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GENETIC DIFFERENTIATION BETWEEN SYMPATRIC AND ALLOPATRIC WINTERING POPULATIONS OF SNOW GEESE

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ABSTRACT.—Blackwater National Wildlife Refuge on the Delmarva Peninsula, Maryland, USA has been the wintering area of a small population of Lesser Snow Geese (*Chen caerulescens caerulescens*; LSGO) since the 1930s. Snow Geese primarily pair in wintering areas and gene flow could be restricted between this and other LSGO wintering populations. Winter pair formation also could facilitate interbreeding with sympatric but morphologically differentiated Greater Snow Geese (*C. c. atlantica*; GSGO).We sequenced 658 bp of the mitochondrial DNA control region for 68 Snow Geese from East Coast and Louisiana wintering populations to examine the level of genetic differentiation among populations and subspecies. We found no evidence for genetic differentiation between LSGO populations but, consistent with morphological differences, LSGO and GSGO were significantly differentiated. We also found a lack of genetic differentiation between different LSGO morphotypes from Louisiana. We examined available banding data and found the breeding range of Delmarva LSGO overlaps extensively with LSGO that winter in Louisiana, and documented movements between wintering populations. Our results suggest the Delmarva population of LSGO is not a unique population unit apart from Mid-Continent Snow Geese. *Received 30 August 2007. Accepted 23 September 2008.*

A small population of Lesser Snow Geese (*Chen caerulescens caerulescens*; LSGO) has been wintering on the Delmarva Peninsula on the east coast of the United States, mostly at Blackwater National Wildlife Refuge (NWR), Maryland since the 1930s (Bellrose 1976). Historically, LSGO were migrants in the Pacific Flyway and the Mid-Continent Region (Central and Mississippi flyways) of North America, and wintered from the Mississippi River west to California. Snow Geese that historically wintered in the Atlantic Flyway were a distinct subspecies, the Greater Snow Goose (*C. c. atlantica*; GSGO) (Mowbray et al. 2000). Colonization of the Atlantic Flyway by LSGO may have two important consequences. First, the Delmarva LSGO may constitute a unique population unit if gene flow is restricted between this and other LSGO populations. Second, recent secondary contact between LSGO and GSGO may facilitate interbreeding between these subspecies.

Information concerning the genetic identity of LSGO on the Delmarva Peninsula is important because a plan to increase the harvest rate of Snow Geese in the Atlantic Flyway has been implemented. The plan is intended to direct actions to control the continental GSGO population, which has been steadily increasing since the 1960s (Reed et al. 1998). As the population has grown, increased grazing pressure has resulted in severe marsh erosion and a decline in the quality of local wintering areas (Smith and Odum 1981, Giroux et al. 1998). A higher harvest rate could help stabilize the population at 1,000,000 birds or fewer and prevent further degradation of staging and wintering areas. The Mid-continent LSGO population also has increased during the last 40 years and has been subjected to liberalized harvest rates (Ankney 1996, Rockwell et al. 1997). If Delmarva LSGO are genetically distinct from other LSGO, waterfowl managers may desire to treat them as a unique management unit (Moritz 1994) with separate population goals.

Genetic differentiation in mitochondrial DNA (mtDNA) has been observed among breeding populations of LSGO (Quinn 1992, Weckstein et al. 2002). The Delmarva LSGO population breeds along Hudson Bay where its range overlaps with LSGO that winter in Louisiana and Texas (the Mid-Continent Population) (Bellrose 1976). These wintering populations likely share breeding areas and genetic differentiation might not be

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expected. Pair formation primarily occurs in wintering areas (Cooke 1987, McKinney 1992, Mowbray et al. 2000, Ganter et al. 2005), and this behavior could restrict gene flow and genetically isolate Delmarva LSGO from other wintering populations (Robertson and Cooke 1999).

The founder event in the 1930s, when the Delmarva LSGO winter population became established, also could have contributed to population differentiation. The original founders likely carried a subset of the total genetic diversity in the Mid-Continent Region; restricted gene flow and genetic drift could have caused further loss of genetic diversity, resulting in genetic differentiation between Mid-Continent and Atlantic Flyway wintering populations. Thus, the Delmarva LSGO population might exhibit low genetic diversity relative to Mid-Continent LSGO.

