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INTERCONTINENTAL GENE FLOW AMONG WESTERN ARCTIC POPULATIONS OF LESSER SNOW GEESE

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Abstract. Quantifying the spatial genetic structure of highly vagile species of birds is important in predicting their degree of population demographic and genetic independence during changing environmental conditions, and in assessing their abundance and distribution. In the western Arctic, Lesser Snow Geese (*Chen caerulescens caerulescens*) provide an example useful for evaluating spatial population genetic structure and the relative contribution of male and female philopatry to breeding and wintering locales. We analyzed biparentally inherited microsatellite loci and maternally inherited mtDNA sequences from geese breeding at Wrangel Island (Russia) and Banks Island (Canada) to estimate gene flow among populations whose geographic overlap during breeding and winter differ. Significant differences in the frequencies of mtDNA haplotypes contrast with the homogeneity of allele frequencies for microsatellite loci. Coalescence simulations revealed high variability and asymmetry between males and females in rates and direction of gene flow between populations. Our results highlight the importance of wintering areas to demographic independence and spatial genetic structure of these populations. Male-mediated gene flow among the populations on northern Wrangel Island, southern Wrangel Island, and Banks Island has been substantial. A high rate of female-mediated gene flow from southern Wrangel Island to Banks Island suggests that population exchange can be achieved when populations winter in a common area. Conversely, when birds from different breeding populations do not share a common wintering area, the probability of population exchange is likely to be dramatically reduced.

Key words: *Lesser Snow Goose,* Chen caerulescens caerulescens, *mtDNA, microsatellites, gene flow, philopatry, spatial genetic structure*

Flujo Génico Intercontinental entre Poblaciones de *Chen caerulescens caerulescens* del Oeste del Ártico

Resumen. Cuantificar la estructura genética espacial de especies de aves con alta movilidad es importante para predecir el grado de independencia demográfica y genética de las poblaciones en momentos de condiciones ambientales cambiantes, y para evaluar su abundancia y distribución. En el oeste del Ártico, *Chen caerulescens caerulescens* representa un ejemplo útil para evaluar la estructura génetica poblacional en el espacio y para estimar la contribución relativa de la filopatría a los sitios de cría y de invernada por parte de los machos y de las hembras. Utilizando muestras de aves reproductoras de las islas de Wrangel (Rusia) y Banks (Canadá), analizamos loci microsatelitales heredados biparentalmente y secuencias de genes de ADNmt heredados por la línea materna para estimar el flujo genético entre poblaciones cuyas distribuciones geográficas se superponen durante la época de cría pero difieren en el invierno. Las diferencias significativas en las frecuencias de haplotipos de ADNmt contrastan con la homogeneidad en las frecuencias alélicas de los microsatélites. Las simulaciones basadas en coalescencia revelaron una alta variabilidad y asimetría entre machos y hembras en las tasas y en la dirección del flujo génico entre poblaciones. Nuestros resultados resaltan la importancia de las áreas de invernada para la independencia demográfica y para la estructura genética espacial de estas poblaciones. El flujo génico mediado por los machos entre las poblaciones del norte de la isla Wrangel, del sur de ésta y de la isla Banks ha sido sustancial. La alta tasa de flujo génico mediada por las hembras entre el sur de la isla Wrangel y la isla Banks sugiere que el intercambio entre poblaciones puede alcanzarse cuando los miembros de éstas pasan el invierno en un área común. Por el contrario, cuando los individuos de poblaciones distintas no comparten un área de invernada, la probabilidad de intercambio poblacional se reduciría dramáticamente.

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INTRODUCTION

Knowledge of levels of spatial genetic structure (or demographic isolation) in highly vagile birds is important for understanding population demographics and genetic independence, particularly for species whose abundance and distribution have changed. Ecological and life-history characteristics of the Anseriformes, including degree of philopatry and sex-specificity of fidelity to nesting and wintering sites, fidelity to migration routes, breeding behavior, and recent range expansions, can have a profound effect on the degree of genetic drift and patterns of gene flow, and resulting spatial genetic structure (Greenwood and Harvey 1982, Anderson et al. 1992, Ely and Scribner 1994, Robertson and Cooke 1999). Significant spatial genetic structure among breeding populations may result from natal philopatry of females (Chesser 1991a, b), even though populations share migratory pathways and wintering areas (Ely and Scribner 1994, Scribner et al. 2003). Alternatively, fidelity to wintering grounds, followed by pair formation on or near these areas, may be critical in defining regional patterns of spatial genetic structure of goose populations (Prevett 1972, Cooke 1987, Cooke et al. 1988, Ryder and Alisauskas 1995, Robertson and Cooke 1999, Ganter et al. 2005).

Lesser Snow Geese (*Chen caerulescens caerulescens*) in the western Arctic provide a unique opportunity for evaluation of the relative importance of philopatry to breeding or wintering areas and their contribution to spatial genetic structure. The majority of Lesser Snow Geese in the western Arctic breed in two large colonies and follow separate migration routes between their breeding and winter ranges (Johnson 1996; Fig. 1). One colony on Banks Island (BI), Northwest Territories, Canada, has increased dramatically since 1953, but at a rate slower than those that have damaged habitats in the central Arctic (Abraham and Jefferies 1997, Batt 1997, Hines et al. 1999b, Kerbes et al. 1999). Although a portion of the Banks Island population continues south into western Texas and central Mexico, most of it migrates through northern California to winter in the Central Valley of California (Fig. 1). A second Lesser Snow Goose population in the western arctic nests on Wrangel Island in northeastern Russia (Bousfield and Syroechkovsky 1985, Syroechkovsky and Litvin 1986). Wrangel Island's population has fluctuated greatly, from 60 000 to over 150 000 individuals (Kerbes et al. 1999). The Wrangel population is of international conservation importance because it is the only remaining Snow Goose colony in Russia and the only population of Snow Geese wintering in Canada (Boyd 1995, Kuznetsov et al. 1998, Mowbray et al. 2000).

