SURVIVAL OF GREATER WHITE-FRONTED GEESE: EFFECTS OF YEAR, SEASON, SEX, AND BODY CONDITION

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Abstract: Information regarding the magnitude and variation in survival rates is necessary for understanding the causes of large changes in population size. We examined survival of greater white-fronted geese (*Anser albifrons frontalis*) in the Pacific Flyway during 1979–82. The population declined by 75% in the decade preceding our study but was stable during our investigation. Annual survival of adults (0.749, SE = 0.045) was 7% higher than during an earlier study. We developed a simple population model which suggests that recent (1985–96) survival rates may be as much as 10% higher in adults than the 1979–82 rate, which corresponds to population increases observed since 1985. Survival of adult females varied seasonally; monthly survival during a period of winter when no hunting or migration occurred was higher (0.986, SE = 0.015) than monthly survival at other times (0.964, SE = 0.006). Survival of adult males varied among years and with a general seasonal trend inverse to that for females. An index of body condition was positively related to survival of adult females in fall and spring, but not for adult males or immature geese. Monthly survival of immatures was lower during their first hunting season (0.886, SE = 0.026) than during all subsequent seasons (0.963, SE = 0.007). Annual survival of immatures beginning 1 October, immediately before the hunting season, was 0.471. Corresponding variations in survival rates, population numbers, and hunting regulations suggest that hunting may have influenced survival in this population of greater white-fronted geese.

JOURNAL OF WILDLIFE MANAGEMENT 63(4):1239–1249

Key words: *Anser albifrons frontalis*, body condition, California, demographics, greater white-fronted goose, harvest, mark–recapture, model selection, population model, survival analysis.

Greater white-fronted geese are important to hunters in central and western North America, but few data exist on their survival rates (Ely and Dzubin 1994). Timm and Dau's (1979) study of the Pacific Flyway population is the only published work reporting survival rates of greater white-fronted geese in North America that was based on modern band–recovery or mark–recapture techniques (e.g., Brownie et al. 1985, Lebreton et al. 1992). The Pacific Flyway population of greater white-fronted geese has fluctuated markedly since the late 1960s. Since Timm and Dau's (1979) study in 1967–69, greater white-fronted goose numbers declined rapidly until reaching their nadir about 1980 (O'Neill 1979, Ely and Dzubin 1994). Greater white-fronted goose numbers subsequently increased as evidenced from fall surveys in the Klamath Basin in northern California and southern Oregon, and summer surveys in the Yukon–Kuskokwim Delta (YKD), Alaska; these surveys documented a 10–12% annual increase between 1985 and 1996 (U.S. Fish and Wildlife Service [USFWS], unpublished data). Harvest regulations have been altered to compensate for these dynamics and suggest an influence of harvest on survival (Raveling 1984, Sedinger 1996; USFWS, unpublished data).

We used mark–recapture techniques to study survival patterns in Pacific Flyway greater white-fronted geese during 1979–82, a period when the population was relatively stable (Ely and Dzubin 1994). Our objectives were 3-fold. First, we estimated annual rates of survival and compared these to estimates by Timm and Dau (1979). We used a simple population model to examine the relation between survival rates and population change at several discrete times during the past 3 decades, with these times corresponding to different population trends and harvest regulations. Second, we partitioned and compared survival among seasonal periods that corresponded to differing mortality risks (e.g., presence or absence of hunting, migration, or breeding). Third, we tested if survival patterns were related to an index of body condition (i.e., mass adjusted for body size; Brown 1997). Sev-

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eral recent studies have found mass or condition to be related to survival for immature geese (Owen and Black 1989, Schmutz 1993, Sedinger et al. 1995), but such relations have not been examined for adults. Body mass and condition in geese are highly dynamic (Raveling 1979, Ankney 1982) and are influenced by food and habitat resources; thus, any relations of body condition to survival imply that management should consider these factors in addition to harvest.

STUDY AREA AND METHODS

Most (>80%) greater white-fronted geese in the Pacific Flyway breed on the YKD, stage in spring and fall in the Klamath Basin, and winter in the Central Valley of California (Ely and Dzubin 1994, Ely and Takekawa 1996). Our study focused on the YKD population. We limited potential erroneous inclusion of birds from the more southerly Bristol Bay population by banding some geese on the YKD (14% of the birds in this study) and excluding from analyses birds banded in California and Oregon in September. Bristol Bay greater white-fronted geese pass through the Klamath Basin earlier than YKD greater white-fronted geese and then winter primarily in Mexico (Ely and Takekawa 1996). All resighting occurred in the Klamath Basin of Oregon or in California.