The close proximity of LSGO and GSGO (hereafter East Coast GSGO) wintering in Delmarva could facilitate interbreeding between the two morphologically differentiated subspecies and result in genetic homogenization (Rhymer and Simberloff 1996). GSGO generally are larger than LSGO and frequencies of plumage-color phases differ between subspecies. LSGO are either a white- or blue-phase; blue-phase are common in Louisiana and Maryland ($\sim$ 50%) but are rarer in western states. GSGO usually are white-phase (Bellrose 1976, Cooke 1987, Avise et al. 1992, Mundy et al. 2004). Avise et al. (1992) found that LSGO and GSGO shared two distinct mtDNA clades (both clades also were shared with the Snow Goose's sister species, the Ross's Goose [*Chen rossii*]). Avise et al. (1992) found a lack of genetic differentiation between subspecies and among populations of LSGO. However, direct sequencing of mtDNA revealed significant differentiation among LSGO populations (Quinn 1992, Weckstein et al. 2002). Sequence data previously were not available for GSGO and a comparison of mtDNA sequences between LSGO and GSGO would contribute to better understanding genetic differentiation between these subspecies.

Alisauskas (1998) documented that different morphotypes of Mid-Continent LSGO used different habitats (Jónsson 2005, Jónsson and Afton 2006). Geese feeding in coastal marshes had overall larger body sizes than did those feeding in rice-prairies (hereafter rice and coastal LSGO). Whether these morphotypes are genetically differentiated is not known.

Our objective was to ascertain whether LSGO from the Delmarva Peninsula represent a distinct population from Mid-Continental LSGO and sympatric GSGO, and constitute a unique population unit. We analyzed mitochondrial DNA sequences to test for genetic differences between these groups. We also tested for genetic differentiation between Louisiana LSGO morphotypes. Finally, we examined banding data to (1) identify the extent of breeding range overlap between Delmarva and Louisiana Snow Geese, and (2) search for evidence of movements between Delmarva and other wintering areas.

METHODS

Sample Collection.—We sampled foot-webbing from wintering LSGO and GSGO ($n = 28$ geese) at Blackwater NWR in Maryland (Fig. 1). We sampled foot-webbing from rice prairie LSGO in the vicinity of Cameron Prairie NWR and coastal marsh LSGO from Rockefeller State Wildlife Refuge ($n = 20$ geese) in Louisiana. We collected muscle samples from hunter-harvested GSGO at Chincoteague NWR and Back Bay NWR in Virginia, and from Bombay Hook NWR in Delaware ($n = 19$ geese). Gender of individuals was assigned either by cloacal examination (Hochbaum 1942) or by amplifying chromosomes following Kahn et al. (1998).

Morphology.—We measured culmen length, head length, total tarsus length, and flattened wing length for each goose following Dzubin and Cooch (1992). We compared morphometrics of adult geese from Blackwater NWR with adult LSGO (4 males, 4 females) from Louisiana and with adult GSGO from the east coast (exclusive of Blackwater NWR). We compared our measurements to previously published measurements of LSGO and GSGO (Alisauskas 1998, Mowbray et al. 2000). We classified an individual as LSGO if all measurements were within the range of measurements from Louisiana LSGO and/or within the standard deviations reported in Alisauskas (1998). All geese consistently larger than known LSGO and within the range of the published GSGO morphometrics (Mowbray et al. 2000) were classified as GSGO. Individuals, that had some size measurements that grouped with LSGO but others that grouped with GSGO were classified as unknowns in our analysis.

Genetics.—We extracted DNA from tissue samples using the DNeasy Tissue Kit (Qiagen, Valencia, CA, USA). We amplified a 658 bp fragment of the mtDNA control region using primers L78 and H774 (Sorenson and Fleischer