The Wrangel population is composed of two subpopulations that currently nest in one mixed colony and migrate south together but winter in geographically separate areas of the Pacific Flyway (Bousfield and Syroechkovsky 1985). The northern (NWI) subpopulation winters in the Skagit–Fraser delta; the southern (SWI) subpopulation winters in California (Fig. 1). On the wintering grounds in California and during spring migration, BI geese mix with the SWI geese, while the NWI population is isolated on winter grounds farther north and during spring migration (Kelley et al. 2001). Winter harvest of sympatric BI and SWI populations could be detrimental to the Wrangel Island population (Williams et al. 2008), which historically has been smaller and less productive than the BI population.

Patterns of migration and population overlap in the breeding and winter ranges likely influence the rates of gene flow among the three populations. Colonially nesting Lesser Snow Geese pair mainly on the winter grounds or during spring migration (Cooke et al. 1975, Ganter et al. 2005), and fidelity to winter areas is greater than to breeding areas (Cooke et al. 1975, Cooke and Sulzbach 1978, Cooke and Abraham 1980, Ganter and Cooke 1998, Williams et al. 2008). Pairing while the NWI and SWI subpopulations are geographically segregated (i.e., during winter and early spring) may limit gene flow. Rates of gene flow between SWI geese and BI geese may be higher because they winter together and follow similar migration pathways in spring (Fig. 1). Thus, the Wrangel population may represent important past connectivity between Asian and North American Anseriformes, and the SWI subpopulation may be the link of gene flow between the continents. Such migration patterns may also facilitate the intercontinental movement of diseases such as avian influenza (Koehler et al. 2008), avian cholera (Samuel et al. 2005), or West Nile virus (Rappole and Hubálek 2003).

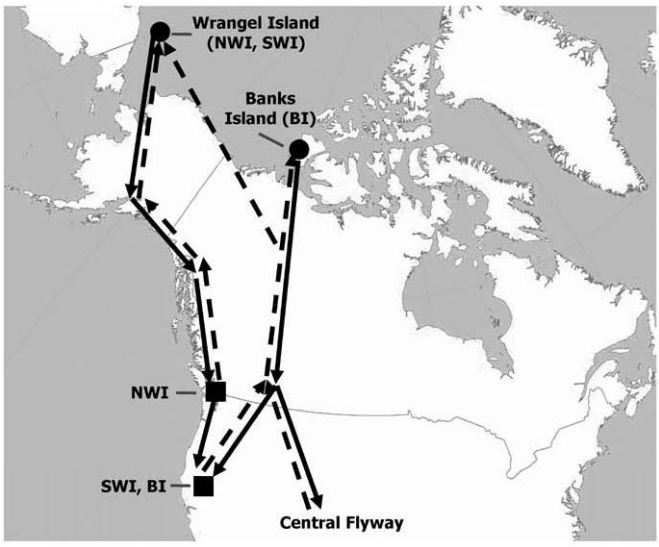

FIGURE 1. Breeding (circles) and winter (squares) distributions of the Lesser Snow Geese breeding on Wrangel Island and Banks Island. Solid arrows, pathways of fall migration south to wintering grounds; dashed arrows, routes of spring migration north to breeding areas. Approximately equal proportions of geese breeding on Wrangel Island winter in the British Columbia and Washington (NWI) and in California's Central Valley (SWI). Lesser Snow Geese from Banks Island (75% of the population; BI) winter in the Central Valley with the SWI wintering population.

Genetic studies of the Wrangel and Banks Island populations that use nuclear and mitochondrial DNA loci can reveal signatures of past vicariance and admixture. Several studies have revealed the existence of two evolutionarily distinct mitochondrial DNA lineages of the Lesser Snow Goose (Avise et al. 1992, Quinn 1992, Weckstein et al. 2002). Hypotheses for the geographic origin of these clades and the mechanisms that facilitated the mixture of clades over the species' range and between the Lesser Snow and Ross's (*Chen rossii*) Geese have been proposed, but population-level genetic data from critical western arctic populations have not been assessed.

Our primary objective was to estimate levels of spatial genetic structure among major populations and subpopulations of western arctic Lesser Snow Geese and to evaluate whether affiliation to breeding or wintering sites and gene flow mediated by males or females contributed to this structure differently. Identifying levels of exchange among breeding and wintering groups of western arctic Snow Geese is essential to predicting future recruitment into the Wrangel Island populations and for the design of effective management for them.

METHODS

SAMPLE COLLECTIONS

Blood samples for genetic analysis were collected in summer 1994 from flightless Lesser Snow Geese at Banks and Wrangel islands. Flocks of molting juveniles and adults were captured during July and August in mobile corral nets by means of an all-terrain vehicle or on foot on Wrangel Island and by helicopter driving on Banks Island (Cooch 1953, Timm and Bromley 1976). Because birds were captured in large molting flocks, rather than family groups, we were not able to identify mated pairs with offspring in our samples. Numbers of birds sampled (Fig. 1) were 76 for NWI, 85 for SWI, and 81 for BI. Blood was placed into tubes containing high-salt buffer (Longmire et al. 1997) and stored at ambient temperatures in the field. Samples were frozen when returned to the laboratory. Sampled geese were marked with metal U.S. Fish and Wildlife Service leg bands and colored plastic neck bands (Samuel et al. 2001) as part of a larger study of avian cholera in Snow Geese of the western Canadian Arctic and Wrangel Island (Kerbes and Meeres 1999, Samuel et al. 1999).