Marking

We used cannon and rocket nets to capture greater white-fronted geese in fall, winter, and spring in Oregon and California. Flightless greater white-fronted geese were captured in July in Alaska with corral traps (Cooch 1953). We sexed all geese by cloacal examination and fitted each with a metal USFWS leg band and a uniquely coded plastic neck collar. During a subset of capture events, we measured body mass and lengths of culmen and tarsus and bill width to index body size. Ely and Raveling (1989) provide dates and general locations for most capture events.

Neck-Collar Retention

We estimated rates of neck-collar retention by using responses to hunter questionnaires. We mailed a questionnaire to all hunters that harvested a leg-banded goose and reported the band number to the U.S. Geological Survey Bird Banding Lab within 3 years of banding. Hunters were asked if the bird had a collar. For geese known to have been leg-banded and neck-collared, responses to the question about presence of a neck collar and time since banding provided data for estimating retention rates. We estimated an annual rate of retention by using program SURVIV (White 1983).

Observations and Definition of Survival Periods

We observed greater white-fronted geese in Oregon and California from first arrival in early September 1979–81 until departure in late April–early May 1980–82. Ely (1992) previously divided each year's observations into 6 periods relevant to management and biology of this species. We used sightings from 3 of these periods for survival analysis. The periods were (1) time of arrival of geese in September until opening of the hunting season in mid-October; (2) end of hunting in late January through the end of February; and (3) 1 April through the departure of geese, usually by the first week in May. We chose these 3 periods because they include meaningful phenomena in our seasonal estimates (e.g., legal harvest or migration). We refer to the survival interval between the first 2 sighting periods as the Fall–Harvest season because all regulated fall and early winter harvest south of Alaska occurred within this interval. We refer to the survival interval between the third and first sighting periods as the Migrating–Breeding season because both spring and fall migrations, breeding and wing molt, and subsistence hunting on the YKD occurred during this interval. The survival interval between the second and third sighting periods is termed No–Harvest because greater white-fronted geese were neither hunted during this period nor were they migrating. Based on midpoints of the sighting periods, the Fall–Harvest intervals lasted 4.33 months, No–Harvest lasted 2.33 months, and Migrating–Breeding lasted 5.33 months. These fractional months were used to adjust survival estimates to monthly rates and thus enable comparison among seasons.

Survival Rate Estimation and Model Selection

We conducted separate analyses for greater white-fronted geese banded as adults and immatures. Given the 3-year duration of this study, some birds banded as immatures were of known age and acquired adult plumage. We used these birds to estimate survival of 1- and

2-year-old birds. We did not include them in the adult analysis, because few of these birds would have entered the breeding population (some breed at 2 yr, but most not until 3 yr old; Warren et al. 1992, Ely and Dzubin 1994). We analyzed adult females and males separately because the large number of paired birds in our sample would create an inflated sample size with misleading estimates of variance (Ely 1993, Schmutz et al. 1995).

We used Cormack-Jolly-Seber (CJS) models to estimate survival rates from mark–resight data (Lebreton et al. 1992). For these analyses, a bird was denoted as resighted if it was observed subsequent to banding ≥1 times during a sighting period. We used the first sighting of an individual, rather than its time of banding, as its first entry in the capture history matrix so as to minimize possible biases from capture effects and to maintain consistency in definition of survival intervals.

We constructed a series of models to examine variation in resighting and monthly survival rates relative to season and year. We began model selection by first examining the fit of the general (all parameters) model, which estimated season and year-specific parameters for both survival and resighting rates. If this model did not fit, we used a variance inflation factor ($\hat{c}$) during analysis for both model selection and parameter estimation. Our measure of fit and $\hat{c}$ was derived from the deviance, which is calculated as $-2 \times$ the difference between the likelihood value for the saturated model and the likelihood for the model being considered (Lebreton et al. 1992). An initial estimate of fit and $\hat{c}$ was generated by dividing the deviance of the general model by the deviance degrees of freedom (McCullagh and Nelder 1989). To generate a less biased estimate of $\hat{c}$, we divided this $\hat{c}$ by the mean $\hat{c}$ obtained from a set of parametric bootstrap samples that were created via Monte Carlo simulations with parameters and sample size from the general model and with no extra-binomial variation (overdispersion) in the data (Efron and Tibshirani 1993, White and Burnham 1999). This estimate of $\hat{c}$ reflects how the deviance of the general model for the observed data was inflated relative to that from an identical model where data were not overdispersed, and they fit the general model.

