, Alaska. Bias adjustments are based on linear regressions between the proportion of the staging population that was sampled, and survival estimates are calculated from those sampled proportions. Regression coefficients were used to calculate a predicted survival rate given that the entire population was sampled.

Variable/bias adjustment	Adult F	Adult M
r^2, P (postbanding)	0.78, <0.01	0.89, <0.01
Predictive equation	$0.660x + 0.187$	$0.649x + 0.364$
Survival esitmate[a]	0.684 (0.041[b])	0.862 (0.046)
Predicted survival estimate[c]	0.847 (0.055)	1.013 (0.033)
Predicted survival estimate adjusted for collar loss	0.850 (0.055)	1.017 (0.033)
Monthly survival estimate	0.933 (0.026)	1.007 (0.014)

[a] Survival estimate generated from resightings at all 4 staging areas (84% of the population) under a fully parameterized model in RELEASE (Burnham et al. 1987).
[b] SEs of survival estimates in parentheses.
[c] Calculated by substituting 1.0 for x in the predictive equation. Variance derived with the delta method (Seber 1982:7).

Confidence in these estimates can be assessed by examining sources of potential bias created by violation of assumptions and by comparison of rates with those for other goose species. Prominent assumptions in mark-resight studies of survival include (1) homogeneity in survival and resighting probabilities among members of a group (e.g., adult males), (2) absence of permanent emigration from the study area, (3) marker retainment, and (4) absence of a marker effect on survival. Heterogeneity in resighting probabilities is inherent in most studies, yet it does not bias survival estimates when occurring at small or moderate levels (Carothers 1979). Permanent emigration is equivalent to an extreme form of heterogeneity in resighting probability and results in negative bias if one interprets $1 - \hat{S}'$ as strictly reflecting mortality. We expected some permanent emigration and resultant negative bias in postbanding periods because geese commonly exhibit philopatry and we did not sample all staging areas. Because we conditioned analyses by treating first observations as the time of banding, we essentially created philopatric subpopulations for each staging area sampled. We feel this analysis eliminated gross heterogeneity in resighting probabilities.

Loss of neck collars was negligible in some studies (Hestbeck and Malecki 1989) and significant in others (Nichols et al. 1992). If collar loss rates are known, survival rates can be appropriately adjusted. We could not obtain an empirical estimate of collar loss rate for emperor geese. However, we feel that use of a collar-loss rate estimate for cackling Canada geese was sufficient. Similar collar materials and banding methods were applied to these 2 sympatrically breeding species. In addition, no aspect of behavior or use of nonbreeding habitat by emperor geese logically induces suspicion of a loss rate greater than that for cackling Canada geese.

Neck collars may affect survival, but quantifying effects is difficult (Zicus et al. 1983, Samuel et al. 1990). Because we used data for individuals only after their first resighting, we eliminated banding effects or initial adjustment to wearing neck collars. Zicus et al. (1983) documented mortality in Canada geese due to accumulation of ice on neck collars. No ice was observed on collars of 105 emperor geese seen in the Aleutian Islands during winter 1988–92 (V. Byrd, U.S. Fish and Wildl. Serv., Homer, Alas., pers. commun.). However, we noticed increased feather wear beneath neck collars on some recaptured geese. Such wear could increase thermoregulatory costs, especially during winter. For our study, we have no data to support a neck-collar effect. However, we do not discount the possibility of such an effect, particularly on juveniles, on the basis of relatively low survival estimates as compared with other goose species (see below).

Annual survival estimates among adult geese vary. Survival in an unhunted population of barnacle geese (*Branta leucopsis*) was 0.845–0.956 (Owen and Black 1989*a*). In contrast, for a population of Canada geese in Utah, where hunting was believed to be additive to natural mortality, survival was 0.379–0.553 (Rexstad 1992). Kirby et al. (1986) found survival in black brant (*B. bernicla*) varied (0.591–0.984) between these two extremes. Although the context for such large variation in survival among species and populations is not discussed here, its magnitude suggests that our estimate of annual survival for adult emperor geese (0.631) is plausible.