Most NWI geese can be reliably distinguished from SWI geese (Baranyuk and Syroechkovsky 1994, Baranyuk et al. 1999) by facial staining acquired in the winter range. During winter, NWI geese forage in tidal marshes and acquire a reddish stain on their head and face (Baranyuk and Syroechkovsky 1994, Baranyuk et al. 1999). SWI geese feed mainly in agricultural fields on waste grain, retaining their white plumage (Baranyuk et al. 1999). We used the amount of facial staining (scored on a scale from 0 for none to 6 for strong staining) to identify SWI (score 0–1) and NWI (score 5–6) geese on the breeding grounds (Kuznetsov et al. 1998, Baranyuk et al. 1999, Williams et al. 2008). Previous observations of neck-banded birds have recorded high fidelity (97%) of Wrangel Island geese with face-plumage scores <2 to southern wintering areas and (89%) of those with scores of 5 or 6 to northern wintering areas (Williams et al. 2008).

ANALYSIS OF MICROSATELLITE LOCI

We extracted DNA from all samples with DNeasy extraction kits (Qiagen, Inc., Valencia, CA). Ten biparentally inherited loci were polymorphic in one or more breeding populations and were used for subsequent analyses. These loci were dinucleotide microsatellites Bcaμ1, Bcaμ5, Bcaμ9, Bcaμ11, Hhiμ1, Hhiμ3 (Buchholz et al. 1998), Aalμ1 (Fields and Scribner 1997), Sfiμ10 (F:5′-TTTTGTCCCCATTCAGGATT-3′; R:5′-GCGTGCTTGAATCCTTGTG-3′; S. Libants, unpubl. data), and CR-G (F:5′- GTAGGCAAAGCAAGTCTGAAGTT-3′; R:5′-GCAACCACCAGCAGTCACTACAA-3′; A. Baker, unpubl. data), and penta-nucleotide microsatellite locus TTUCG-1 (Cathey et al. 1998). Each locus was amplified by PCR in 25-μL reaction volumes, including 100–150 ng DNA, 10-25 pmol of each primer, PCR buffer (10 mM Tris-HCl, pH 8.3, 50 mM KCl, 1.5 mM $MgCl_2$, 100 μg mL^{-1} gelatin, 0.01% NP-40, 0.01% Triton-X 100), 0.5 units of Taq DNA polymerase, and 100–200 μM dNTPs. Forward primers of each locus-specific primer pair were labeled with either HEX or *6-Fam* by the manufacturer (Integrated DNA Technologies, Inc., Coralville, IA). Most thermocycler conditions included a denaturing step of 94 °C for 2 min, followed by 30–35 cycles of 94 °C for 1 min, annealing temperature for 1 min [51 °C (Hhiμ1, Sfiμ10), 56 °C (Bcaμ1, Bcaμ9, Hhiμ3, CR-G), 58 °C (Bcaμ11 and TTUCG-1), 60 °C (Bcaμ5)], and 72 °C for 1 min. Conditions for Aalμ1 included a denaturing step of 94 °C for 2 min and 30 cycles of 94 °C for 1 min and 50 °C for 2 min. Products were visualized with a FMBIO II laser scanner (Hitachi Software Engineering Co., South San Francisco, CA) after electrophoresis on denaturing 6% acrylamide gels. Two experienced laboratory technicians scored the genotypes by comparison to 20-base-pair standards and reference samples of known allelic size.

ANALYSIS OF mtDNA

PCR amplification of the mitochondrial control region. A portion of the 5′ end of the mitochondrial control region approximately 400 bp in size was amplified by PCR from genomic Snow Goose DNA with the primers 16775L (5′-TTGTTCTCAACTACAGGAAC-3′) and 287H-M (5′-TAGAGAGTTGTTCTTAGGGT-3′) (Quinn 1992) for direct DNA sequencing. The reactions were carried out in 25-mL volumes including 1 μL of 250-mM B-mercaptoethanol, 2.5 μL of 2-mM dNTP mix, 4 μL of 25-mM $MgCl_2$, 15 pmol of each primer, 0.5 unit of ChromaTaq DNA polymerase, and 2.5 μL of ChromaTaq 10× PCR buffer (Denville Scientific, Metuchen, NJ). Thermocycling conditions were as follows: 2 min at 94 °C, 35 cycles of 40 sec at 94 °C, 40 sec at 57 °C, and 40 sec at 72 °C and a final extension of 5 min at 72 °C.

PCR product sequencing and processing. PCR products of the mitochondrial control region were cleaned with a Qiaquick PCR purification kit (Qiagen, Valencia, CA) to remove unincorporated nucleotides and primers. We determined gene sequences by automated fluorescent DNA cycle sequencing, using the internal primer LCHENCRI (5′-TTGGTTATGCATATTCGTGC-3′) as described by Weckstein et al. (2002) and the Big Dye Terminator kit version 3.1 (Applied Biosystems, Foster City, CA), visualizing them on an ABI 3730xl DNA sequencer (Applied Biosystems, Foster City, CA). All sequencing was carried out at the Michigan State University Research Technology Support Facility. We inspected chromatograms, aligned sequences by eye, and trimmed them with the computer program MEGA4 (Tamura et al. 2007). We examined sequences for transposed nuclear sequences (Sorenson and Fleischer 1996) by comparing them with sequences available in GenBank. We obtained control-region sequences from 161 Snow Geese, 51 from BI, 51 from NWI, and 59 from SWI. The final sequence alignment, which includes the 178-bp region reported previously (Quinn 1992, Weckstein et al. 2002), was 205 bp in length. We identified and assigned to haplotypes to individual sequences with the program Collapse 1.2 (available from http://darwin.uvigo.es). Sequences representing the mitochondrial control-region haplotypes collected and identified during this study have been deposited in GenBank under accession numbers HQ121366–HQ121398.

Measures of genetic diversity. We calculated microsatellite allele frequencies, allelic richness, expected and observed heterozygosities, degree of deviation of observed genotypic frequencies from Hardy–Weinberg equilibrium (for single loci), and linkage disequilibrium (across loci) with program FSTAT version 2.9.3 (Goudet et al. 1996, Goudet 2001). We estimated nucleotide and haplotype diversity for each population in program Arlequin version 2.0 (Schneider et al. 2000) for DNA sequences.