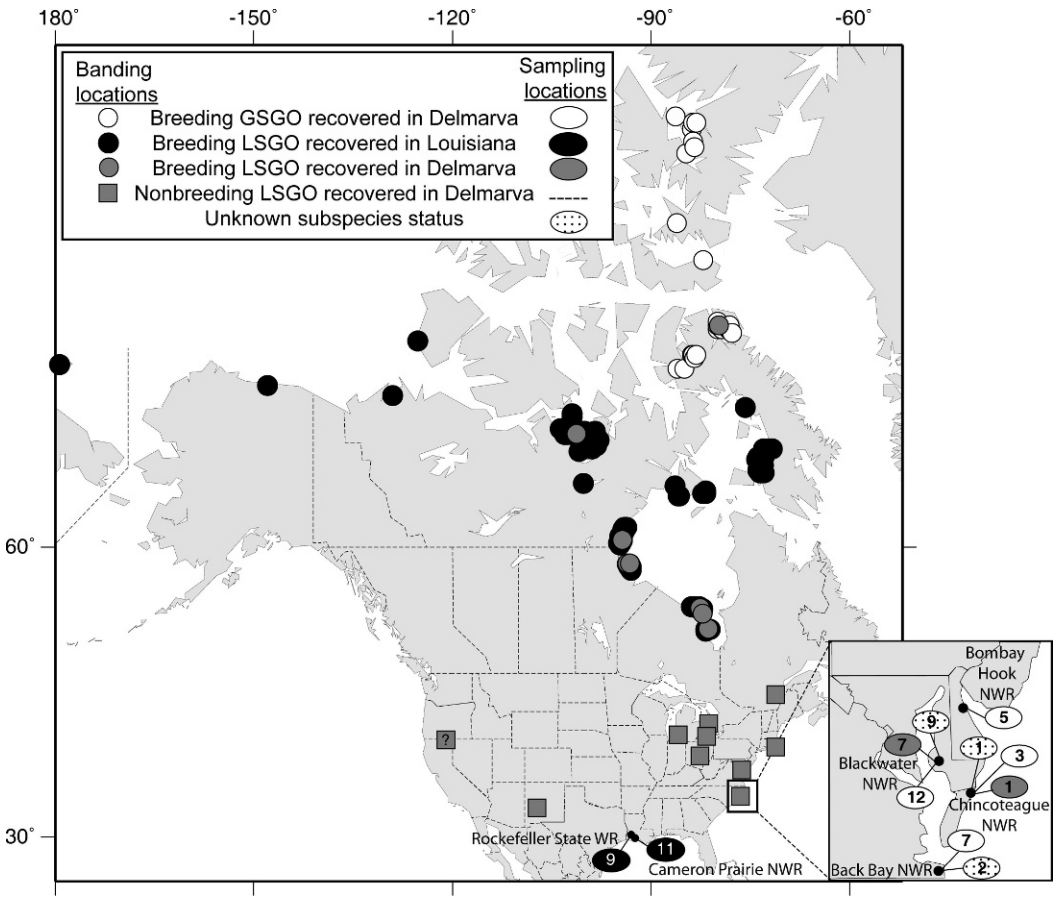

FIG. 1. Banding and recovery locations (circles and squares) and sample sizes (ellipses) for genetic comparisons of Snow Geese. Circles indicate Snow Geese banded during the breeding season recovered on the Delmarva Peninsula (gray = LSGO, white = GSGO) or Louisiana (black). Squares indicate banding or recovery points of LSGO also observed in Delmarva. The question mark indicated an LSGO that was banded in California and recovered in Maryland, although the exact recovery location was not reported.

1996, Sorenson et al. 1999). PCR products were sequenced in both directions using these primers. Both PCR and cycle-sequencing followed the protocols of McCracken et al. (2001). We sequenced products on an ABI 3100 automated sequencer (Applied Biosystems Inc., Foster City, CA, USA) and aligned sequences using Sequencher sequence analysis software (Genecodes Corporation Inc., Ann Arbor, MI, USA). All sequences were submitted to GenBank (accession numbers FJ905228-FJ905294). We compared our sequences to published mtDNA control region sequences and to a Snow Goose nuclear copy (GenBank accession number M95434; Quinn 1992) to ensure that we amplified mtDNA and not a homologous nuclear copy.

We constructed haplotype networks to illustrate phylogenetic relationships among Snow Goose haplotypes using the median joining algorithm in Network v.4.1 (Bandelt et al. 1999). The level of differentiation among populations and subspecies was examined by calculating pairwise Φ_{ST} and conventional F_{ST} between all groups in Arlequin v. 3.01 (Excoffier et al. 2005). We also calculated S_{NN} (nearest-neighbor statistic; Hudson 2000) among populations. S_{NN} estimates how frequently similar pairs of sequences come from the same population; this statistic has more power than other tests of genetic differentiation when sample sizes are small (Hudson 2000). We pooled geese for these tests of genetic differentiation into four groups: Louisiana LSGO,

Delmarva LSGO, GSGO, and ''unknown'' subspecies status.