Annual survival estimates for juvenile geese are less common and usually pertain to the period from just prior to fledging to 1 year later. Francis et al. (1992) observed large variation in point estimates of survival for juvenile lesser snow geese (*C. caerulescens caerulescens*) (about 0.10–0.70) in a long-term study. Our juvenile survival estimates are lower than the lowest years in this and other (Samuel et al. 1990, Rexstad 1992) longer-term (6–19 yr) studies. We detected no annual variation in juvenile survival in emperor geese; however, the short duration of our study may have precluded detection of such variation. Such comparatively low survival estimates for juvenile emperor geese cause concern that these estimates may contain negative bias. However, we cannot be certain of the existence or cause of such bias.

Natural mortality among juvenile emperor geese may be high. Their survival during migration and first fall is dependent upon their condition during late summer while still on the breeding grounds (Schmutz 1993). Migration mortality in juvenile geese can be important, as observed for barnacle geese (Owen and Black 1989*b*). Unlike most other geese, emperor geese use winter habitats without agricultural foods. Relatively high survival rates documented for other geese may be a consequence of the use of agricultural foods. Lack of agricultural foods and the relatively high latitude and inclement weather of their winter habitat in the Aleutian Islands may lead to comparatively high natural mortality in juvenile and adult emperor geese.

The lower survival of adult females relative to males during postbanding periods suggests that females may incur an increased cost of reproduction relative to males. However, Laing (1991) found that female emperor geese during brood rearing fed less than other species of geese, and inferred that emperor geese were therefore not nutritionally stressed during brood rearing. Most studies of geese have failed to find differences in survival relative to sex (e.g., Samuel et al. 1990, Francis and Cooke 1992, Rexstad 1992). Owen and Black (1989*a*) observed higher relative survival in males than in females for barnacle geese, whereas Raveling et al. (1992) observed the opposite in cackling Canada geese. The observed differences for emperor goose males and females did not persist for the entire year as we failed to detect survival differences between males and females for overwinter or oversummer periods.

An alternative explanation for these observed differences between males and females in survival is that they are not real and are merely an artifact of greater philopatry by females to staging areas (Rohwer and Anderson 1988). Postbanding survival estimates are biased by philopatry to unsampled staging areas (Appendix A). Under an assumed context of female-based philopatry, if a goose that uses unsampled staging areas loses its mate and then re-pairs, a female with a new male would likely continue to use the same unsampled staging areas whereas a male with a new female would likely go to the staging area used by the female. If these new females used staging areas we sampled, then we would observe their banded mates, and survival estimates of males for postbanding periods would be inflated compared with that of females. However, we have not detected differences between sexes relative to their philopatry to staging areas (Schmutz, unpubl. data).

The effects of human harvest on waterfowl populations is subject to debate (Nichols et al. 1984). Correlative studies have inferred that goose harvest is additive to natural mortality (Francis et al. 1992, Rexstad 1992). Compensatory mortality implies that density dependent processes reduce survival (Anderson and Burnham 1976). This study and Petersen's (1992) occurred while the emperor goose population was approximately half of or less than recent historic levels (U.S. Fish and Wildl. Serv. 1989); thus, the influence of density-dependent processes during these studies was probably not significant. We speculate that current harvest of emperor geese may be largely additive to natural mortality.

Adult survival rates during 1982–85 (Petersen 1992) and 1988–91 (this study) were not different. This suggests that harvest rates during the 2 periods were similar, despite agreements in 1985 with native groups to stop subsistence harvest and a sport-hunting closure in 1986 (U.S. Fish and Wildl. Serv. 1989). Our tests had reasonably good power (≥63%) to detect changes in survival rates of ≥10% between the 2 studies.

