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Authors
Avise, John C
Alisauskas, Ray T
Nelson, William S
et al.

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MATRIARCHAL POPULATION GENETIC STRUCTURE IN AN AVIAN SPECIES WITH FEMALE NATAL PHILOPATRY

John C. Avise,[1] Ray T. Alisauskas,[2] William S. Nelson,[1] and C. Davison Ankney[3]
[1]*Department of Genetics, University of Georgia, Athens, GA 30602 USA*
[2]*Canadian Wildlife Service, 115 Perimeter Road, Saskatoon, Saskatchewan S7N 0X4 CANADA*
[3]*Department of Zoology, University of Western Ontario, London, Ontario N6A 5B7 CANADA*

Abstract.—We employ mitochondrial (mt) DNA markers to examine the matrilineal component of population genetic structure in the snow goose *Chen caerulescens*. From banding returns, it is known that females typically nest at their natal or prior nest site, whereas males pair with females on mixed wintering grounds and mediate considerable nuclear gene flow between geographically separate breeding colonies. Despite site philopatry documented for females, mtDNA markers show no clear distinctions between nesting populations across the species' range from Wrangel Island, USSR to Baffin Island in the eastern Canadian Arctic. Two major mtDNA clades (as well as rare haplotypes) are distributed widely and provide one of the few available examples of a phylogeographic pattern in which phylogenetic discontinuity in a gene tree exists without obvious geographic localization within a species' range. The major mtDNA clades may have differentiated in Pleistocene refugia, and colonized current nesting sites through recent range expansion via pulsed or continual low-level dispersal by females. The contrast between results of banding returns and mtDNA distributions in the snow goose raises general issues regarding population structure: direct contemporary observations on dispersal and gene flow can in some cases convey a misleading impression of phylogeographic population structure, because they fail to access the evolutionary component of population connectedness; conversely, geographic distributions of genetic markers can provide a misleading impression of contemporary dispersal and gene flow because they retain a record of evolutionary events and past demographic parameters that may differ from those of the present. An understanding of population structure requires integration of both evolutionary (genetic) and contemporary (direct observational) perspectives.

Key words.—Gene flow, matrilines, mitochondrial DNA, natal homing, phylogeography, population structure.

The degree of faithfulness to natal site or to social group is often sex-biased. For example, lion prides consist of matrilineally related females, and most inter-pride movement is by males (Schaller, 1972). Conversely, Florida scrub jays live in extended family groups in which accession of territories is patrilineal, and most dispersal is by females (Woolfenden and Fitzpatrick, 1984). In general, most mammalian species with asymmetric philopatry exhibit male-biased dispersal, whereas most such avian species exhibit female-biased dispersal (Greenwood, 1980; Greenwood and Harvey, 1982). One likely consequence of sex-biased dispersal and gene flow is that a species may exhibit qualitatively different patterns of geographic population structure at genes with biparental transmission (most nuclear loci) versus those at which trans-

mission occurs through only one sex [e.g., mitochondrial (mt) DNA, the mammalian Y chromosome of heterogametic males, and the avian W chromosome of heterogametic females (Cooke et al., 1975; Rabenold et al., 1991)].

Waterfowl (Anatidae) provide exceptions to the prevalent pattern of male biased philopatry in birds. In many species of migratory geese and ducks, pair formation occurs on the wintering grounds, where considerable mixing of birds from different nesting areas can take place (e.g., Cooke, 1987; Weller, 1965). Yet a mated pair commonly returns to the female's natal or prior nesting area, such that most flow of nuclear genes is thought to be male-mediated. According to Greenwood (1980; p. 1144), among all bird species "The lesser snow goose is the best documented example of male biased natal and breeding dispersal. . . ." For example, among 223 banded goslings of snow geese that returned to breed at their natal colony, only eight (3.6%) were males;

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[1] Please address correspondence and reprint requests to John C. Avise.

whereas among 55 banded goslings recovered from a breeding colony other than their natal site, only four (7.3%) were females (Cooke et al., 1975). This life history pattern suggests considerable intercolony gene flow mediated by males, an expectation consistent with results of both allozyme (Cooke et al., 1988) and nuclear RFLP studies (Quinn, 1988; see also Quinn and White, 1987). It also suggests that female-mediated gene flow may be quite limited.

Here we assess the matrilineal component of population structure within and among geographic samples of lesser and greater snow geese (*Chen caerulescens caerulescens* and *C. c. atlantica,* respectively) representing distinct nesting colonies, and their close relative the Ross' goose (*C. rossi*), through analyses of restriction site variation in mitochondrial DNA. Despite the evidence for philopatry by female snow geese, it is not a foregone conclusion that significant mtDNA differences will exist among colonies, for at least two reasons: (a) females occasionally do breed at non-natal locales (Geramita and Cooke, 1982; Hanson et al., 1972), and even a low level of intercolony exchange of breeding individuals may override the effects of genetic drift of neutral alleles under an equilibrium model of population structure (Slatkin, 1985, 1987); and (b) most of the current breeding range of the snow goose, which extends from Wrangel Island, USSR across the Canadian Arctic to Baffin Island, was no doubt uninhabitable during the last ice age, and therefore must have been colonized within the last several thousand years. Thus breeding colonies that today may be relatively isolated with respect to matrilineal exchange could nonetheless be closely related through recent evolutionary interconnections.