We selected among models by using Akaike's Information Criterion, adjusted for small sample size (AIC_c; Burnham and Anderson 1998, White and Burnham 1999). If $\hat{c}$ was >1.0, we used a modified AIC_c, the quasi-likelihood AIC_c ($QAIC_c$; Anderson et al. 1994, Burnham and Anderson 1998). The best model was that with the lowest AIC_c. If several models had a low AIC_c, then we were uncertain which model best represented the data. Because the estimated value for a parameter depended on which model was used for estimation, we accounted for uncertainty in selecting the best model by deriving weighted estimates (Buckland et al. 1997). All survival rate analyses were conducted with program MARK (White and Burnham 1999).

We also calculated an annual rate of survival by conducting a similar analysis as above, except we used survival rates that pertained to each seasonal interval rather than monthly periods. Additionally, we pooled sexes to facilitate comparison of our annual survival estimate to Timm and Dau's (1979). The annual survival rate was the product of the 3 seasonal rates, with the variance being a function of the 3 seasonal rate variances and covariances, adjusted by $\hat{c}$ (Stromborg et al. 1988:592). We also adjusted the estimate of annual survival by dividing by neck-collar retention rate (Nichols et al. 1992) and assumed no covariance between neck-collar retention and seasonal survival for calculation of variance (Seber 1982:9). We compared our annual survival rate to Timm and Dau's (1979) estimate by using a 1-tailed Z test (Brownie et al. 1985). We expected that survival rates may have increased because fall harvest during our study (Sedinger 1996) was only half that reported by Timm and Dau (1979).

Population Model

We constructed a simple deterministic model (Leslie 1945, Caswell 1989), using a postbreeding census to estimate population growth rate (λ) from estimates for various reproductive and survival parameters. We estimated λ with this model for 3 different periods of study among which survival rates may have varied: (1) 1967–69 (Timm and Dau 1979), (2) 1979–82 (this study), and (3) 1985–96. Survival estimates are available for the first 2 periods. For comparison, we also estimated λ for these 2 periods from fall counts in the Klamath Basin (O'Neill 1979, Ely and Dzubin 1994), using log-linear regression (Eberhardt 1985). Immature survival rates were not directly available for 1967–69. We provided an estimate of immature survival for the

model by assuming that the amount of difference between adult and immature survival rates observed during 1979–82 also occurred during other study periods. No published estimates of survival exist for this population for the third period, 1985–96, but estimates of λ are available from surveys of the YKD breeding grounds (Butler et al. 1995; USFWS, unpublished data). Therefore, we calculated the survival rates necessary for this later study period, given the reproductive parameters and the observed λ. We derived estimates of reproductive parameters from Ely and Dzubin (1994) or literature cited therein, and we assumed such parameters did not change among the 3 periods of study.

Effects of Body Condition

We indexed body condition by adjusting live mass by an index for body size (Moser and Rusch 1988). Specifically, our body size measure for adults was the first principal component derived from culmen, tarsus, and bill width measurements. The latter 2 measurements were obtained for <50% of immatures. Thus, we used culmen as our body size index for these birds. We regressed live mass against the body size index and Julian date of capture within a banding period and used the residuals in our survival analysis. Because body condition in geese is temporally dynamic (Ankney 1982), we expected that a time-specific assessment of body condition would be relevant to survival for only a short period of time. Thus, we tested the effect of body condition on survival for the first 2 seasonal intervals immediately following banding. Unlike the survival rate analysis described above, we did not enter birds into the analysis when they were first resighted. Instead, we used their time of banding as their entry point into analysis. For each bird, we constructed a 4-occasion capture history where the final occasion was a pooled occasion consisting of all subsequent resighting periods. Because interval lengths and the potential influences of biological factors differed among seasons, we conducted 1 set of analyses for birds captured between 8 October and 8 November of each year, and another set of analyses for those captured during April. We used program MARK and selected among models by using AIC_c.

