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Genetic Differentiation Between Wintering Populations of Lesser Snow Geese Nesting on Wrangel Island

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Arctic breeding populations of Lesser Snow Geese (*Chen c. caerulescens*) range from Baffin Island in eastern Canada to Wrangel Island, Russia, which is located 650 km west of Alaska (Bellrose 1980). Although hundreds of thousands of Lesser Snow Geese may have occupied the Russian arctic in the mid-1800s (see Takekawa et al. 1994), the Wrangel Island birds constitute the only remnant colony on the Asian continent (Syroechkovsky and Litvin 1986) and may represent a matriarchal population for the species (Quinn 1992). In the past 30 years, the Wrangel Island colony has declined from more than 200,000 to less than 75,000 breeding adults (Pacific Flyway Technical Subcommittee 1992, V. Baranyuk unpubl. data), which has resulted in increasing concern about its conservation and management.

The Wrangel Island colony consists of two wintering populations that migrate to different regions and are faithful to their wintering areas (McKelvey et al. 1989). The larger northern population (about 60% of the total from Wrangel) migrates to the Fraser River delta of British Columbia and the Skagit River delta of northern Washington, whereas the southern population flies 600 km farther south to the Central Valley of California (Rienecker 1965, Teplov and Shevryova 1965, Jeffrey and Kaiser 1979, Priklonsky and Sapetin 1979). The northern population is isolated from other Lesser Snow Geese during the winter, but the southern population mixes with geese from Banks Island, Canada and from the smaller Anderson and Sagavirniktok River deltas (Dzubin 1974, Johnson 1995, Syroechkovsky et al. 1994).

Although Lesser Snow Geese are colonially nesting birds that typically show little genetic structuring (Ely and Scribner 1994), there are potential differences in genetic exchange at Wrangel Island because the birds pair during the winter (Cooke et al. 1975). However, a recent study (Syroechkovsky et al. 1994) suggests that gene flow between wintering

populations is large and that little genetic variation should be exhibited. Here, we examine the genetic differentiation between these two wintering populations through use of electrophoretic analyses of proteins and enzymes in blood samples taken from geese captured at the Wrangel Island breeding colony.

Methods.—Blood samples were collected from geese at the Wrangel Island Nature Reserve during July and August, 1991 to 1993. After hatching, geese molted in mixed flocks on small tundra lakes, and flightless adults and goslings were captured by herding them into a net corral (Cooch 1953). Breeding adults were sexed by cloacal eversion, measured and banded, and blood samples (4 mL) were drawn from an underwing vein into a heparinized tube. Blood and plasma were separated in the field and the samples were stored on ice until transported to a laboratory.

At the breeding colony, adults from the northern wintering population are reliably distinguished from the southern population by staining on their head and face (Baranyuk and Syroechkovsky 1994). Geese from the northern population forage in coastal marshes and pastures (Boyd 1995), but the feathers on their face and head acquire a red stain because of the ferrous salts in the soil and water on the river deltas where they feed (Hohn 1955, Baranyuk and Syroechkovsky 1994). Geese from the southern population feed mainly in rice fields on waste grains (Pacific Flyway Technical Subcommittee 1992) and lack the red staining. Only geese with dark red stains (northern population) or without stains (southern population) were used in our analyses.

Males and females from each population were analyzed separately because females are generally more philopatric to natal colonies than are males (Cooke et al. 1975, Syroechkovsky et al. 1994). Sample sizes included 53 geese from the southern population and 63 from the northern population in 1991, 27 and 31 in 1992, and 85 and 80 in 1993.

