Management and Conservation Article

Winter Fidelity and Apparent Survival of Lesser Snow Goose Populations in the Pacific Flyway

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ABSTRACT The Beringia region of the Arctic contains 2 colonies of lesser snow geese (*Chen caerulescens caerulescens*) breeding on Wrangel Island, Russia, and Banks Island, Canada, and wintering in North America. The Wrangel Island population is composed of 2 subpopulations from a sympatric breeding colony but separate wintering areas, whereas the Banks Island population shares a sympatric wintering area in California, USA, with one of the Wrangel Island subpopulations. The Wrangel Island colony represents the last major snow goose population in Russia and has fluctuated considerably since 1970, whereas the Banks Island population has more than doubled. The reasons for these changes are unclear, but hypotheses include independent population demographics (survival and recruitment) and immigration and emigration among breeding or wintering populations. These demographic and movement patterns have important ecological and management implications for understanding goose population structure, harvest of admixed populations, and gene flow among populations with separate breeding or wintering areas. From 1993 to 1996, we neckbanded molting birds at their breeding colonies and resighted birds on the wintering grounds. We used multistate mark–recapture models to evaluate apparent survival rates, resighting rates, winter fidelity, and potential exchange among these populations. We also compared the utility of face stain in Wrangel Island breeding geese as a predictor of their wintering area. Our results showed similar apparent survival rates between subpopulations of Wrangel Island snow geese and lower apparent survival, but higher emigration, for the Banks Island birds. Males had lower apparent survival than females, most likely due to differences in neckband loss. Transition between wintering areas was low (<3%), with equal movement between northern and southern wintering areas for Wrangel Island birds and little evidence of exchange between the Banks and northern Wrangel Island populations. Face staining was an unreliable indicator of wintering area. Our findings suggest that northern and southern Wrangel Island subpopulations should be considered a metapopulation in better understanding and managing Pacific Flyway lesser snow geese. Yet the absence of a strong population connection between Banks Island and Wrangel Island geese suggests that these breeding colonies can be managed as separate but overlapping populations. Additionally, winter population fidelity may be more important in lesser snow geese than in other species, and both breeding and wintering areas are important components of population management for sympatric wintering populations. (JOURNAL OF WILDLIFE MANAGEMENT 72(1):159–167; 2008)

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The western Arctic contains 2 large breeding colonies of lesser snow geese (*Chen caerulescens caerulescens*) that follow separate migration routes between their breeding and wintering areas (Johnson 1996). One colony at the Egg River on Banks Island (BI), Northwest Territories, Canada (Fig. 1), has increased 4.2% per year since 1953, but at a much slower growth rate than central Arctic lesser snow geese that have damaged Arctic habitats (Abraham and Jefferies 1997; Batt 1997; Hines et al. 1999*b*; Kerbes et al. 1999; Samelius et al., in press). In the fall, the BI population migrates through the prairies of western Canada and into Montana, USA (Bellrose 1980, Samuel et al. 1999; Fig. 1). Although a proportion of the BI population continues south into western Texas, USA, and central Mexico, most of the population migrates through northern California, USA, to winter in the Central Valley of California (Hines et al. 1999*a*). Recent evidence suggests that an increasing proportion of BI birds may be wintering in Texas and Mexico.

The second lesser snow goose breeding population in the western Arctic occurs on Wrangel Island (WI) in northeastern Russia (Bousfield and Syroechkovsky 1985, Syroechkovsky and Litvin 1986). The WI population has significant conservation status and international importance because it is the only remaining snow goose colony in Russia and the only wintering population of snow geese in Canada (Boyd 1995, Kuznetsov et al. 1998, Mowbray et al. 2000). The WI population levels have fluctuated dramatically and experienced inconsistent annual nest success, which is an important driver of population growth for the WI population (<10% of the population nesting during 6 yr of the past 30 yr; Kerbes et al. 1999, V. Baranyuk, Russian Ministry of Environment, unpublished data). The WI population is composed of 2 subpopulations, which nest in one mixed colony but winter in geographically separate areas in the Pacific Flyway (Bousfield and Syroechkovsky 1985; Fig. 1). In fall, the northern Wrangel Island (NWI) subpopulation migrates down the Pacific coast to the Fraser and Skagit River deltas of British Columbia, Canada, and Washington, USA. The southern Wrangel Island (SWI)