Because extant mtDNA genotypes retain a phylogenetic record of matrilineal relationship (Avise, 1989; Moritz et al., 1987; Wilson et al., 1985), issues of past as well as contemporary gene flow can be addressed. Many vertebrate species, including some birds (Avise and Ball, 1991), exhibit strong mtDNA phylogeographic differentiation across their ranges (Avise et al., 1987). If colonies of snow geese also prove to be strongly subdivided for mtDNA, the site philopatry of females would likely be an important factor contributing to the maintenance of this contemporary population genetic structure. Furthermore, colony-specific mtDNA markers would be of great utility in determining the natal origins, migration pathways, and wintering grounds of wild-caught individuals of either sex. On the other hand, an absence of significant mtDNA differentiation among snow geese colonies would indicate that contemporary observations on dispersal behavior can be inadequate or even misleading predictors of evolutionary components of population genetic structure of this (or other) species.

MATERIALS AND METHODS

A total of 160 geese was collected on nesting grounds, or on migration or wintering sites from which general nesting locale could in some cases be inferred from prior experience with band returns and colony-specific migration pathways (Fig. 1). Geese collected on nesting territory included: lesser snow goose from Queen Maud Gulf, Northwest Territories, Canada ($N = 50$) and from the Anderson River Delta, Northwest Territories ($N = 21$); and Ross' goose from Queen Maud Gulf, Northwest Territories ($N = 31$). Birds collected away from breeding areas included lesser snow geese from Skagit Co., Washington [from banding returns, these are thought with high certainty to nest on Wrangel Island, USSR ($N = 10$)], Southern Manitoba [assignable with high probability to eastern breeding locales in Hudson Bay or Baffin Island, Canada ($N = 23$)], and central California [that nest either at Wrangel Island, Anderson River Delta, or Queen Maud Gulf ($N = 12$)]; and greater snow geese from Cap Tourmente, Quebec [known to nest in region 6 in Fig. 1 ($N = 13$)]. No sampled geese were known to be close relatives (e.g., nestmates, or parent-offspring). To minimize the potential confounding factor of intercolony movement by males on mtDNA distributions, most individuals collected (81%) were females.

Fresh heart and liver were shipped to the lab on the MSB-Ca^{++} buffer of Lansman et al. (1981). Within seven days of collection, isolation of closed-circular mtDNA through CsCI-gradients was initiated. Purified mtDNA was then digested with restriction

FIG. 1. Major nesting areas for lesser snow geese (1, Wrangel Island, USSR; 2, Anderson River Delta, Northwest Territories, Canada; 3, Queen Maud Gulf, Northwest Territories, Canada; 4, Southampton Island/ Baffin Island, Canada; 5, Hudson Bay, Canada) and for greater snow geese (6, Bylot Island, Canada). Major migration pathways are also shown, as shaded corridors (from Bellrose, 1976). Heavy arrows indicate collection sites, two of which were nesting locales and four were from migration or wintering areas. Lesser snow geese collected in Skagit Co., Washington are known to nest at colony 1; those from Southern Manitoba, Canada most likely are from nesting colonies in areas 4 and 5; and those collected in central California probably derive from nesting areas 1, 2, and/or 3. Greater snow geese from Cap Tourmente, Quebec, Canada come from nesting area 6. Ross' geese nest almost exclusively at Queen Maud Gulf (location 3).

TABLE 1. Descriptions of the mtDNA clones observed in samples of the white geese complex. Letters (from left to right) designate multi-fragment gel profiles produced by digestion with *Ava*I, *Ava*II, *Bam*HI, *Bcl*I, *Bgl*I, *Bst*EII, *Cla*I, *Eco*RI, *Hinc*II, *Hind*III, *Msp*I, *Pst*I, *Pvu*II, *Sac*I, *Spe*I, *Sst*II, *Stu*I, and *Xba*I. Letters in boldface type indicate digestion profiles that differed from those in the most common haplotype, clone "a."

MtDNA clone	Genotypic description																		Numbers of geese	
																			Snow	Ross'
a	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	63	3
b	C	C	C	C	C	C	C	C	C	C	C	C	C	C	**D**	C	C	C	6	
c	C	C	C	C	C	C	C	C	C	C	C	C	C	C	**E**	C	C	C	4	
d	C	C	C	C	C	C	C	C	C	C	**B**	C	C	C	C	C	C	C	1	
e	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	**B**	C	1	
f	C	C	C	C	C	C	C	C	**D**	C	C	C	C	C	C	C	C	C	2	
g	C	**D**	C	**B**	C	C	**B**	C	C	C	**D**	**D**	C	C	**B**	C	**E**	C	8	
h	**D**	**D**	C	**B**	C	C	**B**	C	C	C	**D**	**D**	C	C	**B**	C	**E**	C	32	28
i	C	**D**	C	**B**	C	C	**B**	C	C	**B**	**D**	**D**	C	C	**B**	C	**E**	C	6	
j	**D**	**D**	C	**B**	C	C	**B**	C	C	**B**	**D**	**D**	C	C	**B**	C	**E**	C	5	
k	**D**	**D**	C	**B**	C	C	**B**	C	C	C	**E**	**D**	C	C	**B**	C	**E**	C	1	
																		Totals	129	31

enzymes according to manufacturers' recommendations. Resulting fragments were radioactively end-labeled with ^{35}S nucleotides and separated by molecular weight through 1.0–1.6% agarose gels, according to standard procedures (Lansman et al., 1981; Maniatis et al., 1982). Autoradiographs revealed mtDNA digestion profiles that constitute the "raw" data. Eighteen informative restriction endonucleases (those producing at least two cuts in the mtDNA molecule) were employed in this study (Table 1). An additional enzyme (*Bgl*II) produced only one cut in our assays, and is considered further only in the context of map construction. Maps for selected restriction sites were developed by double-digestion procedures.