Banding Data Analysis.—We obtained available band recovery data for Delmarva LSGO from the Bird Banding Laboratory (USGS, Bird Banding Laboratory, Laurel, MD, USA); 24 records were obtained of LSGO that were either banded or recovered on the Delmarva Peninsula. Fourteen individuals were banded in July or early-August and likely represented birds banded on or near their breeding areas. We also obtained records of 4,740 LSGO and 1,328 GSGO that were banded on or near their breeding sites and recovered in Louisiana (LSGO) and Delmarva (GSGO), respectively.

RESULTS

Morphology.—Culmen length, head length, and flattened wing length were informative of subspecies designation (Fig. 2). Total tarsus length overlapped substantially between Louisiana LSGO and East Coast GSGO and was not used (data not shown). We classified five (both blue- and white-phase) geese from Blackwater NWR and a blue-phase goose from Chincoteague NWR as LSGO based on these measurements (Fig. 2). Twelve geese from Blackwater NWR were classified as GSGO because they were comparable in size to GSGO from other locations and consistently larger than LSGO (Fig. 2). We classified nine Blackwater NWR geese and three other Atlantic Flyway geese as unknown. We also designated two blue-phase geese from Blackwater NWR, for which size measurements were not available, as LSGO (plumage color and a visual qualitative assessment of body size suggested they were LSGO).

Genetics.—We found 12 different haplotypes that clustered into two distinct mitochondrial clades. Within Clade A, 60.0% of Delmarva LSGO, 86.7% of Louisiana LSGO, and 81.8% of GSGO shared a common haplotype. Clade B haplotypes that were common in LSGO were rare in GSGO, and haplotypes common in GSGO were absent in LSGO. Haplotypes common in GSGO also were common in the unknown group.

All pairwise Φ_{ST} were non-significant (Table 1) indicating that nucleotide diversity did not differ among populations or subspecies. Pairwise F_{ST} between LSGO and GSGO populations were positive (although non-significant), whereas the pairwise F_{ST} between LSGO populations was negative and non-significant (Table 1). S_{NN} values were small and significant ($P < 0.05$) for all comparisons between LSGO and GSGO. Comparisons between populations of the same subspecies resulted in S_{NN} values that were larger and non-significant (Table 1). The 12 ''unknown'' individuals were well differentiated from both LSGO populations, but similar to GSGO. We also compared the rice and coastal Louisiana LSGO and found these morphotypes did not differ significantly for any measures of differentiation.

Banding Data.—Five of 14 LSGO banded in breeding areas and subsequently recovered on Delmarva were banded on the south coast of Hudson/St. James Bay, six were banded on the west coast of Hudson Bay, two were banded along Queen Maud Gulf, and one was banded on Baffin Island (Fig. 1). The remaining six LSGO recovered on Delmarva were banded during the nonbreeding season at locations south of their normal breeding range (Fig. 1); the four individuals banded on Delmarva also were recovered at different locations during the nonbreeding season. One individual banded in New Mexico was recovered on Delmarva and an individual banded in California was recovered in Maryland (latitude and longitude coordinates were not reported for this recovery), indicating movements occur between wintering populations.

DISCUSSION

The available banding and genetic data suggest that Delmarva LSGO are not a unique population unit. First, Delmarva LSGO were not genetically differentiated in mtDNA from Louisiana LSGO. Second, banding data suggest that LSGO that winter in Delmarva breed in several different colonies and overlap with LSGO from other wintering populations (e.g., Louisiana). Third, movement was documented between widely disjunct wintering populations. These results suggest that connectivity between wintering populations of LSGO has prevented population differentiation; Johnson (1996) also observed that a small percentage of LSGO moved between flyways over different winters and within the same winter. However, Delmarva LSGO were moderately differentiated from sympatric GSGO, which is consistent with observed morphological differences and subspecies designations.

Delmarva LSGO and Blackwater GSGO are sympatric in winter (and could form pairs), but we suspect there is only limited interbreeding between subspecies (e.g., Ankney 1975). We found a Blue Goose that was more similar in size to