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Figure 1. The predicted approximate proportions of the northern Wrangel Island and southern Wrangel Island, Russia, and Banks Island, Canada, breeding lesser snow geese subpopulations that migrate to their wintering grounds.

these areas is crucial in defining goose population structure (Cooke et al. 1988, Robertson and Cooke 1999). Additionally, winter fidelity has received only limited attention for migratory waterfowl (Robertson and Cooke 1999). However, because pair-bond formation likely occurs on the wintering grounds, population mixing, movement of birds between wintering areas, and other large-scale movements during winter may influence demographics (immigration and emigration) or gene flow between populations (Prevett 1972, Cooke 1987, Robertson and Cooke 1999).

Lesser snow geese in the western Arctic provide an interesting case study of potential for population structuring, movement, and winter fidelity. On the wintering grounds, BI geese mix with similar Ross's geese (*Chen rossii*) that breed in the central Arctic and with the SWI geese from Wrangel Island, forming a generally indistinguishable panmixia of species and populations (Kelley et al. 2001). In contrast, NWI geese winter in a geographically separate region. To further complicate population assessment of the BI, SWI, and NWI geese, there is some evidence for exchange among these subpopulations (Hines et al. 1999a). Not only is there potential population exchange between WI wintering subpopulations, but SWI birds wintering in California could be mixing with BI birds.

Three significant challenges exist for the future management of lesser snow geese in the Pacific Flyway. First, expanding BI populations may threaten Arctic breeding areas and require population reductions similar to the central Arctic populations. Second, admixing of SWI and BI populations on wintering areas in California makes harvest management difficult because significant reduction of the BI population is likely to adversely impact the SWI population. Third, there are inherent challenges surrounding the international management (Russia, Canada, United States) and special conservation concerns associated with the fluctuating WI population. In response to these problems, the 1992 Pacific Flyway Council identified a comprehensive demographic assessment of western Arctic lesser snow geese, with specific attention to the WI population as an important management goal.

Our goal was to understand wintering fidelity and survival of lesser snow geese on Wrangel and Banks islands. Our specific objectives were to 1) compare the utility of face stain in WI breeding geese as a predictor of wintering area; 2) evaluate movement and potential demographic exchange among the BI, SWI, and NWI subpopulations to help understand emigration, immigration, and gene flow among these subpopulations; and 3) evaluate apparent survival rates among these populations to help understand population trends and harvest impacts.

STUDY AREA

We captured molting, flightless lesser snow geese during July and August on Wrangel Island, Russia (71°20′N, 179°40′W), and on Banks Island, Northwest Territories, Canada (72°20′N, 125°10′W). Wrangel Island is a 7,300-km^2 island approximately 140 km off the coast of far eastern

subpopulation also migrates primarily down the Pacific coast but continues through southern Oregon, USA, and northern California to winter in the Central Valley of California (Bousfield and Syroechkovsky 1985, Armstrong et al. 1999); a smaller portion of the SWI subpopulation migrates through Prairie Canada to wintering areas in California. During winter, the NWI birds acquire red face-staining patterns from feeding in the iron oxide sediments of the Skagit–Fraser estuaries, and the amount of stain has been used to distinguish the NWI and SWI birds (which do not acquire face staining) on their breeding area (Hohn 1955, Baranyuk and Syroechkovsky 1994, Baranyuk et al. 1999).

An understanding of arctic goose population structuring, including breeding, wintering, and migration areas and admixing among populations, is critical for their conservation and management. The characteristics of population structuring help to accurately define appropriate population units, identify constraints on population dynamics, establish harvest regulations, and determine interactions among goose metapopulations (Esler 2000). Because both breeding and wintering areas may have important yet separate demographic influences on goose population dynamics, fidelity to

Siberia. The island was designated a World Heritage site in 2004. More than 98% of the Asian lesser snow geese nest on Wrangel Island, and most of these birds nest at the Tundra River colony (Baranyuk 1992). Banks Island covers an area of 70,000 km^2 situated in the Inuvik region of the Northwest Territories and is Canada's fifth largest island. Over 95% of the western Canadian Arctic population of lesser snow geese nested at the Egg River colony on Banks Island (Kerbes et al. 1999). Individual birds with neck collars were identified by resighting at key staging areas during migration and on wintering areas in Canada and the United States, primarily in the Pacific Flyway.