For most enzymes, differences between mtDNA digestion profiles clearly were attributable to particular restriction site gains or losses (the only possible exceptions involved *Msp*I and *Stu*I, where it was necessary to posit two or three site changes to account for some profile interconversions). Data were thus coded into a presence-absence site matrix, and used to generate parsimony networks by the exhaustive search algorithm of PAUP (Phylogenetic Analysis Using Parsimony, version 3.0, provided by D. L. Swofford). Bootstrap confidence values on putative clades were determined from 200 replicates. The computer program MacClade was employed for additional visual inspection of alternative branching arrangements, and for generation of consistency index (C. I.) values.

The restriction site matrix was also used to estimate sequence divergence (*p*) values between mtDNA clones (Nei and Li, 1979), and these were clustered by the unweighted pair-group method with arithmetic means (UPGMA) (Sneath and Sokal, 1973). Genotypic ("nucleon") and nucleotide diversities were calculated following Nei and Tajima (1981) and Nei (1987; p. 256).

RESULTS AND DISCUSSION
Restriction Site Variation

A mean of 81 restriction sites per individual was scored, representing approximately 438 base-pairs of enzyme recognition sequence. Among the 160 assayed geese, a total of 11 different mtDNA genotypes was observed (Table 1). For the snow goose samples considered collectively, genotypic diversity (the probability that randomly drawn pairs of individuals differ detectably in mtDNA genotype) was $g = 0.69$, and nucleotide diversity (mean estimated sequence divergence between individuals) was $p_{mean} = 0.006$. These values are similar to those for several other avian species similarly assayed (Avise and Ball, 1991). Respective values in the sample of Ross' goose were considerably lower, $g = 0.18$ and $p_{mean} = 0.002$. Snow geese are relatively abundant ($\cong 2,000,000$ pairs) with a broad geographic breeding range across the Nearctic, whereas the Ross' goose is less common ($\cong 200,000$ pairs) with nearly all nesting at Queen Maud Gulf. Thus the greater composite mtDNA
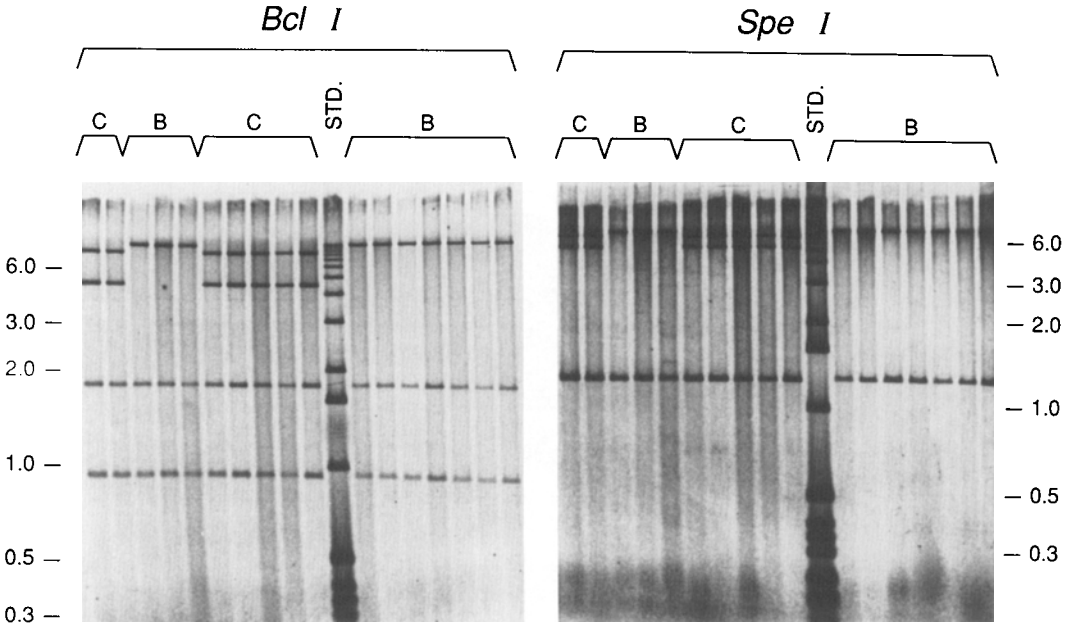
FIG. 2.   *Bcl*I and *Spe*I digests of 17 representative snow geese (arranged in the same order on the two gels). In each gel, the eleventh lane from the left is a 1-kilobase molecular weight standard with selected sizes (in kilobase pairs) indicated in the margins. Differences between the "B" and "C" digestion patterns for *Bcl*I and *Spe*I each are due to a single restriction site gain/loss; the variable sites map to distinct positions in the mtDNA genome (Fig. 3).

variability in snow geese might be expected. However, caution is required in interpreting these variability estimates, because as shown below the primary determinant of level of mtDNA variation in any assayed goose population was the particular frequency distribution (and equitability) of haplotypes representing two highly distinct mtDNA clonal lineages. Some snow goose breeding populations exhibited both mtDNA lineages in high frequency, so variability estimates were essentially as great as those for the species continent-wide (e.g., genotypic and nucleotide diversities in Queen Maud snow geese were $g = 0.64$ and $p_{mean} = 0.006$, respectively). From this perspective, the lower variability in the Ross' goose can be attributed in part to the preponderance there (90% frequency) of one of the two major mtDNA clades.