RESULTS

Marking, Resighting, and Neck-Collar Retention

Data from 1,224 captured and banded geese were used in survival analyses, including 490 juveniles and 734 birds >1-year old. Resighting rates varied seasonally (range = 0.415–0.742). The arithmetic averages of resighting rates for seasons and years were 0.583 for adult females, 0.561 for adult males, and 0.574 for immatures (best model for immatures did not include a sex effect).

We received 184 responses to questionnaires from hunters who had harvested neck-collared geese. These geese were harvested from 1–1,354 days after banding. A total of 178 (97%) geese was reported to have retained their neck collar; annual neck-collar retention rate was 0.955 (SE = 0.055).

Annual Survival of Adults

Annual survival was estimated as the product of seasonal estimates and was 0.749 (SE = 0.045), after adjusting for neck-collar retention. This estimate did not differ from Timm and Dau's (1979) estimate of 0.679 from 1967 to 1969 (P = 0.145). However, power to detect this magnitude of difference was low, considering the 95% confidence interval of the estimated difference overlapped zero (−0.060–0.200).

Seasonal Survival of Adults

The best model, as indexed by $QAIC_c$, indicated monthly survival of females was similar among years and between Fall–Harvest and Migrating–Breeding seasons, but these estimates were lower than during the No–Harvest season (Table 1, Fig. 1). The best model for males included variation in survival among years (Table 1). Parameter estimates averaged across models with $QAIC_c$ weights (Table 1) indicated that survival of males was generally higher than females during Fall–Harvest and Migrating–Breeding seasons, but lower during the No–Harvest season (Fig. 1).

Immature Survival

Analysis of survival data for immatures required more complex models. We expected the greatest disparity in survival among ages to be between geese in their first fall (Fall–Harvest) and subsequent ages. We found no evidence of a sex effect (Models 1 and 2; Table 2). The most parsimonious model indicated monthly survival was lowest in the first Fall–Harvest period (0.886, SE = 0.026). Survival for subsequent periods was greater (0.963, SE = 0.007) and

Table 1. Models used to estimate seasonal survival rates ($\hat{\phi}$) of adult greater white-fronted geese. We conducted separate analyses for females and males. The best model had the lowest quasi-likelihood Akaike's Information Criterion, adjusted for small sample size ($QAIC_c$)[a].

Model parameters	Number of parameters in model	Females		Males	
		$QAIC_c$	$QAIC_c$ weight[b]	$QAIC_c$	$QAIC_c$ weight
$\phi_{year * season}$	14	9.94	0.01	1.87	0.20
ϕ_{season}	9	2.04	0.19	2.16	0.17
ϕ_{hunt}[c]	8	0	0.54		
ϕ_{year}	9	5.05	0.04	0	0.51
ϕ	7	1.80	0.22	2.82	0.12

[a] Variance inflation factors, $\hat{c}$, were 1.274 for females and 1.130 for males.
[b] The $QAIC_c$ weights reflect the likelihood that the considered model was the best model, given these particular data, and these weights were used to calculate weighted parameter estimates (Burnham and Anderson 1998).
[c] Survival set to be equal (constrained) between 2 seasons with hunting, but different from the 1 season without hunting.

without additional variation among ages or seasons (Table 2).

We multiplied seasonal estimates and adjusted for neck-collar loss to estimate annual survival of immatures. Annual survival their first year (1 Oct–30 Sep) was 0.471 (SE = 0.048). Due to low survival during the first Fall–Harvest period, the previous estimate was lower than when annual survival was calculated starting on 1 February (0.645, SE = 0.051).

Population Model

Using the survival rates estimated above and values for reproductive parameters derived from the literature (Table 3), our estimate of λ for 1979–82 was consistent with fall counts that indicated this population was at or near its nadir during this time, and relatively stable (i.e., λ approx 1.0; O'Neill 1979, Ely and Dzubin 1994). Using survival rates based on Timm and Dau (1979), our estimate of λ was similar to the rate of decline in fall counts at the Klamath Basin (λ = 0.879 for 1965–78; O'Neill 1979). Combining reproductive parameters with adult and immature survival rates of 0.85 and 0.56 for 1985–96 yielded an estimate of λ (1.101), similar to that observed from surveys of the YKD (1.121) and the Klamath Basin (1.113; USFWS, unpublished data). Estimated fall age ratios of (31.0–32.7% juveniles) approximated the long-term average for this population (32.1%; Ely and Dzubin 1994; Table 3).