METHODS

At Wrangel Island (1993–1996), we captured geese by driving birds into corral nets using an all-terrain vehicle or on foot, whereas on Banks Island (1994–1996), we used helicopter-drive trapping techniques with portable nets (Cooch 1953, Timm and Bromley 1976). We leg-banded geese with United States Fish and Wildlife Service metal rings, and marked many of the adult geese (>1 yr of age) with plastic neck collars engraved with a unique 3-character code. Wrangel Island neck collars were red with white characters, and Banks Island neck collars were black with white characters (Samuel et al. 2001).

We evaluated the probability that Wrangel Island birds captured on the breeding areas and resighted between December and January in the first year after banding would have fidelity to their respective winter areas. To this end, we evaluated the level of face staining (0 = no face stain, up to 6 = strong face stain) during capture on breeding areas as a predictor of wintering in Washington or British Columbia compared to California the following season. Face stain was consistently recorded by one biologist (V. V. Baranyuk) during all years of banding. We used logistic regression to evaluate the probability of WI geese marked in the summer being observed on the northern or southern wintering areas based on year of banding, face stain, or sex. We calculated the estimated number and proportion of WI geese observed on the northern or southern wintering areas by dividing the observed number of geese by the average resighting rates obtained for each wintering area.

Once birds were on the wintering grounds, neck collars allowed resighting of individual geese both within Skagit–Fraser estuaries in Washington and British Columbia and in the Central Valley of California during the fall–spring, 1993–1999. To ensure birds had reached their final wintering area, we only used resightings of marked geese obtained from December through January each year (Bellrose 1980, Armstrong et al. 1999). We used observations of neckbands on wintering areas to construct a complete history protocol needed to estimate apparent survival (φ) between winters, movement between wintering areas (ψ), and resighting rates (p; Burnham et al. 1987, Hestbeck et al. 1991, Williams et al. 2001). We used the multistrata analysis with live recaptures and simulated annealing in Program MARK (White 2004) to model survival, transition, and resighting probabilities for subpopulations. Our initial model contained 120 parameters for 5 years, 3 rates (survival, transition, and resighting probability), 2 sexes, 2 wintering areas (WA–BC and CA), and 2 breeding populations (BI and WI). Because the WI birds shared breeding areas and we never observed BI birds in the northern wintering area, we simplified our analysis of the 3 different subpopulations of geese (NWI, SWI, and BI). We reduced the number of parameters by constraining some parameters: 1) because we initially captured no birds in 1993 on BI, we set these annual survival and resighting probability parameters to zero; and 2) because we observed no BI birds wintering in northern areas, we set transition rates for BI birds from California to Washington–British Columbia and survival and resighting probability Washington–British Columbia to zero for BI birds. Therefore, our global model included 76 estimated parameters. We evaluated 22 nested models to calculate yearly apparent survival (φ), transition (ψ), and resighting (p) probabilities of male and female snow geese for any given year and banded on BI and WI. We established the nested models to evaluate hypotheses related to time-constant versus time-specific demographic rates, similarity in demographic parameters among the 3 goose populations, and differences in demographic parameters between male and female geese.

We estimated apparent survival rates for all populations because our analyses did not account for neckband loss or emigration of geese outside their expected wintering areas, and each of these factors can produce an underestimate of true survival (Samuel et al. 2001). In a similar manner, winter fidelity can be determined from transition rates (winter fidelity = 1.0 − transition probability), provided there is little permanent emigration. We evaluated the goodness of fit and variance inflation factor ($\hat{c}$) for the global model to determine if our data were overdispersed and whether the use of quasi-Akaike's Information Criterion (QAIC$_c$) would be warranted over AIC. We used Program UCARE to obtain an estimate of the goodness of fit for the global model and found no indication of overdispersion or heterogeneity ($\chi^2_{25} = 19.68$, $\hat{c} = 0.787$; Choquet et al. 2003). As a result we used AIC values, AIC differences (Δ_i), highest AIC weights (w_i), and likelihood ratio tests within MARK to evaluate the reliability of alternative models (Johnson and Omland 2004). We used the Δ_i value for nested models to interpret the relative support for an alternative model compared to the best model based on the following criteria: between 0 and 2 there is substantial empirical support for the alternate model, whereas a value between 4 and 7 indicates considerably less support for the alternate, and a value >10 indicates essentially no support (Burnham and Anderson 2002). We compared annual survival estimates from the best-fit model parameters using Program CONTRAST ($P \leq 0.05$; Sauer and Williams 1989).