Among all assayed geese, two mtDNA haplotypes ("a" and "h") were common, collectively accounting for 79% of all specimens, whereas each of the remaining genotypes was observed in only 1–8 individuals (Table 1). Haplotypes "a" and "h"

differed in digestion profiles for 8 of the 18 informative restriction enzymes (examples in Fig. 2), and estimated sequence divergence was $p = 0.011$. All rare genotypes were genetically close to one or the other of these two common forms, typically differing at only one or two assayed restriction sites.

To confirm that the multi-enzyme distinction betwen genotypes "a" and 'h" was not due to a single molecular event such as a localized genomic re-arrangement [see Desjardins and Morais (1990) for documentation of a change in mtDNA gene order in birds relative to mammals] or to a duplication/deletion that might simultaneously have altered several mtDNA digestion profiles, particular restriction sites were mapped using double digestion procedures (Fig. 3). Included among the enzymes distinguishing "a" and "h" were *Pst*I, *Spe*I, *Cla*I, and *Bcl*I, each of which exhibited a site in "a" that was missing from "h" (*Ava*II, *Msp*I, and *Stu*I show site gains in the same direction of comparison). These mapped variable sites were scattered widely about the mtDNA genome. Thus the diges-
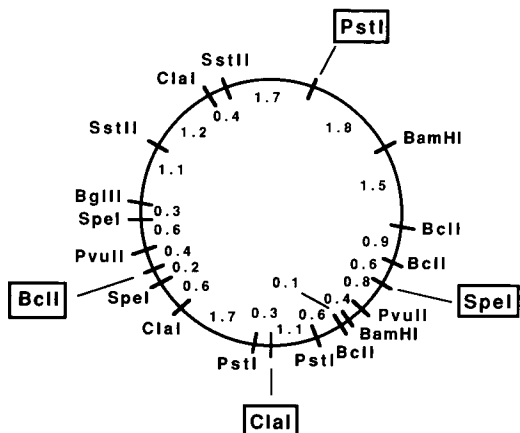
FIG. 3. Map of restriction sites for selected endonucleases in the snow goose-Ross' goose complex. Approximate distances between sites are given in kilobases. The presence versus absence of the four sites enclosed within boxes contributed to the distinction between the two major mtDNA clades.
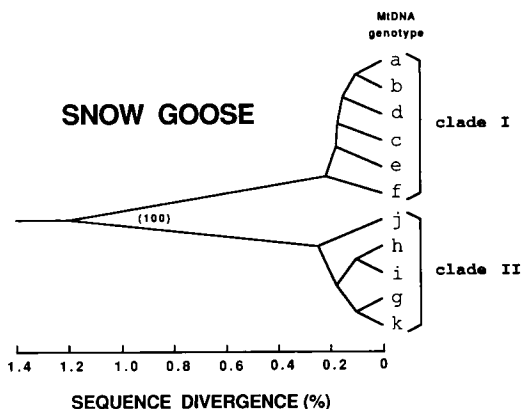

FIG. 4. Estimated phylogeny for the 11 mtDNA genotypes observed in snow geese, presented here as a UPGMA phenogram. In parsimony analyses, this and several alternative minimum-length networks (17 steps) were found, but all involved minor rearrangements within clades I and II. The distinction between these two clades was supported at the 100% level by bootstrapping, whereas no other lineage was identified in more than 65% of the bootstrap replicates. The consistency index in the associated parsimony network was 0.94.

tion profile differences distinguishing "a" and "h" reflect numerous independently arisen mutations.

A grouping of mtDNA haplotypes into two distinct lineages (henceforth designated clades I and II) was evident in both the parsimony and UPGMA analyses (Fig. 4). Thus in the UPGMA phenogram, the *largest* clustering distance within either assemblage was $p \cong 0.002$, whereas the two distinct groups joined at a clustering level six times higher, $p \cong 0.012$; and in the parsimony networks, bootstrapping supported the separation of two major clades at the 100% level, whereas no other putative clade was identified in more than 65% of bootstrap replicates. Furthermore, rearrangements of branches within clades I or II (relative to Fig. 4) sometimes resulted in equally parsimonious networks. For all of these reasons, most attention will henceforth be focused on the distributions of the two highly differentiated and statistically supportable mtDNA clades.

Shields and Wilson (1987) previously assayed mtDNA from one specimen each of snow and Ross' goose and three other species of *Anser* (=*Chen*) and a related genus *Branta*. In their phylogeny reconstruction, snow and Ross' geese were one another's closest relatives, differing by an estimated mtDNA sequence divergence of $p = 0.008$,

whereas the nearest assayed outgroup (the white-fronted goose, *Anser albifrons*) differed from either by $p > 0.025$. Based on these authors' descriptions of fragment patterns, several of which involved the same enzymes employed in the current study, their specimen of snow goose belonged to mtDNA clade I whereas their Ross' goose sample belonged to clade II. Thus the differences they reported between Ross' and snow geese currently can be found as polymorphisms within both species.