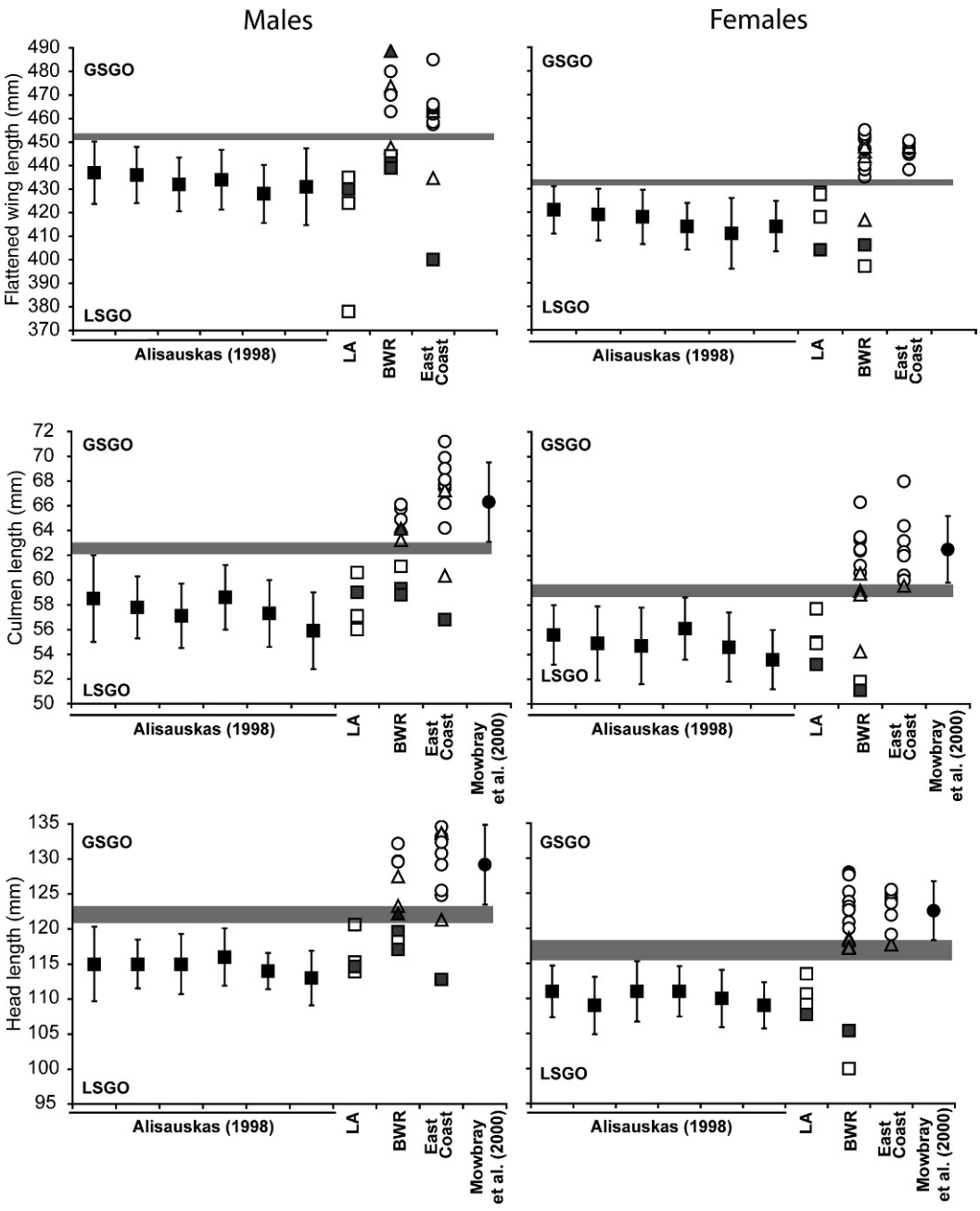

FIG. 2. Snow Goose morphometrics: flattened wing length, culmen length, and head length. Squares represent geese that were consistently within the LSGO size range, and circles represent geese that were consistently within the GSGO range. Triangles denote geese that had some measurements consistent with both LSGO and GSGO or that were ambiguous (i.e., within the gray region); these individuals were treated as ''unknowns''. Shaded shapes represent blue-morph geese. The measurements from Alisauskas (1998) represent geese populations in three different wintering habitats from 2 different years.

TABLE 1. Pairwise Φ_{ST}, F_{ST}, and S_{NN} values among populations and subspecies of Snow Geese. * indicates strong differentiation between pairs ($P < 0.05$); ** indicates significant differentiation after a Bonferroni correction for six pairwise comparisons (critical $P = 0.008$).