We used a combination of parameter variables with subscript–superscript notation to define model parameters and thereby alternative nested model structures. We used subscripts to designate either sex-similar versus sex-specific

Table 1. Number of lesser adult snow geese captured and resighted on Wrangel Island, Russia, and Banks Island, Canada, breeding grounds and the number neckband observations on the wintering grounds, 1993–1999, Washington, USA,–British Columbia, Canada, and California, USA.

Breeding and wintering populations	Yr						
	1993	1994	1995	1996	1997	1998	1999
Breeding grounds (Jul)							
Banks Island	0	288	1,034	1,065	0	10	0
Wrangel Island	543	737	513	1,080	23	22	0
Wintering grounds (Dec–Jan)[a]							
WA and BC	0	188	477	146	196	507	178
CA (southern Wrangel Island geese)	0	172	332	390	691	448	13
CA (Banks Island geese)	0	0	113	514	741	548	19

[a] Note winter observations span across yr; for example, 1994 winter observations occurred during Dec 1993 and Jan 1994.

and time-constant versus time-specific parameter estimates and superscripts to designate parameter differences among the 3 wintering goose populations. Because we never observed BI geese in the northern wintering areas of the Fraser–Skagit rivers, we considered only 3 goose populations (BI, NWI, SWI). For example, we used this notation to identify population-similar and time-specific transition rates (ψ_t), population-specific and time-constant resighting rates (p^P), or time-constant apparent survival rates that were similar between NWI and SWI ($\phi^{NWI=SWI}$). Using this notation, a hypothetical model structure with year-, sex-, and population-specific apparent survival rates, year- and population-specific transition rates, and year-specific resighting rates with equal resighting between BI and SWI geese would be $\phi_{x \times t}^P \psi_t^P p_t^{BI=SWI}$.

RESULTS

Large numbers of captures at each of the breeding areas and neckband observations at each of the wintering grounds during 1993–1999 provided the ability to estimate apparent survival, resighting, and transition rates for adult geese from each of the 3 subpopulations (Table 1). During the breeding season, we leg-banded or neck-collared 2,373 adult geese from the BI population and 2,873 adult geese from the WI population. In December and January, we resighted 1,692 (803 M and 889 F) neck-banded geese in Washington or British Columbia, all from the WI population. We also resighted 3,981 (1,820 M and 2,161 F) neck-banded geese in California, 2,046 from the WI population, and 1,935 from the BI population.

Logistic regression indicated a significant effect associated with face stain ($P < 0.05$) and a significantly different pattern in 1994 ($P < 0.05$) compared to other banding years. The estimated proportion of birds observed at each wintering area based on resighting rates indicated that birds with a high degree of face staining ($\geq$level 5) had a high likelihood (>88%) of wintering in Washington and British Columbia (Table 2). Additionally, birds with low degrees of face staining ($\leq$level 1) showed a high probability ($\geq$90%) of wintering in California. However, birds with intermediate face staining (levels 2–4) were not consistently associated with winter areas in Washington–British Columbia or California. We focused our evaluation on fidelity to

wintering areas because of the large number of birds that had an undetermined level of face staining, the uncertainty in predicting individual fidelity from breeding to wintering grounds for birds with intermediate levels of face staining (scores 2–4 in Table 2), and the difficulty in obtaining sufficient recapture or resighting data at summer breeding colonies.

We evaluated 22 nested models of yearly apparent survival (ϕ), transition (ψ), and resighting (p) probabilities of male and female snow geese for any given year and banded on BI and WI for the lowest AIC values, lowest Δ_i, and highest w_i (Table 3). Given these criteria, our best model, with males and females exhibiting an additive effect on survival, showed strong support in describing the data: $\phi_{x+t}^P \psi^{NWI=SWI} p_{t*}^{BI=SWI}$, with $\Delta_i = 0$ and $w_i = 0.991$. This model estimated the following parameters: 1) apparent survival (ϕ), transition (ψ), and resighting (p) probabilities were time dependent with a neckband observation probability of 100% at the last time step and were not influenced by sex; 2) annual survival probabilities were different and additive between males and females; 3) annual resighting probabilities of BI birds in California equaled annual resighting probabilities of SWI birds in California (except for 1993–1994); and 4) transitions between California to Washington–British Columbia were equal with Washington–British Columbia to California for WI birds.