Plumage Colors, Taxonomic Units, and the Major mtDNA Clades

Representatives of both mtDNA clades were ubiquitously distributed in the white goose complex (Tables 2 and 3), being present in samples from: (1) all nesting colonies, migration, and wintering locales; (2) both taxonomic subspecies of the snow goose (the greater and lesser races); (3) both sexes; (4) both color morphs (blue and white) of the lesser snow goose (see beyond); and (5) Ross' goose [albeit with a low frequency (10%) for clade I].

With available sample sizes, there is highly significant heterogeneity in frequency of

TABLE 2. Observed numbers of individuals belonging to mtDNA clades I and II in various collections of snow and Ross' geese. G-tests for heterogeneity are described in Sokal and Rohlf (1969).

Collection	mtDNA clade I	mtDNA clade II	(Freq. of clade I)
Nesting locale known			
Lesser snow goose			
(1) Wrangel Island	4	6	(0.40)
(2) Anderson River Delta	15	6	(0.71)
(3) Queen Maud Gulf	32	18	(0.64)
Greater snow goose			
(4) Cap Tourmente	7	6	(0.54)
Ross' goose			
(5) Queen Maud Gulf	3	28	(0.10)
Nesting locale uncertain			
Lesser snow goose			
(6) Southern Manitoba migrants	12	11	(0.52)
(7) Central California winterers	7	5	(0.58)
G-tests for heterogeneity among collections:			
All collections [(1)–(7)]	$G_H = 32.1$;	$df = 6$;	$P < 0.005$
Snow geese only [(1)–(4), (6), (7)]	$G_H = 3.9$;	$df = 5$;	NS
Snow goose nesting locales [(1)–(4)]	$G_H = 3.2$;	$df = 3$;	NS
Snow goose nesting locale females	$G_H = 2.0$;	$df = 3$;	NS

the two major mtDNA clades across all collections (Table 2). However, removal of the frequency outlier (Ross' goose) eliminates the statistical significance, such that no heterogeneity can be demonstrated among the six collections of snow geese. This lack of heterogeneity is not attributable to the inclusion of wintering and migratory populations (which may involve mixtures of birds from separate nesting sites) because the G-statistic among nesting locales alone remains non-significant with our sample sizes

TABLE 3. G-tests for independence (with Yate's correction for small sample size, Sokal and Rohlf, 1969) between mtDNA clade and color morph in collections of lesser snow geese where both plumage phases were present in high frequency.[1]

Collection site Plumage morph	mtDNA clade I	mtDNA clade II	Test statistic
South Manitoba migrants			
Blue color phase	5	3	
White color phase	7	8	$G = 0.06$; NS
Queen Maud Gulf nesters			
Blue color phase	14	5	
White color phase	18	13	$G = 0.68$; NS

[1] For these pooled collections, tests for association between mtDNA clade and plumage color were also non-significant: $G = 1.24$.

(Table 2). Nor is the lack of heterogeneity among nesting locales due to the inclusion of males, because their removal does not alter the outcome of the statistical test (Table 2).

Lesser snow geese exhibit two distinctive plumage color phases, blue and white. From pedigree studies, the polymorphism appears attributable to a single major gene with an allele for blue incompletely dominant over a recessive allele for white (Cooke, 1987). Birds exhibit positive assortative mating with respect to these morphs, with mate choice influenced via a developmental mechanism whereby goslings imprint and later preferentially mate with the color phase of their parents and siblings (Cooch and Beardmore, 1959; Cooke and Cooch, 1968; Cooke et al., 1972; Cooke and McNally, 1975; Cooke et al., 1976). However, imprinting is incomplete, and perhaps 10–15% of individuals "err" when selecting a mate (Cooke, 1987). Cooke et al. (1988) review historical and other evidence that the two color phases were formerly allopatric (blue predominating in eastern populations), that range shifts over the last 70 years have resulted from changes in winter feeding ranges, and that the current merger is taking place without evidence of reduced hybrid fitness.

Has the divergence between mtDNA clades I and II resulted from the same allopatric population separation proposed to be involved with the evoluton of plumage color differences? If so, genetic associations might yet be retained between the nuclear alleles for plumage coloration and mtDNA genotypes. However, with our samples we have no evidence for such associations, either between or within populations. Thus an east to west decline in frequency of the blue color morph across breeding populations of the lesser snow goose (Cooke, 1987) is not paralleled by a similar frequency cline for the mtDNA clades (Table2). Within locales where both color phases co-occur in high frequency and thereby permit tests for correlation (such as at Queen Maud Gulf and among the southern Manitoba migrants), no mtDNA/plumage color associations are evident in our samples (Table 3). Finally, blue plumage is undocumented in the greater snow goose and is extremely rare in the Ross' goose (McLandress and McLandress, 1979), yet both taxa contained representatives of both mtDNA clades. Overall, we have no evidence that the distinction between mtDNA clades was generated by the same evolutionary vicariant events hypothesized to have influenced the plumage color polymorphism.