Demographic changes in populations leave distinctive signatures on the distribution of pair-wise differences between individuals in the number of base-pair substitutions. Tajima's *D* (Tajima 1989) is based on the difference between two estimates of base-pair variation ($\theta = N_e\mu$). Under the neutral model, two estimators of θ (the number of segregating sites and average number of pair-wise base-pair differences estimated for all haplotypes within a population) should be the same. *D* statistically different from zero indicates deviance from the expectation of neutrality and may have resulted from past population changes. In addition, smooth and unimodal distributions of pair-wise base-pair differences are expected in populations that have increased. Ragged distributions of pair-wise differences are characteristic of populations that have been in demographic equilibrium (Harpending 1994). We estimated Harpending's raggedness statistic (*r*) in Arlequin, and it and Tajima's *D* served as indicators of past demographic history (i.e., evidence of population expansion).

Analysis of population genetic structure. We estimated interpopulation variance in frequencies of microsatellite alleles and mtDNA control-region haplotypes in program Arlequin with and without weighting for allele or haplotype evolutionary relationships based on allele size or haplotype-sequence divergence (F_{ST} and R_{ST} for microsatellites and F_{ST} and Φ_{ST} for mtDNA, respectively). Significance of *F*-statistics was based on 95% confidence intervals determined by bootstrapping (1000 replicates) across loci. For tests of Hardy–Weinberg, gametic disequilibrium, and *F*-statistics, we adjusted nominal significance levels (α) to account for multiple testing with sequential Bonferroni corrections (Rice 1989).

Analysis of gene flow. We conducted analyses to estimate rates of past migration among Snow Goose populations and to estimate evolutionary effective population sizes. We calculated the evolutionary effective population size (θ; $4N_e\mu$ or $N_f\mu$ for nuclear and maternally inherited loci, respectively), number of migrants per generation (N_em), and number of female migrants per generation (N_fm) among the three western arctic Snow Goose populations for nuclear microsatellite and mtDNA, respectively, using program Migrate version 3.1.6 (Beerli and Felsenstein 2001, Beerli 2002). N_e and N_f in these models represent the evolutionary effective total and female population sizes, respectively, and μ is the rate of mutation to new alleles. The parameters estimated are mutation-scaled effective population size (θ_i) and mutation-scaled migration (M_i) for each of *i* sampled populations. The parameter θ is interpreted as the effective population size and mutation rate per site per generation ($xN_e\mu$ or $xN_f\mu$) where *x* is a multiplier that depends on ploidy and inheritance (e.g., $x = 4$ for biparentally inherited microsatellites and 1 for maternally inherited mtDNA).

We evaluated six models. Model 1 was an *N*-island model with equal θ and equal and symmetrical interpopulation rates of migration. Model 2 assumed variable θ with a constant and symmetrical rate of migration among populations. Model 3 was a "breeding ground" model that assumed equal θ with equal and symmetric rates of migration for populations that share a breeding area (SWI and NWI) and different rates of migration between breeding populations. Model 4 assumed constant θ with variable and nonsymmetrical rates of migration among populations. Model 5 was a "wintering ground" model that assumed constant θ with equal and symmetric migration rates between populations that share a common wintering area and θ differing between populations that did not. Model 6 was a full model in which parameter estimates for and all pair-wise and migration rates were allowed to vary.

We ran Migrate with maximum-likelihood search parameters including ten short chains (1000 genealogies per chain), four long chains (10 000 genealogies per chain), and four adaptively heated chains (start temperatures 1, 1.5, 3, and 10 000; swapping interval = 1). All models were run three times to ensure the convergence of parameter estimates. We used empirical estimates of F_{ST} for the initial run and output estimates of F_{ST} in subsequent runs. We evaluated alternative models for goodness of fit given the data with a log-likelihood

ratio test and for model selection by AIC (Burnham and Anderson 2002). The statistics resulting from the log-likelihood ratio test are equivalent to a χ^2 distribution with the degrees of freedom equal to the difference in the number of parameters estimated in the two models (Beerli and Felsenstein 2001).

RESULTS

Nine of 10 microsatellite loci used were polymorphic in all three populations, with 2 to 17 alleles present within each population (Table 1). No microsatellite locus deviated significantly from Hardy–Weinberg expectations in any population. Loci were genetically independent, as we detected no evidence of gametic disequilibrium for any interlocus combination in any population ($P > 0.05$). Tajima's D and Harpending's raggedness statistics were significant only for the SWI population, indicating a past demographic expansion.

We resolved 33 mtDNA haplotypes from two evolutionarily divergent clades across the three populations and subpopulations (Fig. 2, Table 1). Each of the three had a large number of private haplotypes (seen in only a single population): 6 for NWI, 5 for SWI, and 8 for BI. The majority of the private haplotypes were from mitochondrial clade II (Table 1). The populations' estimated levels of genetic diversity were concordant (Table 2), as evidenced by similar inbreeding coefficients (F_{IS} range 0.035–0.050), heterozygosity (range 0.535–0.544), and allelic richness (range 7.23–7.49) for nuclear loci, as well as number of haplotypes (range 16–17) and haplotype diversity (range 0.805–0.892) for mtDNA (Table 2). Nucleotide diversity for SWI and BI was higher than for NWI because of the equitable distribution of haplotypes from two genetically different clades that have been previously recognized (Quinn 1992, Avise et al. 1992, Weckstein et al. 2002; Fig. 2, Table 1). The frequencies of clade I haplotypes for SWI and BI were 0.475 and 0.532, respectively, compared to the highly skewed distribution of frequencies of clade I and clade II types for NWI (0.197 and 0.803, respectively; Table 1).