In the model, resighting probabilities on the California wintering grounds were generally high (74–90%). However, resighting rates on the Washington–British Columbia wintering grounds was highly variable (18–92%; Table 4), probably driven by annual variation in observer effort. As a result, standard errors for the survival and transition probabilities were variable (3–8%). Our model indicated <3% of the WI birds changed winter areas from one year to the next and these transition rates were similar between both wintering areas. Yearly survival estimates of BI birds were moderately low (49.0–64.5%) for 1994–1996 but improved (75.9–83.4%) during 1996–1997 (Table 4). Our models indicated that female survival was consistently 4–10% higher than male survival across populations and years. Within individual populations, BI females had higher apparent survival (10%) than males ($\chi^2_1 = 5.06$, $P < 0.01$), but there was no difference between males and

Table 2. Number of banded lesser snow geese on the Wrangel Island, Russia, breeding grounds exhibiting 7 levels of face stain (from wintering the previous year in WA or migrating through as in the case of wintering CA birds migrating back to Wrangel Island) that migrated back to either California, USA, or Washington, USA,–British Columbia, Canada, the following winter, 1993–1999.

Face stain[a]	CA		WA		Estimated proportion of birds wintering in WA (%)[b]
	n	%	n	%	
0	98	96.1	4	3.9	5.7
1	422	97.7	10	2.3	3.4
2	105	82.0	23	18.0	24.6
3	65	47.8	71	52.2	61.8
4	47	29.0	115	71.0	78.5
5	41	16.1	214	83.9	88.6
6	1	0.8	123	99.2	99.6
Undetermined	128		130		

[a] Levels of face stain (i.e., 0 = no stain, 6 = face highly stained).
[b] Adjusted proportion calculated from average resighting rates for CA = 0.836 and WA = 0.562.

females in the 2 WI subpopulations ($\chi^2_1 > 1.35$, $P > 0.14$). Across sexes and years, apparent survival rates for WI birds were similar for birds wintering in Washington–British Columbia (63.2–80.5%) or California (63.1–79.9%) between 1993–1994 and 1996–1997 ($\chi^2_1 = 0.05$, $P = 0.83$). Across sexes and years, WI birds had higher apparent survival than BI birds ($\chi^2_1 = 15.37$, $P < 0.001$).

Our analysis using resighting data provides a statistically powerful approach to evaluate within flyway movement, resighting rates, and apparent survival between our pop-

ulations. However, this analysis also ignores potential biases in apparent survival resulting from site fidelity and neckband retention (apparent survival [ϕ] = true survival [S] × site fidelity [F] × neckband retention [NB]). In our case, lack of fidelity (or permanent emigration) would occur when birds emigrated outside our observation areas in the Pacific Flyway. To assess this problem, we ran a simplified Burnham (1993) model on the leg-band recovery data to estimate true survival (S). Average true survival (S) was similar among all 3 populations: 0.644 (SE = 0.055) for BI, 0.636 (SE = 0.058) for NWI, and 0.705 (SE = 0.044) for SWI. In addition, the proportion of bands recovered outside the Pacific Flyway was 4% (4/97) for BI, 0% (0/121) for SWI, and 2% (1/69) for NWI, indicating strong fidelity of birds to their winter areas. These results suggest that lower apparent survival rates estimated for the BI birds, especially males, likely resulted from lower neckband retention for this population or the combination of fidelity and neckband retention (F × NB; Samuel et al. 2001).

DISCUSSION

Previous studies on lesser snow geese breeding on Wrangel Island indicated that face staining can be a limited predictor of whether birds wintered in the Fraser–Skagit region (higher levels of red face stain) or in California (Baranyuk and Syroechkovsky 1994, Baranyuk et al. 1999). Our results, based on twice as many observations, also showed that prediction of wintering areas was unreliable for geese with intermediate face stain (levels 2–4). This suggests that some

Table 3. Models estimating apparent survival (ϕ), transition (ψ), and resighting probabilities (p) of Wrangel Island, Russia (WI; including southern Wrangel Island [SWI] and northern Wrangel Island [NWI]), and Banks Island, Canada (BI), lesser snow geese in the Pacific Flyway, 1993–1999. We calculated Akaike's Information Criterion (AIC), AIC differences (Δ_i), AIC model weight (w_i), and model likelihood and deviance for each model.