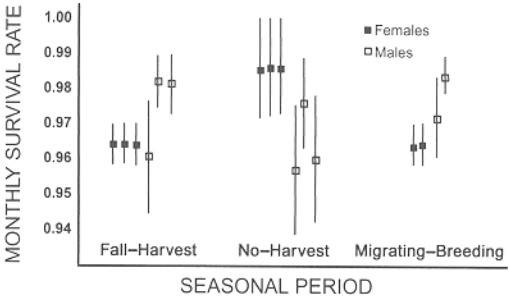

Fig. 1. Monthly survival rates in 3 seasons (Fall–Harvest, No–Harvest, Migrating–Breeding) for adult greater white-fronted geese. From left to right within sex and season groupings, estimates refer to 1979–80, 1980–81, and 1981–82. Vertical bars denote ±1 standard error, adjusted for variance inflation and model selection uncertainty (Buckland et al. 1997, Burnham and Anderson 1998).

Effects of Body Condition

Body mass residuals (which account for body size and condition) of adult females were positively correlated with survival probability in the first season subsequent to capture for birds captured in fall and spring (Table 4, Fig. 2); the sum of AIC_c weights for models with a condition effect was 0.71 in fall and 0.85 in spring. The slopes of these relations did not differ between seasons (Z = 0.043, P = 0.482). We found no compelling evidence for a relation between survival in the first season subsequent to capture and body condition for adult males captured in fall or spring, or for immatures captured in fall (Table 4); the sum of AIC_c weights for models with a condition effect were ≤0.45 for each of these 3 groups. Although the model with a positive second season (No–Harvest) condition effect had the lowest AIC_c for adult males in fall, the model with no condition effects fit nearly as well (AIC_c = 0.22, sum of AIC_c weights for models with a condition effect = 0.61).

DISCUSSION

Sex Differences

Seasonal survival rates differed between females and males, which implies that the mor-

Table 2. Models used to estimate seasonal survival rates ($\hat{\phi}$) of immature greater white-fronted geese. The best model is that with the lowest Akaike Information Criterion, adjusted for small sample size (AIC_c; Burnham and Anderson 1998).

Models	Model description	Number of parameters in model	AIC_c weight	AIC_c
1	ϕ varies among 2 sexes, 3 seasons, all age classes (<1-, 1-, 2-yr-olds), and years (3 yr for <1-yr-olds, 2 yr for 1-yr-olds).	42	0	28.75
2	ϕ varies among 3 seasons, all age classes, and years.	24	0	9.49
3	ϕ varies among 3 seasons and all age classes, but not among years for ≥1-yr-olds.	22	0.02	6.09
4	ϕ varies among 3 seasons and years for <1-yr-olds. No year or age variation among ≥1-yr-olds.	20	0.04	5.07
5	ϕ varies among 3 seasons and years for <1-yr-olds. No age, seasonal, or year variation in ≥1-yr-olds.	18	0.01	9.33
6	Variation in ϕ similar to Model 5 except that No–Harvest and Migrating–Breeding survival of <1-yr-olds are constrained to be equal.	16	0.04	5.38
7	Variation in ϕ similar to Model 6 except that annual variation is only for the Fall–Harvest period of <1-yr-olds.	14	0.16	2.35
8	ϕ varies among 3 constrained seasons: Fall–Harvest of <1-yr-olds, other seasons of <1-yr-olds, and all subsequent periods. No age, seasonal, or year variation in ≥1-yr-olds.	12	0.20	1.98
9	ϕ varies between 2 constrained seasons: Fall–Harvest of <1-yr-olds and all subsequent periods. No age, seasonal, or year variation in ≥1-yr-olds.	11	0.53	0
10	No variation in ϕ.	10	0	32.30

tality process may differ between sexes. Adult females survived at higher rates than adult males during the No–Harvest season but at lower rates during the Fall–Harvest and Migrating–Breeding seasons. Perhaps female greater white-fronted geese are more vulnerable to hunting mortality than males, which has been observed in greater snow geese (*Chen caerulescens atlantica*; Giroux and Bédard 1986), or they suffer greater mortality during migration, breeding, or molting. In contrast, males experienced greater mortality than females during midwinter when neither hunting nor migration occurred, and primary mortality agents were predation and disease (McLandress 1983). Male greater white-fronted geese more frequently engaged in vigilance and defense against predators during this time period than females (C. R. Ely, unpublished data), and thus may incur greater mortality from this protective behavior. Sex differences in survival among seasons also have been observed in cackling Canada geese (*Branta canadensis minima*; Raveling et al. 1992) and emperor geese (*C. canagica*;