The presence of the particular genotypes "a" and "h" in the Ross' and snow goose suggests that mtDNA sequences were distributed to these species at a recent time postdating the split in the mtDNA gene tree. Whether this distribution reflects a recent speciation involving retention by both species of the ancestral polymorphism, and/or whether secondary hybridization and introgression are responsible, remains uncertain. However, a secondary hybridization scenario appears favored on two grounds: (a) Ross' and snow geese are known to hybridize in captivity (Sibley, 1938) and are thought also to do so in nature, as judged by the occasional appearance of morphologically intermediate forms (Palmer, 1976; Trauger et al., 1971; Alisauskas, unpubl. data); and (b) the low frequency of mtDNA clade I in the Ross' goose makes it unlikely to have been long-retained as part of an ancestral polymorphism. Available evidence from the nuclear genome is consistent with either recent speciation or secondary introgression scenarios: Ross' and Snow Geese were essentially indistinguishable in allelic composition [Nei's (1972) $D \cong 0.002$] at 18 allozyme loci assayed (Patton and Avise, 1985).

The Bimodal Distribution of mtDNA Distances

The salient finding of this study is the ubiquitous distribution of two distinct mtDNA clades throughout populations of the snow (and Ross') goose complex. This phylogeographic pattern, in which a deep phylogenetic discontinuity in the mtDNA gene tree exists without clade localization (category II in the classification scheme of Avise et al., 1987), is most unusual, having been reported previously in only a few species (Avise et al., 1984a, 1990; Wayne et al., 1990). Normally, mtDNA clades distinguished by large sequence gaps are localized, and geographically oriented in ways suggestive of origins through long-term zoogeographic impediments to gene flow (Avise, 1992; Avise et al., 1987).

Figure 5 (bottom) plots the frequency histogram of estimated mtDNA genetic distances among all 12,720 pairwise comparisons of the 160 assayed geese. As expected, the distribution is strongly bimodal, and departs dramatically from the unimodal geometric distributions predicted at equilibrium under neutrality theory for a single population or series of populations with high gene flow (Avise et al., 1988). In most other species, such multimodal mtDNA distance distributions are attributable to within- versus between-region comparisons associated with sharp biogeographic discontinuities in mtDNA phylogeny. For example, both the sharp-tailed sparrow (*Ammodramus caudacutus*) and the seaside sparrow (*A. maritimus*) exhibit bimodal mtDNA distance distributions remarkably similar to that for the snow goose (Fig. 5), but in these species, results stem from the occurrence of two divergent mtDNA clades confined to separate regions within the respective species' ranges (Avise and Nelson, 1989; Rising and Avise, unpubl. data).

Avise et al. (1987) suggest that examples of phylogeographic category II are most likely to result from secondary admixture
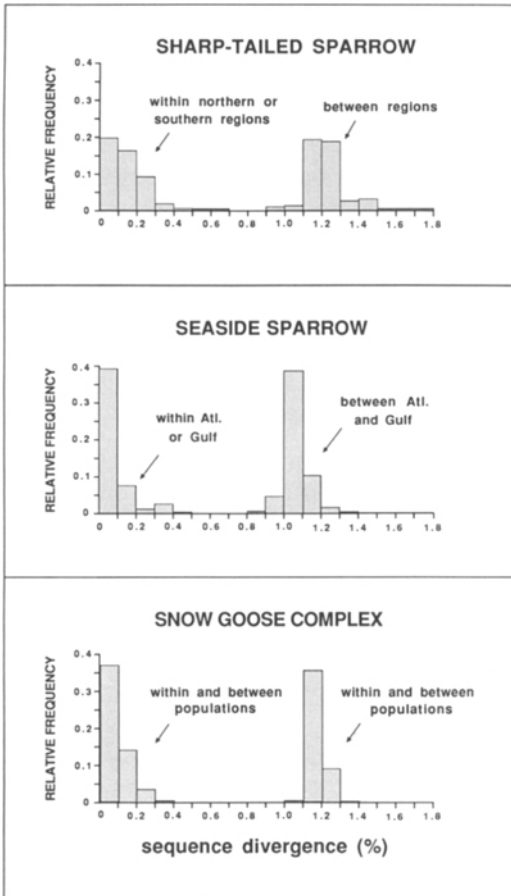
FIG. 5. Frequency histograms of mtDNA genetic distance estimates within sharp-tailed sparrows (Rising and Avise, unpubl. data), seaside sparrow (Avise and Nelson, 1989), and the snow-Ross' goose complex. Within each of the sparrow species, the bimodal distributions are attributable to pronounced phylogeographic partitions. However, in the snow geese the two distinct clades underlying the bimodal distribution are not geographically localized, but rather occur in all surveyed populations. A total of 12,720 pairwise comparisons of individuals is included in the histogram for geese.

between allopatrically evolved populations from which deep splits in the gene tree derive. In the current context, this implies the existence of two Pleistocene population isolates from which snow goose females subsequently dispersed and mixed widely. The net nucleotide divergence between the major snow goose mtDNA clades (after correction for within-clade variation) is $p \cong 0.011$. Shields and Wilson (1987) present evidence that a conventional vertebrate mtDNA "clock" calibration of 0.01 substi-

tutions/bp/lineage/Myr (Brown et al., 1979) applies to geese as well. Using this calibration, the putative population separation in the snow goose dates to about 550,000 years before present.