Model[a]	AIC_c	Δ_i	w_i	Likelihood	Parameters	Deviance
$\phi_{x+t}^{P} \psi^{NWI=SWI} p_{t^*}^{BI=SWI}$	7,865.9	0	0.9991	1.0000	26	392.57
$\phi_{t}^{P} \psi^{NWI=SWI} p_{t^*}^{BI=SWI}$	7,881.8	15.91	0.0004	0.0004	23	414.54
$\phi_{t}^{P} \psi_{t}^{P} p_{t^*}^{BI=SWI}$	7,883.8	17.89	0.0001	0.0001	32	398.33
$\phi_{t}^{P} \psi^{P} p_{t^*}^{BI=SWI}$	7,883.8	17.92	0.0001	0.0001	24	414.52
$\phi_{x\times t}^{P} \psi_{x}^{NWI=SWI} p_{x\times t^*}^{BI=SWI}$	7,883.8	17.96	0.0001	0.0001	46	369.99
$\phi_{t}^{P} \psi_{t}^{NWI=SWI} p_{t^*}^{BI=SWI}$	7,884.5	18.59	0.0001	0.0001	27	409.14
$\phi_{x\times t}^{P} \psi_{x}^{P} p_{x\times t^*}^{BI=SWI}$	7,886.7	20.81	0.0000	0.0000	48	368.77
$\phi_{t}^{P} \psi_{t}^{P} p_{t^*}^{P}$	7,886.7	20.84	0.0000	0.0000	35	395.20
$\phi_{t}^{P} \psi_{t}^{P} p_{t}^{P}$	7,892.8	26.92	0.0000	0.0000	38	395.20
$\phi_{x}^{P} \psi_{x}^{P} p_{x\times t}^{P}$	7,893.9	27.99	0.0000	0.0000	38	396.27
$\phi_{t}^{BI=SWI} \psi^{NWI=SWI} p_{t^*}^{BI=SWI}$	7,895.3	29.39	0.0000	0.0000	19	436.08
$\phi^{P} \psi^{P} p_{t}^{P}$	7,896.4	30.47	0.0000	0.0000	19	437.16
$\phi_{x\times t}^{P} \psi_{x\times t}^{P} p_{x\times t^*}^{BI=SWI}$	7,900.1	34.25	0.0000	0.0000	64	349.54
$\phi_{x\times t}^{P} \psi_{x\times t}^{P} p_{x\times t^*}^{P}$	7,909.0	43.1	0.0000	0.0000	70	346.08
$\phi_{x\times t}^{P} \psi_{x\times t}^{P} p_{x\times t}^{P}$	7,921.3	55.43	0.0000	0.0000	76	346.08
$\phi_{t}^{NWI=SWI} \psi^{P} p_{t^*}^{BI=SWI}$	8,035.5	169.58	0.0000	0.0000	18	578.28
$\phi_{t}^{P} \psi_{t}^{P} p_{*}^{P}$	8,210.3	344.44	0.0000	0.0000	26	737.01
$\phi_{x\times t}^{P} \psi^{NWI=SWI} p_{x\times t^*}^{BI=SWI}$	8,382.2	516.28	0.0000	0.0000	20	920.95
$\phi^{P} \psi^{NWI=SWI} p_{t^*}^{BI=SWI}$	9,516.9	1,651.00	0.0000	0.0000	12	2,071.83
$\phi_{x}^{P} \psi_{x}^{P} p_{x}^{P}$	9,592.2	1,726.30	0.0000	0.0000	16	2,139.08
$\phi^{P} \psi^{P} p^{P}$	9,594.9	1,728.90	0.0000	0.0000	8	2,157.79
$\phi^{NWI=SWI} \psi^{NWI=SWI} p_{t^*}^{BI=SWI}$	9,640.6	1,774.60	0.0000	0.0000	10	2,199.47

[a] Variables with superscript P indicate rates were population specific. Probabilities with a subscript t indicate rates were time specific. Probabilities with subscript x indicate rates were sex specific. Resighting probability p_{t^*} indicates rates were time specific, but we constrained final year resighting rates to 1.0. Resighting probability p_* rates were constant, but we constrained final year rates to 1.0.