We summarized pair-wise interpopulation differences in microsatellite allele frequency across the ten microsatellite loci and for mtDNA sequences as the proportion of total genetic diversity partitioned between each pair of populations. None of the differences in microsatellite loci were significant (Table 3), indicating allele frequencies were similar across populations (mean F_{ST} across all populations = 0.0007, $P > 0.05$). Results did not vary whether allele frequencies were weighted on the basis of evolutionary relationships among alleles (R_{ST}) or not (F_{ST}). In contrast, the populations differed significantly in mtDNA haplotype frequencies (mean $F_{ST} = 0.047$, mean $\Phi_{ST} = 0.126$, $P < 0.001$; Table 3). The largest interpopulation Φ_{ST} was that between the BI and NWI populations (0.237). Frequencies of mitochondrial DNA haplotypes in the NWI and SWI subpopulations also differed significantly ($\Phi_{ST} = 0.127$, Table 3). Differences in mtDNA haplotype frequencies between the BI and SWI populations were much smaller ($\Phi_{ST} = 0.020$, $P > 0.05$).

TABLE 1. Frequencies of alleles at 10 biparentally inherited microsatellite loci and of mtDNA haplotypes from clades I and II in three populations of the Lesser Snow Goose breeding in the western Arctic.

		Population[a]		
Locus	Allele	NWI	SWI	BI
Microsatellites (*n*)		71	79	79
Bcaμ9	98	0.000	0.006	0.000
	102	0.487	0.424	0.411
	104	0.013	0.006	0.013
	106	0.173	0.129	0.196
	108	0.033	0.053	0.070
	110	0.127	0.147	0.127
	112	0.160	0.235	0.171
	114	0.007	0.000	0.013
TTUCG-1	165	0.007	0.000	0.000
	180	0.007	0.006	0.013
	185	0.013	0.012	0.006
	190	0.020	0.029	0.070
	195	0.053	0.053	0.038
	200	0.073	0.024	0.044
	205	0.087	0.071	0.063
	210	0.087	0.088	0.095
	215	0.100	0.106	0.127
	220	0.087	0.171	0.133
	225	0.127	0.106	0.076
	230	0.153	0.106	0.139
	235	0.067	0.071	0.101
	240	0.033	0.106	0.057
	245	0.020	0.018	0.019
	250	0.033	0.018	0.006
	255	0.000	0.000	0.013
	280	0.000	0.006	0.000
	290	0.007	0.006	0.000
	300	0.020	0.006	0.000
	305	0.007	0.000	0.000
Bcaμ1	112	0.013	0.000	0.006
	114	0.013	0.029	0.045
	116	0.113	0.094	0.064
	118	0.253	0.276	0.391
	120	0.060	0.047	0.058
	122	0.067	0.129	0.122
	124	0.160	0.129	0.051
	126	0.120	0.129	0.083
	128	0.047	0.071	0.071
	130	0.087	0.065	0.064
	132	0.053	0.012	0.019
	134	0.013	0.012	0.026
	188	0.000	0.006	0.000
Aalμ1	82	0.180	0.190	0.196
	84	0.073	0.065	0.044
	86	0.180	0.119	0.101
	88	0.407	0.423	0.456
	90	0.127	0.173	0.184
	92	0.033	0.030	0.019
Bcaμ5	200	0.987	0.994	1.000

(*continued*)

TABLE 1. Continued.

Locus	Allele	Population[a] NWI	SWI	BI
	202	0.013	0.006	0.000
CRG	164	0.993	0.994	0.975
	166	0.000	0.000	0.012
	168	0.007	0.006	0.012
Hhiμ1	174	0.000	0.012	0.006
	178	0.007	0.000	0.006
	180	0.000	0.000	0.006
	182	0.020	0.018	0.012
	184	0.007	0.006	0.000
	186	0.020	0.006	0.019
	188	0.092	0.071	0.062
	190	0.020	0.053	0.031
	192	0.066	0.141	0.062
	194	0.421	0.335	0.451
	196	0.125	0.106	0.105
	198	0.072	0.071	0.080
	200	0.033	0.029	0.031
	202	0.066	0.065	0.080
	204	0.020	0.029	0.012
	206	0.026	0.041	0.025
	208	0.000	0.006	0.006
	210	0.007	0.006	0.000
	212	0.000	0.006	0.000
	214	0.000	0.000	0.006
Hhiμ3	115	0.237	0.292	0.235
	117	0.020	0.006	0.012
	121	0.007	0.000	0.006
	123	0.171	0.196	0.235
	125	0.553	0.488	0.500
	127	0.013	0.018	0.012
Sfiμ10	126	0.507	0.560	0.481
	128	0.026	0.000	0.000
	130	0.467	0.440	0.519
Bcaμ11	134	0.000	0.006	0.000
	138	0.020	0.018	0.006
	140	0.862	0.887	0.883
	142	0.118	0.089	0.111
mtDNA (*n*)		51	59	51
	A (I)	0.157	0.339	0.353
	B[b] (I)	0.000	0.000	0.020
	C[b] (I)	0.000	0.000	0.020
	D (II)	0.039	0.153	0.275
	E[b] (II)	0.176	0.034	0.020
	F[b] (II)	0.039	0.000	0.020
	G[b] (II)	0.000	0.017	0.020
	H[b] (I)	0.000	0.034	0.020
	I[b] (I)	0.000	0.000	0.059
	J[b] (I)	0.000	0.000	0.039
	K[b] (I)	0.000	0.017	0.020
	L[b] (II)	0.000	0.017	0.020
	M[b] (I)	0.000	0.000	0.020
	N[b] (II)	0.000	0.000	0.020
	O[b] (II)	0.078	0.000	0.039
	Q[b] (II)	0.000	0.000	0.020
	R (I)	0.000	0.000	0.020
	S[b] (II)	0.216	0.203	0.000
	T[b] (II)	0.039	0.000	0.000
	U[b] (II)	0.020	0.017	0.000
	V[b] (II)	0.020	0.000	0.000
	W[b] (II)	0.098	0.000	0.000
	X[b] (II)	0.020	0.000	0.000
	Y[b] (II)	0.020	0.017	0.000
	Z (I)	0.020	0.000	0.000
	AA (II)[b]	0.020	0.000	0.000
	AB[b] (I)	0.020	0.017	0.000
	AC[b] (II)	0.020	0.017	0.000
	AD[b] (I)	0.000	0.017	0.000
	AE (I)	0.000	0.051	0.000
	AF[b] (II)	0.000	0.017	0.000
	AG[b] (II)	0.000	0.017	0.000
	AH[b] (II)	0.000	0.017	0.000