The electrophoretic procedures used to examine

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blood plasma proteins and plasma esterases have been described earlier (Gahne et al. 1977; Kuznetsov 1991, 1995a, 1995b). In addition, electrophoresis of *Ada* was performed in starch (Tris-citrate buffer, pH 7.5) and polyacrylamide (Tris-HCl/Tris-glycine buffers, pH 8.5) gels and revealed six alleles near a single autosomal locus. We examined alleles at 11 gene loci including prealbumin-1 (*Pr-1*), prealbumin-2 (*Pr-2*), prealbumin-4 (*Pr-4*), albumin (*Al*), haptoglobin (*Hp*), postalbumin-X (*Pa-X*), postalbumin-3 (*Pa-3*), transferrin (*Tf*), carboxyl esterase (*Est*), adenosine deaminase (*Ada*), and glucose-6-phosphate isomerase (*Gpi*). Alleles were designated alphabetically in descending order from the most anodal, or numerically when denoting cases where alleles were found subsequent to initial analyses (Kuznetsov 1991). We calculated allele frequencies, percent polymorphic loci with allele frequencies $\leq 95\%$ (Ferguson 1980), and multilocus heterozygosity for all individuals. We calculated *F*-statistics (Nei 1977, Wright 1978) to examine relatedness (positive F_{IS} and F_{IT} values indicating inbreeding and fixation) and shared alleles (F_{ST} values ranging from 0 to 1). A database of the individual genotypes was constructed and analyzed using the program BIOSYS-1 (Swofford and Selander 1981). Differences in allele frequencies were determined with Fisher's exact test (Swofford and Selander 1981), and significance levels ($\alpha'' = \alpha/k$; $\alpha = 0.05$, $k = 44$ comparisons) were conservatively set at $\alpha'' = 0.001$ for multiple comparisons with a Bonferroni correction (Sokal and Rohlf 1994).

Results.—Three (*Pr-1*, *Al*, *Gpi*) of the 11 loci in Lesser Snow Geese from Wrangel Island were monomorphic, but the other eight loci exhibited polymorphism with up to six alleles per locus (Table 1). We found little difference in the number of alleles per locus (Table 2), and Nei's distance (1978) was zero, indicating no separation by sex or wintering population. However, unique alleles were identified in these small samples by wintering population and sex including males (*Pa-X*, *Pa-3*, *Tf*, *Est*) and females (*Est*, *Pr-4*) from the southern wintering population and males (*Pr-2*) and females (*Pr-1*, *Tf*) from the northern wintering population.

Geese from the southern wintering population had fewer (36.4%) polymorphic loci than geese from the northern wintering population (45.5%). We found that heterozygosity varied from 0.094 in males from the southern population to 0.130 in males from the northern population (Table 2). Allelic frequencies in males from the northern population were in Hardy-Weinberg equilibrium ($P > 0.5$), but deficiencies in heterozygotes were located at five loci for females from the northern population (*Pr-1*, $P < 0.001$; *Ada*, $P < 0.008$), and in males (*Pa-3*, $P < 0.004$; *Pa-X*, $P < 0.081$; *Ada*, $P < 0.012$) and females (*Pr-2*, $P < 0.055$) from the southern population. However, the deficiency in heterozygotes was significant only for *Pr-1* ($P < 0.001$) in females from the northern population af-

TABLE 1. Allele frequencies of polymorphic blood plasma proteins and esterases (Kuznetsov 1995a, b) in two wintering populations of Lesser Snow Geese from the Wrangel Island breeding colony. Alleles were designated alphabetically or numerically, denoting cases where they were found subsequent to initial analyses (Kuznetsov 1991), in descending order from the most anodal. Sample sizes are in parentheses. Loci abbreviations are defined in Methods.