Table 3. Demographics of greater white-fronted geese in the Pacific Flyway during Timm and Dau's (1979) study (1967–69) when the population was declining (O'Neill 1979), during our study (1979–82) when it was approximately stable (Ely and Dzubin 1994), and during 1985–96 when it was increasing (USFWS, unpublished data).

Demographic parameter[a]	1967–69	1979–82	1985–96
Adult survival	0.68	0.75	0.85
Immature survival	0.39	0.46	0.56
Breeding propensity (>3-yr-olds)	0.90	0.90	0.90
Breeding propensity (2-yr-olds)	0.25	0.25	0.25
Clutch size	5	5	5
Nesting success	0.60	0.60	0.60
Gosling survival	0.59	0.59	0.59
Survival postfledging to Klamath Basin	0.84	0.84	0.84
Predicted fall age ratio	0.327	0.319	0.310
Predicted population growth rate (λ)	0.869	0.965	1.101

[a] Adult and immature survival estimated as described in text. Breeding propensity approximated from Warren et al. (1992) and Ely and Dzubin (1994). Clutch size derived from Ely and Raveling (1984) and USFWS (unpublished data). Nesting success approximated apparent success rates (U.S. Geological Survey, unpublished data). Gosling survival is the product of partial and total brood loss reported in Ely and Dzubin (1994). Postfledging survival estimated as the ratio of average number of young per family after arrival in Klamath Basin in fall (2.34) divided by the average number of young just prior to fledging (2.8; Ely and Dzubin 1994).

Table 4. Survival of greater white-fronted geese relative to body condition at capture. Fall captures were 8 October–8 November, and spring captures were in April. Condition metrics used in each analysis were the residuals from regressions (1 for each season, age, and sex) of live mass as a function of date of capture and an index of body size. For adults, body size was the first principal component derived from measurements of bill width and lengths of culmen and tarsus. For immatures, culmen length indexed body size. The best model is that with the lowest Akaike's Information Criterion, adjusted for small sample size (AIC_c; Burnham and Anderson 1998).

Model[a]	Number of parameters in model[b]	AIC_c[a]				
		Adult females in fall (n = 78)	Adult males in fall (n = 80)	Adult females in spring (n = 85)	Adult males in spring (n = 84)	Immatures in fall (n = 133)
$\phi_{season * condition}$	6	3.94	3.61	4.21	5.09	3.39
$\phi_{season + condition}$	5	1.81	3.79	2.33	2.92	1.35
$\phi_{season + 1st_condition}$	5	1.81	4.38	2.12	3.12	1.43
$\phi_{season + 2nd_condition}$	5	4.28	1.63	5.88	2.96	1.79
ϕ_{season}	4	2.69	2.27	5.03	1.08	0
$\phi_{* condition}$	5	2.07	1.88	2.06	3.61	6.89
$\phi_{+ condition}$	4	0.15	1.67	0.18	1.82	4.77
$\phi_{1st_condition}$	4	0	2.29	0	2.09	4.94
$\phi_{2nd_condition}$	4	2.30	0	3.74	1.45	5.17
ϕ	3	0.96	0.22	2.90	0	3.54

[a] Season as a subscript indicates the intercept parameter in this model varied seasonally. A + indicates a consistent effect of body condition among seasons, whereas an * indicates a variable effect of condition among seasons. 1st_condition as a subscript indicates a condition effect in the first season after banding, but no condition effect subsequently. The 2nd_condition subscript connotes the opposite interpretation.

[b] Because of additional variation in resighting probabilities for adults in spring and immatures in fall, we estimated 1 extra parameter for each of these models.