(*continued*)

[a]NWI, breeding on Wrangel Island, wintering in British Columbia and Washington ($n = 76$); SWI, breeding on Wrangel Island, wintering in California ($n = 85$); breeding on Banks Island, wintering in California ($n = 81$).
[b]New haplotype not previously documented for the Snow or Ross's Goose.

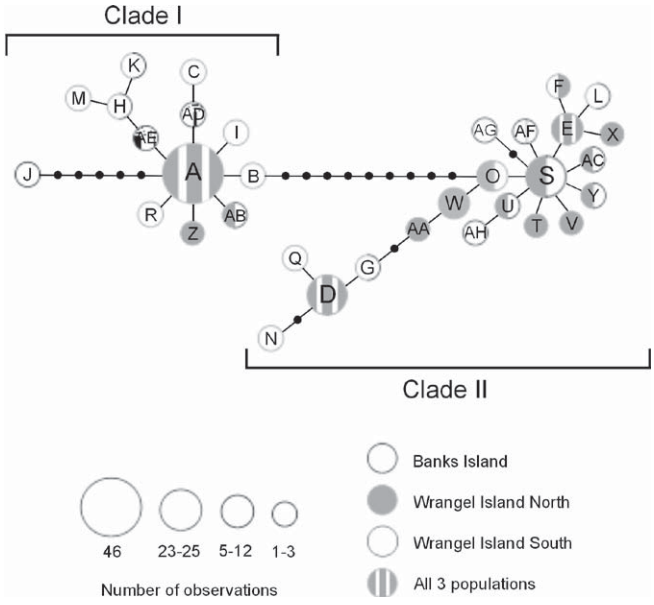

FIGURE 2. Minimum spanning tree of control-region haplotypes of the Snow Geese observed in this study.

TABLE 2. Estimates of population levels of genetic diversity of three populations of Lesser Snow Geese breeding in the western Arctic.

Genetic diversity measure	Wrangel I. N	Wrangel I. S	Banks I.
mtDNA	$n = 51$	$n = 59$	$n = 51$
No. haplotypes	16	17	17
Haplotype diversity	0.892	0.826	0.805
Nucleotide diversity	0.025	0.035	0.035
Tajima's D	0.805	1.675[a]	0.821
Raggedness	0.064	0.095[a]	0.067
Microsatellites	$n = 71$	$n = 79$	$n = 79$
Heterozygosity (H_E)	0.544	0.544	0.535
F_{IS}	0.049	0.05	0.035
Allelic richness	7.49	7.23	7.3

[a]Statistically significant; $P < 0.05$.

Comparisons of competing models of migration and effective population size indicated that model 4 (constant θ with variable and nonsymmetrical migration) was the model of best fit for microsatellite loci ($\ln L = -0.22$; Table 4). Model 6 (full model with different θ and different and nonsymmetrical migration) was the model of best fit for mtDNA ($\ln L = 3.5$; Table 4). For mtDNA, under model 6, for females, the evolutionary effective sizes of the BI (0.024) and NWI (0.017) populations were smaller than that of the SWI population (0.044, Table 5). Estimates of rates of female gene flow between populations were highly variable, differed by two orders of magnitude, and were decidedly asymmetric. For example, the rate of gene flow from BI into SWI was 118 whereas that from SWI into BI was 2064. Rates of female gene flow from BI into NWI were six times the rate estimated from NWI into BI (Table 5A). The rate of female gene flow from SWI into NWI was 4 times that from NWI into SWI (Table 5A). The degree of asymmetry in biparentally inherited microsatellite loci was less than the magnitude of differences in rates of female gene flow estimated for mtDNA (Table 5B).

DISCUSSION

FEMALE- AND MALE-MEDIATED GENE FLOW AMONG POPULATIONS

Our data on spatial genetic structuring imply that female Lesser Snow Geese have more fidelity to winter than to breeding areas, as suggested previously (Ryder and Alisauskas 1995, Robertson and Cooke 1999, Ganter et al. 2005). The subpopulations of Lesser Snow Geese (SWI and NWI) that breed on Wrangel Island differed significantly in mtDNA haplotype frequency (Tables 1, 3), while birds that winter in the same area (SWI and BI) were not genetically differentiated. Coalescence simulations indicated that neither the "breeding ground" or "wintering ground" models (models 3 and 5, respectively; Table 4) fit for our data better than the full model of different and nonsymmetrical rates of gene flow (model 6), likely because of asymmetry in rates of inferred gene flow.