Alternatively, it is conceivable that distinct mtDNA lineages were by chance retained within snow geese in the absence of historical population separation. Under neutrality theory, retention of long-separated mtDNA lineages is most likely when the evolutionary effective population size of females ($N_{f(e)}$) is large (Avise et al., 1984b). However, this scenario appears unlikely for the following reasons. First, as already mentioned, the bimodal distribution of mtDNA distances (Fig. 5) is dramatically different from mean equilibrium expectations for gene genealogies within a non-subdivided population [but see Ball et al. (1990) for examples of idiosyncrasy in gene tree structures within random-mating organismal pedigrees]. Second, if $N_{f(e)}$ was very large, considerably greater mtDNA variation within either mtDNA clade might be expected. However, nucleotide diversities within clades I and II were relatively low: $p_{mean} = 0.0003$ and 0.0009, respectively. Using the approach of Avise et al. (1988), and assuming a generation length in snow geese of three years, these nucleotide diversities translate into estimates of $N_{f(e)} = 5,000$ and $15,000$ for snow goose populations constituting the two respective clades. (These values are much smaller than current-day census sizes of particular snow goose colonies, which can contain a few hundred thousand pairs.)

A final possibility is that representatives of the two mtDNA clades are not neutral, but rather have been buffered against lineage extinction via some form of balancing selection. In theory, conditions for the maintenance of mtDNA polymorphism through selection alone are especially restrictive due to uniparental, haploid transmission (Clark and Lyckegaard, 1988; Gregorius and Ross, 1984). However, even if balancing selection is currently at work, additional factors involving evolutionary population separation (or a large $N_{f(e)}$) are also required to account for accumulation of the numerous mutational differences that distinguish clades I and II.

Female-Mediated Gene Flow

Whatever the origin of the two mtDNA clades, their shared presence across snow goose locales strongly suggests considerable population connectedness and gene flow involving females. It is highly ironic that a lack of geographic localization for distinct mtDNA clades appears in the one avian species prominently cited as the best documented example of female-biased philopatry to nest site (Greenwood, 1980). Indeed, with respect to the major clades, we cannot demonstrate with current sample sizes that the collections represent other than random draws from a single matriarchal gene pool. [Therefore, beyond the conclusion of considerable genetic connection, attempts to further refine or quantify estimates of gene flow (Nm) are unwarranted with current data.]

Several authors have discussed the philosophical distinctions between contemporary gene flow and the recent evolutionary connectedness between populations (Larson et al., 1984; Slatkin, 1987; Avise, 1989). In the current context, several types of past and present population contact likely contribute to the observed similarity in mtDNA composition between snow goose nesting locales. First, the current nesting range of the snow goose was largely uninhabitable during Pleistocene glacial episodes, so most present-day nest sites must have been colonized within about the past 5,000 years, perhaps by females from two or more postulated refugia. Second, inter-colony mixing may occur by massive but episodic pulses of gene flow during periods of colony perturbation. For example, a recent mass exodus of both sexes is suspected for colonies along the west coast of Hudson Bay, where overpopulation and food depletion have prompted a permanent switch of nesting colonies by both males and females (Dzubin, 1979; MacInnes and Kerbes, 1987; Kerbes et al., 1983, 1990). Speculation is that the tremendous recent growth of the Queen Maud colony is due in part to the immigration of birds from the diminishing Hudson Bay colonies. Finally, even under "normal" population demographic conditions, a steady trickle of intercoloy female dispersal undoubtedly takes place. Indisputable evidence from band returns shows

TABLE 4. Geographic distributions of rare mtDNA haplotypes in the snow goose.

mtDNA haplotype	Number of individuals	Collection locale (number of individuals)
b	6	Anderson River Delta (3); Queen Maud Gulf (3).
c	4	Anderson River Delta (2); Skagit Co., WA. (1); Queen Maud Gulf (1).
f	2	Queen Maud Gulf (1); Cap Tourmente (1).
g	8	Anderson River Delta (4); Queen Maud Gulf (2); central CA. winterers (2).
i	6	Anderson River Delta (2); south Manitoba migrants (3); central CA. winterers (1).
j	5	Queen Maud Gulf (1); Skagit Co., WA. (4).

that small numbers of females do nest at non-natal sites and in some cases even change nesting locales in different years. For example, one banded female nested in successive years at locales separated by more than 1200 km, and several such instances of shorter movements between nesting locales are documented (Cooke et al., 1975).

No matter how the gene flow has occurred, mtDNA data indicate that snow goose populations have had extensive and recent matrilineal contact. Not only are the two major mtDNA clades shared between locations, but also rare mtDNA genotypes within clades commonly appear at multiple nesting sites (Table 4). For example, among four individuals exhibiting the rare mtDNA genotype "c" (distinguished by gain of a SpeI site relative to the common "a" haplotype), two derive from the nesting locale at Anderson River Delta, and one each from Wrangel Island and Queen Maud Gulf (Table 4). Indeed, no haplotype observed in more than one individual was confined to a single nesting locale. Thus inter-colony exchange appears to have dispersed even those microevolutionary twigs in the mtDNA tree that probably arose relatively recently.

CONCLUSIONS

The genetic and behavioral results for snow geese prompt the following observations on interpretations of population struc-

ture in any species. First, direct behavioral or marking studies on contemporary populations can in some cases provide a misleading picture of the geographic distributions of genetic traits, because they fail to access the important evolutionary aspects of population connectedness. Conversely, geographic distributions of genetic markers can in some cases provide a misleading picture of contemporary dispersal and gene flow, because they retain a record of evolutionary events and demographic parameters that may differ from those of the present. Thus both evolutionary (genetic) and contemporary (behavioral) perspectives are required for a full appreciation of the geographic population structure of a species.