Locus	Allele	Male		Female		
		South- ern	North- ern	South- ern	North- ern	
<i>Pr-1</i>	(n)	(90)	(76)	(80)	(94)	
	A	0.000	0.000	0.025	0.000	
	B	1.000	1.000	0.975	1.000	
<i>Pr-2</i>	(n)	(90)	(76)	(80)	(94)	
	A	0.017	0.000	0.006	0.011	
	B	0.000	0.007	0.000	0.016	
	B+	0.006	0.000	0.006	0.032	
	C	0.972	0.993	0.981	0.931	
<i>Hp</i>	(n)	(44)	(36)	(42)	(53)	
	A	0.148	0.111	0.119	0.113	
	B	0.852	0.889	0.881	0.887	
	<i>Pa-X</i>	(n)	(44)	(36)	(42)	(53)
		A	0.000	0.028	0.071	0.019
B		0.011	0.014	0.012	0.009	
C		0.989	0.944	0.917	0.972	
<i>Pa-3</i>	(n)	(87)	(72)	(64)	(85)	
	B ₁	0.000	0.007	0.000	0.000	
	C ₁	0.126	0.132	0.195	0.124	
	C ₂	0.868	0.854	0.805	0.865	
	C ₃	0.006	0.007	0.000	0.012	
<i>Tf</i>	(n)	(90)	(76)	(80)	(94)	
	A ₁	0.000	0.000	0.006	0.000	
	B	1.000	0.993	0.994	1.000	
	E	0.000	0.007	0.000	0.000	
<i>Est</i>	(n)	(90)	(76)	(80)	(93)	
	A	0.000	0.007	0.006	0.000	
	B	0.050	0.033	0.063	0.086	
	C	0.944	0.954	0.931	0.914	
<i>Ada</i>	(n)	(90)	(76)	(80)	(94)	
	A	0.511	0.493	0.525	0.479	
	B	0.361	0.349	0.356	0.394	
	C	0.072	0.086	0.050	0.080	
	D	0.028	0.033	0.035	0.021	
	E	0.028	0.026	0.038	0.016	
	F	0.000	0.013	0.006	0.011	

ter *P*-values were adjusted with a Bonferroni correction (Sokal and Rohlf 1994).

We calculated Wright's (1978) *F*-statistics for each polymorphic locus and averaged the values for all loci after weighting by sample size and number of alleles (Table 3). Mean F_{IS} (0.099) and F_{IT} (0.103) values were positive, indicating that Lesser Snow Geese shared more genes than was expected. The largest

TABLE 2. Genetic variability at 11 loci in Lesser Snow Geese from two wintering populations of the Wrangel Island breeding colony. Values are $\bar{x} \pm SE$. A locus was considered polymorphic if the frequency of the most common allele was ≤ 0.95 .

Sex	Sample size per locus	Alleles per locus	% Polymorphic loci	Heterozygosity (direct count)	H-W expectation ^a
Southern population					
Female	81.5 \pm 5.6	2.4 \pm 0.4	36.4	0.114 \pm 0.530	0.117 \pm 0.056
Male	68.5 \pm 4.8	2.5 \pm 0.5	36.4	0.094 \pm 0.042	0.120 \pm 0.058
Northern population					
Female	71.8 \pm 4.6	2.5 \pm 0.4	45.5	0.119 \pm 0.045	0.142 \pm 0.054
Male	85.7 \pm 4.9	2.5 \pm 0.6	45.5	0.130 \pm 0.054	0.131 \pm 0.055

^a Unbiased Hardy-Weinberg estimates (Nei 1978).

positive F_{IS} values occurred at the *Ada*, *Pa-3*, and *Pr-2* loci. The F_{ST} value indicated that only 0.5% of the genetic variation was partitioned among wintering populations and between sexes.

Discussion.—The northern population from Wrangel Island is spatially isolated from other populations of Lesser Snow Geese during the winter (McKelvey et al. 1989), but the southern population constitutes 5 to 10% of the overall wintering admixture in the Central Valley (Syroechkovsky et al. 1994). Populations from Banks and Wrangel islands intermix in the Central Valley during winter (J. Takekawa unpubl. data), and it is likely that considerable interbreeding occurs between the two populations. Syroechkovsky et al. (1994) suggest that genetic exchange may be as much as 9% per generation in wintering populations because of extrapair copulations, intraspecific nest parasitism, fostering, and rare mixed-population matings. Although a few rare alleles occur, our electrophoretic analysis indicates little difference in polymorphism of blood proteins and esterases among wintering populations and between sexes.

However, we found a deficiency of heterozygotes in five loci, and one locus in northern females was significantly deficient (*Pr-1*). Cooke et al. (1988) sug-

gested that such a deficiency of heterozygotes may be explained by scoring errors, null alleles, selection against heterozygotes, inbreeding, and the Wahlund effect (Li 1969). We knew of no evidence for selection against these heterozygotes, and wintering populations clearly were not isolated (Syroechkovsky et al. 1994) in a manner that would suggest inbreeding. If scoring and gel resolution were adequate, the most plausible explanation for a deficiency in heterozygotes in both wintering populations seems to be the Wahlund effect, where two formerly allopatric groups have only recently come into contact (Avise et al. 1987, Quinn 1992).