NWI birds may spend more time feeding in agricultural fields and pasture areas recently created to provide additional goose habitat, and thus geese may no longer be accumulating red face staining that was historically acquired by feeding in estuaries. We suspect that face staining will become a less reliable predictor of wintering area as more agricultural areas are created and birds reduce their use of iron oxide sediments in the Fraser–Skagit region.

The wintering distribution of WI birds shifted from approximately 80% of the 150,000 birds (1970s) in California to approximately equal proportions of the remaining 65,000 birds (1990s) in northern and southern areas, and >60% of the population in northern areas by 2000 (Baranyuk 1995, Boyd 1995, Hines et al. 1999a). It is unknown whether these changes were due to differential survival of wintering birds, movement among wintering areas, recruitment, or other factors. Hines et al. (1999a) hypothesized this shift was driven by lower competition for food resources in the Fraser–Skagit region compared to crowding in California from the increasing BI population. We found approximately 2% of the NWI and SWI subpopulations change winter areas annually, with equal transition rates between winter areas. Because emigration outside the Pacific Flyway appears low for these subpopulations, especially the WI population, fidelity rates can be approximated by $1.0 - $ transition rates. Syroechkovsky et al. (1994) also estimated high winter fidelity rates for WI geese during the late 1970s; however, the data were not sufficient to estimate transition rates between the NWI and SWI wintering populations. Overall, our data suggest high winter fidelity (≥97%) rates, which appear insufficient to account for the shift from California to the Skagit–Fraser region during the last 4 decades; however, the limited time frame of our study does not provide strong evidence to confirm this hypothesis. The pattern of strong wintering fidelity in lesser snow geese is in contrast to patterns for other waterfowl and Canada geese (Owen 1980, Hestbeck et al. 1991, Samuel et al. 1991, Robertson and Cooke 1999), which appear to be influenced by winter weather. We suspect milder winters in the Pacific Flyway compared to the Atlantic or Mississippi flyways may be partially responsible for these differences.

Many species of geese are believed to pair in the winter; thus, patterns of population structure and gene flow may be defined during winter rather than during the breeding season (Robertson and Cooke 1999). Selection pressures leading to winter fidelity could differ substantially from those leading to breeding fidelity. Winter fidelity in the western Arctic lesser snow geese was much greater than breeding fidelity reported for (50–80%) mid-continent birds (Cooke and Sulzbach 1978, Cooke and Abraham 1980, Ganter and Cooke 1998). Survival advantages of strong winter fidelity include a return to familiar areas to avoid predators or exploit food resources, facilitation of mating with partners sharing genetic relatedness, and maintenance of social cohesion among families with long-term pair bonds and extended parental care (Weatherhead and Forbes 1994, Robertson and Cooke 1999). Although our study did not

Table 4. Apparent survival, transition, and resighting probabilities (and SEs) for Wrangel Island, Russia (WI), and Banks Island, Canada (BI), lesser snow goose populations estimated from best fit model based on wintering ground neckband observation between December and January 1993–1994, to December and January 1998–1999. No rates were estimable for the last year, 1998–1999.

Parameter	Wintering grounds	Breeding population origin	Sex	1993–1994 Rate	1993–1994 SE	1994–1995 Rate	1994–1995 SE	1995–1996 Rate	1995–1996 SE	1996–1997 Rate	1996–1997 SE	1997–1998 Rate	1997–1998 SE	$\bar{x}$ Rate	$\bar{x}$ SE
Apparent survival	CA, USA	Banks Island	M			53.32	5.59	49.04	3.02	75.91	7.88			59.42	12.45[a]
			F			64.52	5.15	60.51	2.79	83.38	6.52			69.47	10.63[a]
		Wrangel Island	M	75.25	3.90	76.52	3.11	63.09	3.11	76.58	7.36			72.86	6.97[b]
			F	78.74	3.52	79.89	2.79	67.56	2.87	79.94	6.48			76.53	6.32[b]
	Skagit–Fraser, Canada	Banks Island	M and F												
		Wrangel Island	M	75.51	3.94	74.21	6.39	72.63	7.42	63.23	4.25			71.40	7.35[b]
			F	80.53	3.39	79.42	5.51	78.06	6.36	69.75	3.87			76.94	6.40[b]
Transition		WI subpopulation to BI subpopulation	M and F	2.17	0.31	2.17	0.31	2.17	0.31	2.17	0.31			2.17	0.31[b]
		BI subpopulation to WI subpopulation	M and F												
Resighting	CA	Banks Island	M and F	87.28	3.38	84.75	2.47	89.63	1.66	74.15	6.39	100.00	0.00	82.84	6.96[a]
		Wrangel Island	M and F			84.75	2.47	89.63	1.66	74.15	6.39	100.00	0.00	83.95	6.24[b]
	Skagit–Fraser	Banks Island	M and F												
		Wrangel Island	M and F	92.09	3.24	23.49	2.81	17.68	2.36	91.48	2.84	100.00	0.00	56.19	35.71[b]