Pairwise comparison	Φ_{ST}	F_{ST}	S_{NN}
Delmarva LSGO			
Louisiana LSGO	−0.041	−0.021	0.600
Eastern GSGO	−0.060	0.080	0.753**
Eastern Unknown	−0.046	0.085	0.717*
Louisiana LSGO			
Eastern GSGO	−0.007	0.063*	0.650**
Eastern Unknown	−0.055	0.040	0.674*
Eastern GSGO			
Eastern Unknown	−0.041	−0.049	0.513

GSGO than to LSGO, and a LSGO recovered in Delmarva was banded within the GSGO breeding range supporting some level of interbreeding. We also found several individuals having some size measurements consistent with GSGO and others more similar to LSGO. A hybrid ancestry might explain these intermediate phenotypes, but size measurements overlap between subspecies and are not conclusively diagnostic (Cooke et al. 1995). Individuals with intermediate phenotypes were genetically more similar to GSGO; five unknown individuals had mtDNA haplotypes shared exclusively with GSGO, whereas seven individuals had the most common haplotype that was shared with both subspecies. This genetic similarity suggests these unknowns mostly are small-bodied GSGO or are descendant from pairings between female GSGO and male LSGO because mtDNA is maternally inherited. Nuclear markers are needed to test the identity of our unknown geese.

We observed two flocks of Snow Geese in Blackwater NWR during sample collection. One flock was predominately white morphs and our morphological measurements indicated this flock primarily consisted of GSGO (only 1 of 33 individuals captured from this flock was morphologically more similar to LSGO); this is the first documentation of GSGO using Blackwater NWR. The other flock was ~50% blue-morphs (Roger Stone, pers. obs.), and five of six Blue Geese from Delmarva that we measured were more similar in size to LSGO. These observations suggest that intermixing between flocks is limited, although further observations, ideally from breeding areas, are needed.

We found the two morphs in Louisiana did not exhibit differences in mtDNA, i.e., rice and coastal LSGO were genetically similar, despite significant differences in morphology (Alisauskas 1998, Jónsson 2005). Consistent with this lack of differentiation, Jónsson (2005) found that LSGO move between the two habitats and that both morphotypes have been observed at the same breeding location (Karrak Lake, Nunavut); thus, rice and coastal LSGO have frequent opportunities to pair. Currently, there is limited support for a hypothesis of separate populations because movements between habitats occurred and birds from both habitats frequently were observed within the same flocks (Jónsson 2005). One untested hypothesis is that the different morphs result from nutritional differences between habitat types (Alisauskas 1998).

Snow Geese have two distinct clades of mtDNA haplotypes that are shared between subspecies and with Ross's Geese (Avise et al. 1992, Weckstein et al. 2002). Avise et al. (1992) proposed two hypotheses for this shared polymorphism: (1) interspecific hybridization, and (2) retained ancestral polymorphism. Weckstein et al. (2002) argued that interspecific hybridization was the more likely reason for the shared clades on the basis of documented hybridization between LSGO and Ross's Geese. However, the ancestral polymorphism hypothesis also is consistent with the data. For example, LSGO and GSGO only shared two haplotypes, and both were common and at internal positions within the haplotype network, suggesting they were ancestral (Castelloe and Templeton 1994). These two haplotypes also were shared with Ross's Geese sampled by Weckstein et al. (2002). In contrast, derived haplotypes were subspecies-specific, including two high frequency haplotypes in GSGO (haplotypes 9b and 9c; Fig. 3). This pattern is consistent with an intermediate stage of divergence described by Omland et al. (2006) in which older, ancestral haplotypes were shared between taxa whereas recently derived haplotypes were unique to a single taxon (a pattern they termed ''neotypy''). Conclusively rejecting either the hybridization hypothesis or the ancestral polymorphism hypothesis is not possible with current data, and may require analyses of nuclear DNA (Peters et al. 2007).

Population genetic studies often use Φ_{ST} to examine the level of genetic differentiation because this measure considers the relatedness