MANAGEMENT IMPLICATIONS

Postfledging is a time of high mortality in juvenile geese (Owen and Black 1989*b*, Francis et al. 1992). Habitat conditions on breeding areas affect body mass and thus survival of juvenile emperor geese during migration (Schmutz 1993). Natural mortality during winter periods is also

significant and probably related to availability of quality forage to ensure a positive energy balance. Therefore, recruitment of juveniles and subsequent survival of juveniles and adults is dependent on availability of quality habitat in breeding, staging, and wintering areas. These areas are all remote and not likely to incur immediate habitat change. However, climate change and pollution related to petroleum development are long-term threats, the impact of which, if any, will be difficult to ascertain.

We believe that harvest mortality in emperor geese is currently additive to natural mortality. This implies that the ability to vary harvest rates would induce changes in overall survival rates. However, adult survival rates have not changed since the early to mid-1980s, further implying that management agreements to restrict harvest (U.S. Fish and Wildl. Serv. 1989) have not been effective. Persistent low population levels in emperor geese may be, in part, a consequence of this harvest. Minimizing harvest is desirable, but difficult, and has important socioeconomic and political considerations (Raveling 1984, Mitchell 1986, Pamplin 1986).

LITERATURE CITED

ANDERSON, D. R., AND K. P. BURNHAM. 1976. Population ecology of the mallard: VI. The effect of exploitation on survival. U.S. Fish and Wildl. Serv. Resour. Publ. 128. 66pp.

BURNHAM, K. P., AND D. R. ANDERSON. 1992. Data-based selection of an appropriate biological model: the key to modern data analysis. Pages 16–30 *in* D. R. McCullough and R. H. Barrett, eds. Wildlife 2001: populations. Elsevier Sci. Publ., London, U.K.

———, ———, G. C. WHITE, C. BROWNIE, AND K. H. POLLOCK. 1987. Design and analysis methods for fish survival experiments based on release-recapture. Am. Fish. Soc. Monogr. 5. 437pp.

CAROTHERS, A. D. 1979. Quantifying unequal catchability and its effect on survival estimates in an actual population. J. Anim. Ecol. 48:863–869.

EISENHAUER, D. I., AND C. M. KIRKPATRICK. 1977. Ecology of the emperor goose in Alaska. Wildl. Monogr. 57. 62pp.

FRANCIS, C. M., AND F. COOKE. 1992. Sexual differences in survival and recovery rates of lesser snow geese. J. Wildl. Manage. 56:287–296.

———, M. H. RICHARDS, F. COOKE, AND R. F. ROCKWELL. 1992. Long-term changes in survival rates of lesser snow geese. Ecology 73:1346–1362.

HESTBECK, J. B., AND R. A. MALECKI. 1989. Estimated survival rates of Canada geese within the Atlantic Flyway. J. Wildl. Manage. 53:91–96.

JOLLY, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. Biometrika 52:225–247.

KIRBY, R. E., M. J. CONROY, T. W. BARRY, AND R. H. KERBES. 1986. Survival estimates for North American Atlantic brant, 1956–75. J. Wildl. Manage. 50:29–32.

KLEIN, D. R. 1966. Waterfowl in the economy of the Eskimos on the Yukon-Kuskokwim Delta, Alaska. Arctic 19:319–336.

LAING, K. K. 1991. Habitat and food selection, behavior, and body composition of nesting emperor geese. M.S. Thesis, Univ. California, Davis. 84pp.

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.

MITCHELL, D. C. 1986. Native subsistence hunting of migratory waterfowl in Alaska: a case study demonstrating why politics and wildlife management don't mix. Trans. North Am. Wildl. Nat. Resour. Conf. 55:527–534.

NICHOLS, J. D., J. BART, R. J. LIMPERT, W. J. L. SLADEN, AND J. E. HINES. 1992. Annual survival rates of adult and immature eastern population tundra swans. J. Wildl. Mange. 56:485–494.

———, M. J. CONROY, D. R. ANDERSON, AND K. P. BURNHAM. 1984. Compensatory mortality in waterfowl populations: a review of the evidence and implications for research and management. Trans. North Am. Wildl. Nat. Resour. Conf. 44: 535–554.