Many of the Lesser Snow Geese that bred in the Russian arctic in the past century migrated to wintering grounds in Asia, including China, Japan, and Korea (Takekawa et al. 1994). Some of the Lesser Snow Geese on the Russian coast, particularly those that nested on the Chukotka Peninsula near Wrangel Island, likely migrated to California during the winter (a remnant breeding population of a few hundred individuals marked on the Kolyma River delta migrated to California; M. Kurechi unpubl. data). These geese may have joined the colony at Wrangel Island after being displaced from the arctic coast prior to the 1930s (Bousfield and Syroechkovsky 1985).

Although several colonies of Snow Geese occurred on Wrangel Island in the past century (Mineev 1946), only two colonies remained by the mid-1950s (Syroechkovsky and Krechmar 1981). These colonies may have migrated to different wintering areas or were otherwise isolated from each other, but they combined in 1958 after one was disrupted by a geologic expedition (Syroechkovsky and Krechmar 1981). Only one colony has been present since 1969 (Bousfield and Syroechkovsky 1985).

If the Banks and Wrangel island populations are genetically different, and if the southern population has recently joined the geese wintering in the Central Valley, it could explain a deficiency of heterozygotes. Males from Banks Island that pair with females from the southern population during the win-

TABLE 3. Summary of Wright's (1978) weighted F -statistics for variable loci averaged over all samples.

Locus	F_{IS}	F_{IT}	F_{ST}
<i>Pr-1</i>	1.000	1.000	0.019
<i>Pr-2</i>	0.104	0.115	0.013
<i>Pr-4</i>	-0.025	-0.015	-0.009
<i>Hp</i>	-0.043	-0.041	0.002
<i>Pa-X</i>	0.029	0.046	0.017
<i>Pa-3</i>	0.112	0.118	0.006
<i>Tf</i>	-0.006	-0.002	0.004
<i>Est</i>	0.031	0.036	0.005
<i>Ada</i>	0.156	0.157	0.001
Mean	0.099	0.103	0.005

ter are likely to breed at Wrangel Island (Cooke et al. 1975, Syroechkovsky et al. 1994). We would expect males from the southern wintering population to exhibit genetic variation because of mixing during winter (Syroechkovsky et al. 1994), in contrast to what we would expect for philopatric females or males isolated in the northern population. Unfortunately, we lack samples from Banks Island geese for a direct comparison.

It is possible that we attributed some geese to wintering populations incorrectly based on face staining (Baranyuk and Syroechkovsky 1994). However, studies of collar-marked (R. Kerbes unpubl. data) and radio-marked (J. Takekawa unpubl. data) Snow Geese from Wrangel Island showed that our method was highly reliable if geese with intermediate levels of stain were excluded (as practiced in our study).

Our results suggest that some genetic differentiation exists in wintering populations of Lesser Snow Geese from Wrangel Island despite the general genetic similarity across the North American range of the taxon (Avise et al. 1992). We could not ascertain the origins of these genetic differences, but they may be related to recent consolidation of other populations from Asia with the remaining colony from Wrangel Island. Additional studies, including comparisons with samples of Lesser Snow Geese from Banks Island and other western colonies, would be valuable in providing further insight into this area of research.

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Rejection of Cowbird Eggs by Mourning Doves: A Manifestation of Nest Usurpation?

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Three conditions are known to select for rejection of foreign eggs by birds: (1) nesting in dense colonies in which individuals risk confusing their eggs with

those of nearby conspecifics (Tschanz 1959); (2) conspecific brood parasitism (Jackson 1990); and, most frequently, (3) interspecific brood parasitism (Rothstein 1975b, 1990). The Mourning Dove (*Zenaidura macroura*) is an inappropriate host for parasitic Brown-headed Cowbirds (*Molothrus ater*; hereafter "cowbird"), and as a consequence, it is rarely parasitized (<10 records; Friedmann 1971, Friedmann et al.

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