[a] Does not include 1993–1994, 1997–1998.
[b] Does not include 1997–1998.

explicitly evaluate these hypotheses, strong winter fidelity observed in Pacific Flyway snow geese, coupled with pairing of juvenile geese (or birds with lost mates) on the wintering grounds, would provide an opportunity to maintain genetic isolation among populations. However, this genetic separation would require nonrandom pairing for BI and SWI populations with sympatric wintering grounds. For waterfowl pairing on the wintering grounds, winter fidelity should be male-based if males can defend critical resources and female-based if males cannot defend a critical resource (Emlen and Oring 1977, Greenwood 1980, Robertson and Cooke 1999). Waterfowl in the Pacific Flyway are typically confronted by dynamically shifting resources that are influenced by inter- and intraspecific competition from a multispecies community of consumers. Therefore, it is unclear whether the hypothesized advantages of male-based fidelity for dominant males can be achieved in such a dynamic system. However, we found no difference in sex-based fidelity within adult Pacific Flyway lesser snow geese. We are uncertain whether pairs of geese decide to shift wintering areas, if separate and nearly equal shifts occur for males and females that have lost mates, or whether dynamically shifting resources preclude sex-based fidelity. We suspect many of these shifts are made during fall migration, when most of the WI geese migrate through the northern wintering area, rather than during spring when NWI and SWI geese follow separate migration routes.

Apparent survival rates varied annually and among BI and WI birds wintering in Skagit–Fraser or California during 1993–1997. Survival of BI birds was typically lower than that of SWI birds that wintered sympatrically in California (except in 1996–1997 when apparent survival was similar) and there were no clear differences in survival between SWI and NWI birds. Additionally, females had higher apparent survival than males, especially in the BI population. This was likely a result of lower neckband retention for males than females (as observed by Samuel et al. 2001: BI: 75.6% vs. 83.8% and WI: 87.1% vs. 95.8%). Survival data from the 1980s (Hines et al. 1999b) and 1990s do not support the hypothesis of population shifts because of differential survival between SWI and NWI birds. Although we found higher apparent survival for WI birds than for BI birds, differences in neckband retention rates and permanent emigration of BI birds to the Central Flyway make a direct comparison difficult. Based on an analysis of recovery data, we found that true survival rates were similar between WI and BI populations. Samuel et al. (2001) found that neckband loss was approximately 10–12% higher in BI snow geese than in WI birds, which could be sufficient to account for the differences in apparent survival between these populations. Our limited data also suggest that emigration from wintering areas in California may be slightly higher for BI geese than for SWI geese.

MANAGEMENT IMPLICATIONS

Our findings suggest that NWI and SWI subpopulations should be considered a metapopulation in better under-standing and managing Pacific Flyway lesser snow geese (Brault et al. 1994, Esler 2000). Additionally, the absence of a strong population connection between BI and WI geese suggests that these breeding colonies can be managed as separate but overlapping populations. Additionally, winter population fidelity may be more important in lesser snow geese than in other species and both breeding and wintering areas are important components of population management for sympatric wintering populations. In contrast to the WI population, the BI population has been growing exponentially for the previous 4–5 decades. We suspect that the dramatic and longer-term increase in BI population in contrast to the fluctuating WI population may result from a combination of higher annual nesting success and higher overwinter survival of BI geese, possibly in the Central Flyway. Thus, we recommend continued monitoring of the BI and WI nesting colonies to evaluate population trends, potential habitat impacts at BI, and investigation of population demographics for the Central Flyway subpopulation of BI geese. We caution that efforts to control the BI population by reducing survival rates should occur in locations (e.g., Prairie Canada or nesting grounds) and during times of the year (e.g., breeding or fall migration) when the probabilities of impacting SWI geese are minimized.

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