OWEN, M. 1980. Wild geese of the world. B. T. Batesford Ltd., London, U.K. 236pp.

———, AND J. M. BLACK. 1989*a*. Barnacle geese. Pages 349–362 *in* I. Newton, ed. Lifetime reproduction in birds. Academic Press, New York, N.Y.

———, AND ———. 1989*b*. Factors affecting the survival of barnacle geese on migration from the breeding grounds. J. Anim. Ecol. 58:603–617.

PAMPLIN, W. L., JR. 1986. Cooperative efforts to halt population declines of geese nesting on Alaska's Yukon-Kuskokwim Delta. Trans. North Am. Wildl. Nat. Resour. Conf. 51:487–506.

PETERSEN, M. R. 1992. Reproductive ecology of emperor geese: survival of adult females. Condor 94:398–406.

———, AND R. E. GILL, JR. 1982. Population and status of emperor geese along the north side of the Alaska Peninsula. Wildfowl 33:31–38.

POLLOCK, K. H. 1981. Capture-recapture models allowing for age-dependent survival and capture rates. Biometrics 37:521–529.

———, S. R. WINTERSTEIN, C. M. BUNCK, AND P. D. CURTIS. 1989. Survival analysis in telemetry studies: the staggered entry design. J. Wildl. Manage. 53:7–15.

RAVELING, D. G. 1984. Geese and hunters of Alaska's Yukon Delta: management problems and political dilemmas. Trans. North Am. Wildl. Nat. Resour. Conf. 49:555–575.

———, J. D. NICHOLS, J. E. HINES, D. S. ZEZULAK, J. G. SILVEIRA, J. C. JOHNSON, R. W. ALDRICH,

AND J. A. WELDON. 1992. Survival of cackling Canada geese, 1982–88. J. Wildl. Manage. 56: 63–73.

REXSTAD, E. A. 1992. Effect of hunting on annual survival of Canada geese in Utah. J. Wildl. Manage. 56:297–305.

ROHWER, F. C., AND M. G. ANDERSON. 1988. Female-based philopatry, monogamy, and the timing of pair formation in migratory waterfowl. Current Ornithol. 5:187–221.

SAMUEL, M. D., D. H. RUSCH, AND S. CRAVEN. 1990. Influence of neck bands on recovery and survival rates of Canada geese. J. Wildl. Manage. 54:45–54.

SCHMUTZ, J. A. 1993. Survival and pre-fledging body mass in juvenile emperor geese. Condor 95:222–225.

SEBER, G. A. F. 1965. A note on the multiple recapture census. Biometrika 42:267–292.

———. 1982. The estimation of animal abundance and related parameters. Second ed. Charles Griffin and Co., London, U.K. 654pp.

U.S. FISH AND WILDLIFE SERVICE. 1989. Comprehensive management plans for arctic nesting geese in Alaska. Anchorage, Alas. 96pp.

WHITE, G. C. 1983. Numerical estimation of survival rates from band-recovery and biotelemetry data. J. Wildl. Manage. 47:716–728.

ZICUS, M. C., D. F. SCHULTZ, AND J. A. COOPER. 1983. Canada goose mortality from neckband icing. Wildl. Soc. Bull. 11:286–290.