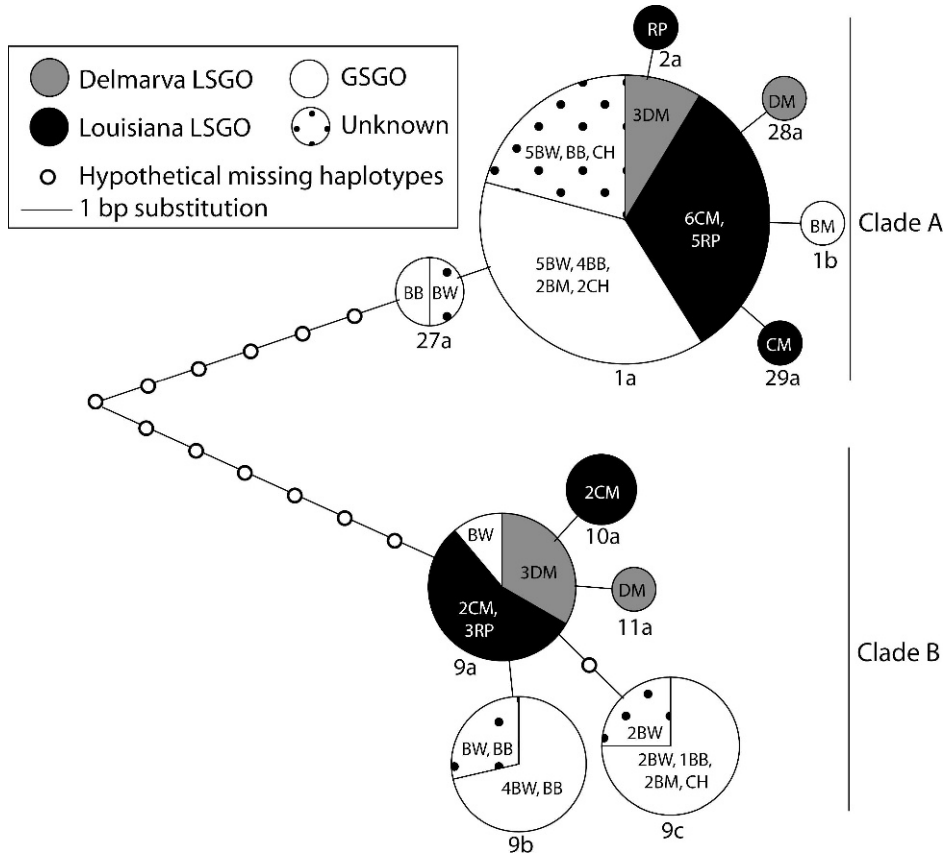

FIG. 3. Haplotype network illustrating phylogenetic relationships among mtDNA control region sequences. The area of the circle is proportional to the number of individuals having that haplotype. Sampling locations and sample sizes are given for each haplotype; DM = Delmarva, RP = rice prairie, CM = coastal marsh, BW = Blackwater, BB = Back Bay, CH = Chincoteague, BM = Bombay Hook. Each haplotype is assigned a number based on which 178 bp Quinn (1992) haplotype it matches; the lowercase letter after the number refers to variation in the additional 480 bp sequenced. Haplotypes 27–29 are unique to our study.

of haplotypes (Excoffier et al. 1992). In contrast, conventional F_{ST} only considers haplotype frequencies. We found that all pairwise comparisons resulted in negative Φ_{ST} (i.e., no population differentiation), but both F_{ST} and S_{NN} suggested the LSGO and GSGO populations are genetically differentiated (although only the S_{NN} values were significant). It is likely the deep genetic divergence between clades A and B contributed disproportionately to within population variation and lowered the power of tests using Φ_{ST} (Peters and Omland 2007). Benedict et al. (2003) found a similar pattern of two deeply divergent clades when examining genetic differentiation between eastern and western subspecies of Sage-grouse (*Centrocercus urophasianus urophasianus* and *C. u. phaios*, respectively) and suggested that weighting haplotypes in such a situation adds more noise than signal. Conventional F_{ST} and S_{NN} may be more powerful statistics for evaluating genetic differentiation when deeply divergent clades are shared between taxa.

Mitochondrial DNA suggests that sympatric LSGO and GSGO are genetically differentiated. Our results and those of Johnson (1996) suggest some level of connectivity between disjunct wintering populations of LSGO despite knowledge that Snow Geese primarily form pairs during winter. Delmarva's LSGO population seemingly does not constitute a unique population unit separate from Mid-Continental geese. However, larger sample sizes are needed to better estimate the magnitude of connectivity among wintering populations. Nuclear DNA is needed to obtain

overall estimates of population connectivity (mtDNA is maternally inherited and reflects only female dispersal), and to better evaluate the likelihood of interbreeding between LSGO and GSGO. Nuclear data also are needed to better understand why species and subspecies of the white-goose complex share deeply divergent mtDNA lineages. Further study of population genetics in the white-goose complex would provide an opportunity to better understand the importance of differing morphology and breeding versus non-breeding discontinuity on population differentiation and species divergence.

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