Schmutz et al. 1994). Sex differences in seasonal survival of geese are evident despite a lack of consistent sex differences in annual survival (Samuel et al. 1990, Francis and Cooke 1992, Rexstad 1992, Schmutz et al. 1994). Annual survival of females and males would be expected to be equal for a monogamous species with long-term pair bonds (Stearns 1992). However, life-history theory does not preclude sex differences in seasonal mortality factors and rates. Our data suggest behavioral differences between males and females may lead to differential vulnerabilities to various mortality factors.

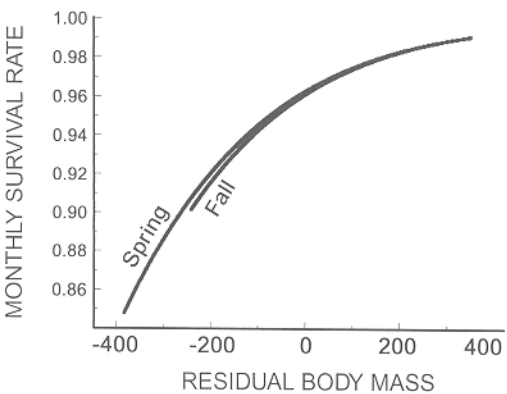

Fig. 2. Probability of adult female greater white-fronted geese surviving the next seasonal interval in relation to their body condition at capture. Body condition was indexed as the residual from a regression of live mass at capture versus capture date and an index of body size. Slope parameters for these relations were calculated via a logit link function and are of the following form: x = intercept + residual mass × slope, where e^x = survival rate ÷ (1 − survival rate). Slope parameters for adult females in fall and spring are 0.00412 (SE = 0.00261) and 0.00398 (SE = 0.00194). These estimates are not conditional on a single best model within Table 4; they reflect the relative likelihood of each considered model being the best representation of the data (Buckland et al. 1997).

Effects of Body Condition

Further indication of sex differences in mortality factors was suggested by the significant relation between body condition and survival for adult females but not adult males. The importance of accumulating nutrient reserves (and thus increasing body condition) in spring for reproduction by adult female geese was demonstrated by Ankney and MacInnes (1978) and Raveling (1979). However, our results indicate such dynamics also influence survival of greater white-fronted geese, at least for adult females. Although male geese also rely on nutrient reserves when breeding, their mass dynamics and reliance on reserves are not as great as for females (Ankney 1977). Body condition of females in spring is therefore important to both reproduction and survival; an extreme example of the consequences of poor condition occurs when female snow geese die of starvation while incubating (Ankney and MacInnes 1978).

We did not find strong evidence for a relation between body condition and survival for immatures, so other factors may exert greater influence on their survival, or our sampling was inadequate to detect such a relation. Although

survival of immature geese from breeding areas to fall or wintering areas has been related to prefledging body mass (Owen and Black 1989, Schmutz 1993), we sampled greater white-fronted geese after they had completed most of their migration. Thus, immatures in the poorest condition in late summer may have died by the time of capture in fall, leaving a population of immatures whose remaining variability in body mass and condition was not related to subsequent survival.

Population Dynamics

Few published data exist that can be compared to our survival data for greater white-fronted geese. Bell et al. (1993) studied survival of Greenland white-fronted geese (*A. a. flavirostris*) in the 1980s. Their reported mean annual survival rate (0.738) was similar to ours for adults; however, for immatures, their mean rate (0.634) was higher than our annual rate beginning on 1 October (0.471), but similar to our annual rate beginning after the Fall–Harvest season on 1 February (0.645). When we combined our survival data with information on other demographic parameters (Ely and Dzubin 1994) into a projection model, we estimated a rate of population growth similar to that derived from aerial surveys in fall (O'Neill 1979). In contrast, when we put Timm and Dau's (1979) survival estimates into this model and maintained the same values for other demographic parameters, we estimated a population growth rate similar to that observed during their earlier study. Therefore, the 7% difference in point estimates of adult survival between our study and Timm and Dau's (1979) study may have influenced growth of this population at these 2 times (i.e., stable during our study, declining during Timm and Dau's [1979]).

Despite our interpretation of the importance of an apparent 7% difference in survival, we acknowledge that we did not detect a statistically significant difference in survival between these 2 studies at $\alpha = 0.05$. We emphasize, however, that use of a specific α is arbitrary and represents a chosen balance between α and β (Tacha et al. 1982). We speculate that the difference in point estimates is real because (1) models of Schmutz et al. (1997) demonstrate that a 7% difference in survival can have a large effect on population growth rate, and (2) the estimated difference in survival may be even larger when one considers potential biases in survival estimates (see below).