Rates of gene flow between populations were not symmetrical, as evidenced by the large disparity in estimates and direction of female-mediated gene flow (Table 5). Estimates of female migration rates suggest that some fraction of SWI females nested on Banks Island and comparatively fewer females from Banks Island bypassed their natal colony during spring migration to nest on Wrangel Island. Estimated rates of female migration from NWI to BI are far lower. Moderate levels of estimated female gene flow between BI and NWI (122) and between BI and SWI (118) suggest that some females extend migration beyond natal areas. However, the much higher estimate of female gene flow between SWI and BI (2063) suggests that females are more likely to stop short than to extend migration beyond natal areas. Stopovers during spring migration are common (Clausen et al. 2003, Drent et al. 2007), possibly because resources are insufficient to both continue migration and successfully breed. Reciprocity of estimates of biparental gene flow between SWI and BI greater than for female-mediated gene flow suggests that males are less likely to discriminate between mates by site of origin. Furthermore, stopping short in fall can also influence demographic trends

TABLE 3. Pair-wise estimates of interpopulation variation in frequencies of mtDNA haplotypes and microsatellite alleles between three populations of the Lesser Snow Goose breeding in the western Arctic. Above diagonal: F_{ST} (mtDNA) and R_{ST} (microsatellites) based on pair-wise distances. Below diagonal: Φ_{ST} based on pair-wise differences in the frequency of alleles and haplotypes only[a].

	Microsatellites			mtDNA		
Population	Wrangel I. N	Wrangel I. S	Banks I.	Wrangel I. N	Wrangel I. S	Banks I.
Wrangel I. N		0.000	0.001		0.127**	0.237**
Wrangel I. S	0.000		0.004	0.034*		0.020
Banks I.	0.005	0.001		0.085**	0.025*	

[a]Levels of significance: *$P < 0.05$; **$P < 0.01$.

TABLE 4. Summary and quantitative evaluation of different coalescence models of interpopulation gene flow (m_{ij}) and evolutionary effective population size (θ) for populations of the Lesser Snow Goose breeding in the western Arctic based on maternally inherited mtDNA and biparentally inherited microsatellite loci.

		Microsatellites			mtDNA		
Model	Hypothesis	LRT (df)	K[a]	ΔAIC	LRT (df)	K	ΔAIC
1	N-island model	1127.9 (9)	2	1113.78	240.85 (9)	2	226.85
2	Variable θ, constant m_{ij}	696.2 (6)	7	692.22	174.08 (6)	7	170.08
3	Constant θ, symmetric breeding m_{ij}	192.77 (5)	7	188.77	31.74 (5)	7	172.91
4	Constant θ, variable m_{ij}	2.21 (3)	8	0.22[b]	7.25 (3)	8	5.25
5	Constant θ, symmetric wintering m_{ij}	391.37 (5)	8	389.37	131.51(5)	8	129.52
6	Full model, variable θ and m_{ij}		9	0		9	0[b]

[a]Number of parameters.
[b]Model of best fit to data according to ΔAIC.

(Newton 2006, Mitchell et al. 2010). If in fall migration SWI geese stop short in British Columbia they could contribute to the asymmetrical gene flow from SWI into NWI.

Estimated rates of female gene flow between the SWI and NWI subpopulations are likewise asymmetrical (Table 5). Our simulations indicated a rate of gene flow of SWI females to NWI four times higher than from NWI to SWI. These genetic results are consistent with historic and recent changes in the winter distribution of Wrangel Island Lesser Snow Geese between California (southern) and the Fraser–Skagit delta (northern). During the 1970s approximately 80% of the Snow Geese nesting on Wrangel Island wintered in California, but when genetic data were collected in the mid-1990s, approximately 60% of them wintered in the Fraser–Skagit region (Baranyuk 1995, Boyd 1995, Hines et al. 1999a). This dramatic shift in winter distribution was not sufficient to homogenize the frequencies of mtDNA haplotypes of NWI and SWI geese, suggesting that other mechanisms affect interactions among individuals on wintering areas and maintain the genetic integrity of birds from different breeding areas. In addition, higher rates of female gene flow between SWI and NWI than between BI and NWI (799 vs. 122, respectively) suggests that SWI females stopping short during fall migration is more likely than BI females extending spring migration to Wrangel Island.

Other factors may also contribute to interbreeding between the NWI and SWI populations. Depending on the degree of asymmetry in arrival times of NWI and SWI females, extra-pair paternity could contribute to gene flow. Fostering and subsequent movement of goslings on Wrangel Island could contribute to gene flow between the island's two subpopulations. Gene flow between NWI and SWI may also be attributed to matrilineal mixing of genes through intraspecific brood parasitism, as observed in other waterfowl (Lank et al. 1989, Larsson et al. 1995), given the overlap of the SWI and NWI subpopulations within the colony.

Genetic differences observed for mtDNA were not reflected in biparentally inherited microsatellite loci (Table 3), suggesting rates of gene flow from males were higher

TABLE 5. (A) Parameter estimates for migration rates (M_{ij} or m_{ij}/μ) estimated for maternally inherited mtDNA ($N_f m$) and biparentally inherited microsatellite loci ($4Nm$) and θ ($N_{ef}\mu$ and $4N_e\mu$ for mtDNA and microsatellites, respectively) for models of best fit (Table 3). (B) Migration estimates expressed as θM to standardize female and biparental estimates for inheritance and ploidy.

		A			B[a]		
Receiving population	θ	Wrangel I. N	Wrangel I. S	Banks I.	Wrangel I. N	Wrangel I. S	Banks I.
mtDNA (full model [model 6]: variable θ and variable and asymmetric migration)							
Wrangel I. N	0.017		799	122		13.6	2.1
Wrangel I. S	0.044	192		118	8.4		5.2
Banks I.	0.024	20	2063		0.5	49.5	
Microsatellites (model [4]: constant θ and variable and asymmetric migration)							
Wrangel I. N	1.126		10	9		11.3	10.13
Wrangel I. S	1.126	15		11	16.9		12.4
Banks I.	1.126	12	14		13.5	15.8	

[a]Standardized estimates of migration rates for mtDNA and microsatellite loci are not strictly comparable because of expected differences in mutation rates.

than from females. Our coalescence-based analysis of frequencies of biparentally inherited microsatellite alleles indicated rates of genetic exchange among the three populations more equitable than that in mtDNA (Table 5B). Discordance between male-mediated and female-mediated gene flow among Lesser Snow Geese in the western Arctic may not be typical for other Lesser Snow Goose populations. Many geographically distinct breeding populations are interconnected seasonally by overlapping migration routes and shared wintering areas (Mowbray et al. 2000, Drake and Alisauskas 2004), allowing extensive gene flow. Consistent with this model of gene flow, past studies of Lesser Snow Geese have found little to no phylogeographic differentiation in frequencies of mtDNA haplotypes in most breeding populations across North America (Avise et al. 1992, Quinn 1992, Weckstein et al. 2002).