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APPENDIX A

We conducted simulations intended to mimic our pattern of resighting effort. Our intent was to see how survival estimates were affected by this effort distribution and how conditioning on first resighting influenced bias in our estimates. We conducted 2 sets of simulations using RELEASE (Burnham et al. 1987); the first simulated the Full dataset, and the second simulated the Subset dataset. Because geese exhibit philopatry to staging areas (Schmutz, unpubl. data), we simulated subpopulations specific to staging areas for each set of simulations. All geese that used unsampled staging areas were simulated by 1 subpopulation. All other geese could have been simulated by another subpopulation, except that sampling began at different times at different staging areas. Thus, we simulated subpopulations according to when sampling began at staging areas, resulting in the following 3 subpopulations: Cinder Lagoon, Nelson Lagoon, and the combination of Port Heiden Bay and Seal Islands. Simulated values for S and $p > 0.05$ (p = resighting probability) were based on initial analyses of the Full dataset, with S equal among all staging areas within each season, and $p = 0.6$ or $p = 0.5$ for the resighting effort at a given staging area in either spring or fall, respectively. For unsampled areas (e.g., Nelson Lagoon during the first resighting period of the study), we simulated $p = 0.05$ to represent the infrequent times when a bird from the Nelson Lagoon subpopulation would be resighted at one of the areas we were then actively monitoring.

The number of geese in each subpopulation was simulated in proportion to the distribution of geese among staging areas as observed during aerial surveys of the entire population (R. J. King, U.S. Fish and Wildl. Serv., Fairbanks, Alas., unpubl. data). The timing of release of these geese into each subpopulation differentiated the 2 simulations. The first simulation (1,000 iterations) represented a single release of banded geese from the Yukon-Kuskokwim Delta that then dispersed to all staging areas (Appendix B). This simulation was analogous to the Full dataset as band-resight histories begin at original banding and a postbanding survival period was estimable. In the second simulation (1,000 iterations), the timing of each of 3 releases pertained to when sampling of that subpopulation began (Appendix B). In this simulation, each release was analogous to their first resighting, thus a release could not happen at a lagoon until resighting effort was expended there. Therefore, in the second simulation, which was representative of the Subset dataset, there was no unsampled subpopulation. These simulations demonstrated that under a Full dataset analysis, strong negative bias (absolute, as opposed to relative), as represented by -0.164 (Appendix B), occurred in estimates for postbanding periods. Positive bias was found in some subsequent periods, particularly the third and fourth periods after banding. In contrast, the simulation of a Subset data analysis showed virtually no bias in survival estimates for any period (Appendix B).

Appendix B. Approximations of bias in estimates of survival (S) for emperor geese under 2 different simulation scenarios. These scenarios were designed to emulate our pattern of resighting effort for individually banded geese on the Alaska Peninsula, 1988–92. One scenario treats birds from all subpopulations as having been banded during the flightless period in 1988 (analogous to the Full dataset). The other scenario treats birds of a given subpopulation as having been banded when resighting first began at that subpopulation (analogous to the Subset dataset).

	Subpopulation													
	Cinder Lagoon			Nelson Lagoon			Pt. Heiden/Seal Isl.			Unsampled				
Period i	p_i[a]	RF_i[b]	RS_i[c]	p_i	RF_i	RS_i	p_i	RF_i	RS_i	p_i	RF_i	RS_i	Full bias[d]	Subset bias
Band 1988		1,250			3,150			4,000			1,600			
Fall 1988	0.60		1,250	0.05			0.05			0.05			−0.164	
Spring 1989	0.50			0.25			0.05			0.05			0.001	0.000
Fall 1989	0.60			0.60		3,150	0.05			0.05			0.055	0.000
Spring 1990	0.50			0.50			0.05			0.05			0.037	0.000
Fall 1990	0.60			0.60			0.60		4,000	0.05			−0.014	0.001
Spring 1991	0.50			0.50			0.50			0.05			−0.002	−0.001
Fall 1991	0.60			0.60			0.60			0.05			−0.005	0.001
Spring 1992	0.50			0.50			0.50			0.05				

[a] Resighting probability.
[b] RF_i refers to the number of banded birds, or "releases," in period i under the simulation of the Full dataset. This number is scaled according to the proportion of all geese that occur in this subpopulation, as determined from independent surveys (R. J. King, U.S. Fish and Wildl. Serv., Fairbanks, Alas., unpubl. data).
[c] RS_i refers to the number of banded birds, or "releases," under the simulation of the Subset dataset.
[d] Bias is estimated by $S_i - E(\hat{S}_i)$.