Our survival estimates based on neck-collared greater white-fronted geese could be biased low for multiple reasons. First, it is possible that hunters were more likely to report neck-collared and banded geese than those with only a leg band (Samuel et al. 1990). If so, then our sample of hunters would underrepresent those who had harvested birds with lost neck collars, resulting in an overestimate of neck-collar retention and an underestimate of survival. Second, neck collars negatively influence survival in some goose populations (Castelli and Trost 1996). If such an effect occurred in our sample population, then our estimated survival rates are less than what was experienced by the population to which we are making inference. We have no data to address these potential biases; instead, we note that if our survival estimates are biased, they are likely biased low and that the true difference in survival between 1967–69 and 1979–82 was larger than reported here.

Subsequent to our study, this greater white-fronted goose population increased markedly. Surveys of breeding populations on the YKD (Butler et al. 1995) indicated a 2–3-fold increase in this population between 1985 and 1996, which is corroborated by similar increases in fall counts (USFWS, unpublished data). Given the assumption that reproductive parameters did not change, our model provides an estimate (0.85) of what annual survival of adults was during 1985–96, which is greater than our estimate for 1979–82 (0.75). The disparity in survival rates between these 2 periods would be less if our estimates for 1979–82 were biased low. A limitation is that we do not know how variable the other demographic parameters in our model were over time. However, our model should be robust to such variations because adult survival is known to have the largest relative effect on population growth for species with life histories similar to those of geese (Eberhardt 1985, Sæther et al. 1996, Rockwell et al. 1997, Schmutz et al. 1997).

MANAGEMENT IMPLICATIONS

Our data and models presented here suggest survival rates of greater white-fronted geese progressively increased from 1967–69 to 1979–82 and 1985–96. Concurrent reductions in harvest and increases in population size suggest harvest management affected survival and pop-

ulation dynamics in these greater white-fronted geese. Bag limits were reduced in 1978 (Raveling 1984); during our study, fall and winter harvest (Sedinger 1996) was less than half that reported during Timm and Dau's (1979) study. The Yukon Delta Goose Management Plan adopted in 1985 resulted in agreements with native communities to limit their spring subsistence harvest and additional restrictions on fall–winter harvest in California and Oregon (Pamplin 1986). After imposition of these restrictions, total annual harvest through 1993 constituted a smaller proportion of the overall population size of greater white-fronted geese than prior to these restrictions (Sedinger 1996). Despite these correlated changes in survival, harvest management, and population size, we cannot conclude that harvest management was indeed a causal mechanism because study design prevented that inference (Anderson et al. 1987, Nichols 1991). Other environmental factors also could have changed between the compared time periods and caused the observed changes in survival and population size.

One such environmental factor that may influence population dynamics since the late 1980s is the availability of foods for wintering geese. Greater white-fronted geese in California eat agricultural foods, primarily rice (Ely and Dzubin 1994). The amount and nature of rice farming changed little between the 1960s and late 1980s; however, burning of rice fields since then has been supplanted by different farming practices that have likely increased available roosting habitats but may have had uncertain effects on the availability of these grains to foraging geese (D. Orthmeyer, U.S. Geological Survey, personal communication). Changes in food availability may influence body condition, which we demonstrated affects survival in this population.

ACKNOWLEDGMENTS

We thank B. J. Aldrich, J. Beam, S. Castillo, E. J. Collins, B. Deuel, R. C. Fields, D. S. Gilmer, J. L. Hainline, J. B. Helvie, E. H. McCollum, E. J. O'Neill, W. C. Reinecker, and J. Romero for logistical support or field assistance. Winema Hunting Lodge supplied housing. D. P. Connelly and J. R. LeDonne made financial and logistical support available. D. G. Raveling provided guidance during the field portion of this project. The Agricultural Experiment station at University of California at Davis provided financial assistance. This manuscript benefitted from reviews by D. V. Derksen, D. Esler, M. S. Lindberg, and J. D. Nichols.

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Received 12 May 1998.
Accepted 5 April 1999.
Associate Editor: Kaminski.