Delayed sexual maturity (Ganter et al. 2005) of Wrangel Island Lesser Snow Geese may increase the degree of natal philopatry if individuals travel between breeding and wintering areas with family groups multiple times prior to establishing pair bonds. The reproductive isolation of breeding populations could be reinforced by the fact that birds from Wrangel Island are likely to pair at ages older and remain in family groups longer than birds from other breeding locales, due to the island's harsh and highly variable high-Arctic climate, low annual breeding success (Bousfield and Syroechkovsky 1985), and delayed age of sexual maturity (Ganter et al. 2005). These demographic factors increase the likelihood that NWI and SWI geese winter in families, further decreasing dispersal and gene flow among wintering populations.

Previous studies of Wrangel Island Lesser Snow Geese were based on resightings of neck collars (Syroechkovsky et al. 1994, Williams et al. 2008) and genetic analyses of protein allozymes (Kuznetsov et al. 1998), which are less variable than microsatellite and mtDNA sequences. On the basis of visual observations of banded individuals, Syroechkovsky et al. (1994) and Williams et al. (2008) estimated the exchange of migrants between the SWI and NWI wintering subpopulations to be approximately 3% per year. There is no evidence of migration between the BI and NWI wintering populations. If Lesser Snow Geese form pair bonds during wintering or spring migration, then limited exchange between wintering areas is consistent with the asymmetric direction and rate of female-mediated gene flow we found. Allozyme analyses of biparentally inherited blood proteins and esterases from samples of NWI and SWI geese found no statistical differences between populations in allele frequency (Kuznetsov et al. 1998), as we observed in biparentally inherited microsatellite loci. Levels of inferred exchange of males are sufficiently high to preclude the accrual of differences in biparentally inherited genes (Waples and Gaggiotti 2006).

Genetic drift may be an additional factor contributing to accrual of genetic differences among populations. If genetic drift were the only factor influencing haplotype-frequency differences between NWI and SWI Snow Geese, we would expect divergence in frequencies of mtDNA clades approximately 4 times greater than those in alleles of nuclear DNA (Birky et al. 1989). However, differences in microsatellite and mtDNA estimates of interpopulation variance in allele and haplotype frequencies, respectively, exceed this threshold substantially (Table 3). Therefore, we conclude that drift alone cannot account for the difference in frequencies of mtDNA haplotypes and microsatellite alleles between the NWI and SWI subpopulations.

Demographic parameters estimated from mtDNA data based on distributions of pair-wise base-pair differences between haplotypes (Tajima's D and Harpending's r; Table 2) and θ (Table 5) were consistent, showing that the SWI population has experienced periods of demographic expansion. The increase in the BI population is too recent for mutations to have arisen, have increased in frequency, and be reflected in the mtDNA population profiles. Given the differences in population growth rates, levels of maternal gene flow between NWI and BI and SWI may be insufficient to provide demographic rescue if a population's viability is threatened.

PHYLOGEOGRAPHIC PATTERNS IN DATA

The degree of sequence divergence between clade I and clade II haplotypes has been repeatedly observed in North American populations (Quinn 1992, Weckstein et al. 2002) and suggests prolonged isolation in different glacial refugia (Ploeger 1968). In addition, large differences in the frequency of haplotypes (Table 1) of two divergent clades (Fig. 2) suggest that Asia could be the origin of clade II haplotypes. Significant differences in mtDNA-haplotype frequencies of NWI and SWI geese may indicate incomplete lineage sorting, considering that in the past the NWI and SWI populations may have been spatially segregated for breeding. Kuznetsov et al. (1998) and Takekawa et al. (1994) reported that Lesser Snow Geese historically nested in multiple colonies on Wrangel Island and that a portion of the island's population may be derived from geese that formerly nested on the coast of the nearby mainland and joined the Wrangel Island colony after being displaced prior to the 1930s (Bousfield and Syroechkovsky 1985). Although inhabiting the same island, the NWI and SWI populations may have been largely isolated in different breeding colonies into the late 1950s (Syroechkovsky and Krechmar 1981, Kuznetsov et al. 1998). Only since 1969 have the majority of geese on Wrangel Island nested in a single large colony (Bousfield and Syroechkovsky 1985), increasing the potential for mixing of geese of the two populations on the breeding grounds. The large disparity in clade II frequency between NWI (0.803) and SWI (0.525) is further reflected in Φ_{ST} (0.127) exceeding F_{ST} (0.037). If the areas in which NWI and SWI winter have remained constant over time, haplotype frequencies of BI and SWI may have been similar for a considerable period.

CONCLUSIONS

Our study highlights how combining direct and indirect measures of dispersal and genetic exchange by using multiple genetic markers with different patterns of inheritance can provide a more comprehensive picture of demographic patterns through time and aid in population assessment. Significant genetic differences between the NWI and SWI populations indicate that these populations should be currently managed as separate populations, or subpopulations, even though most individuals nest within one large breeding colony on Wrangel Island. Genetic differences between NWI and BI Snow Geese, and the lack of such differences between SWI and BI geese wintering in the same region, suggest that management of Lesser Snow Geese of the western Arctic should consider the winter range as well as the breeding range. However, if BI and SWI birds are managed as one unit, we caution that reduction of the overabundant BI population through harvest in winter could significantly reduce the long-term viability and genetic diversity of the SWI breeding population.

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