Second, the lack of dramatic mtDNA differentiation in an avian species with well-documented female site philopatry makes even more impressive the mtDNA phylogeographic discontinuities characterizing regional populations of other species for which data on female movements are largely unavailable (such as the seaside and sharp-tailed sparrows, Fig. 5). Apparently, such species have experienced even less female-mediated interpopulational exchange than has the "site philopatric" snow goose.

Finally, the lack of sharp mtDNA differentiation among populations of the snow goose contrasts with the situation reported in another migratory species thought to exhibit female nesting site philopatry, the green sea turtle (*Chelonia mydas*). Many nesting rookeries of the green turtle are distinguishable by fixed or nearly fixed mtDNA haplotype differences (Meylan et al., 1990; Bowen et al., 1992), a finding consistent with the hypothesis of strong natal homing by females despite extensive movements by juveniles and by adults during the non-nesting season. Given the contrast of mtDNA phylogeographic patterns between species thought to have similar life histories with respect to female dispersal, it is apparent that population genetic structures of various species will require evaluation on a case-by-case basis.

LITERATURE CITED

AVISE, J. C. 1989. Gene trees and organismal histories: A phylogenetic approach to population biology. Evolution 43:1192–1208.

———. 1992. Molecular population structure and the biogeographic history of a regional fauna: A case history with lessons for conservation biology. Oikos 63:62–76.

AVISE, J. C., C. D. ANKNEY, AND W. S. NELSON. 1990. Mitochondrial gene trees and the evolutionary relationship of Mallard and Black Ducks. Evolution 44:1109–1119.

AVISE, J. C., J. ARNOLD, R M. BALL, E. BERMINGHAM, T. LAMB, J. E. NEIGEL, C. A. REEB, AND N. C. SAUNDERS. 1987. Intraspecific phylogeography: The mitochondrial DNA bridge between population genetics and systematics. Annu. Rev. Ecol. Syst. 18:489–522.

AVISE, J. C., AND R. M. BALL, JR. 1991. Mitochondrial DNA and avian microevolution. Acta XX Congressus Internationalis Ornithologici Vol. 1:514–524.

AVISE, J. C., R. M. BALL, AND J. ARNOLD. 1988. Current versus historical population sizes in vertebrate species with high gene flow: A comparison based on mitochondrial DNA lineages and inbreeding theory for neutral mutations. Mol. Biol. Evol. 5:331–344.

AVISE, J. C., E. BERMINGHAM, L. G. KESLER, AND N. C. SAUNDERS. 1984a. Characterization of mitochondrial DNA variability in a hybrid swarm between subspecies of bluegill sunfish (*Lepomis macrochirus*). Evolution 38:931–941.

AVISE, J. C., J. E. NEIGEL, AND J. ARNOLD. 1984b. Demographic influences on mitochondrial DNA lineage survivorship in animal populations. J. Mol. Evol. 20:99–105.

AVISE, J. C., AND W. S. NELSON. 1989. Molecular genetic relationships of the extinct dusky seaside sparrow. Science 243:646–648.

BALL, R. M., JR., J. E. NEIGEL, AND J. C. AVISE. 1990. Gene genealogies within the organismal pedigrees of random mating populations. Evolution 44:360–370.

BELLROSE, F. C. 1976. Ducks, Geese and Swans of North America. Stackpole Books, Harrison, PA USA.

BOWEN, B. W., A. B. MEYLAN, J. P. ROSS, C. J. LIMPUS, G. H. BALAZS, AND J. C. AVISE. 1992. Global population structure and natural history of the green turtle (*Chelonia mydas*) in terms of matriarchal phylogeny. Evolution 46:865–881.

BROWN, W. M., M. GEORGE, JR., AND A. C. WILSON. 1979. Rapid evolution of animal mitochondrial DNA. Proc. Natl. Acad. Sci. 76:1967–1971.

CLARK, A. G., AND E. M. S. LYCKEGAARD. 1988. Natural selection with nuclear and cytoplasmic transmission. III. Joint analyses of segregation and mtDNA in *Drosophila melanogaster*. Genetics 118:471–481.

COOCH, F. G., AND J. A. BEARDMORE. 1959. Assortative mating and reciprocal difference in the blue-snow complex. Nature 183:1833–1834.

COOKE, F. 1987. Lesser snow goose: A long-term population study, pp. 407–432. In F. Cooke and P. A. Buckley (eds.), Avian Genetics. Academic Press, N.Y., USA.

COOKE, F., AND F. G. COOCH. 1968. The genetics of polymorphism in the goose Anser caerulescens. Evolution 22:289–300.

COOKE, F., G. H. FINNEY, AND R. F. ROCKWELL. 1976. Assortative mating in lesser snow geese (Anser caerulescens). Behav. Genet. 6:127–140.

COOKE, F., C. D. MACINNES, AND J. P. PREVETT. 1975. Gene flow between breeding populations of lesser snow geese. Auk 92:493–510.

COOKE, F., AND C. M. McNALLY. 1975. Mate selection and colour preferences in lesser snow geese. Behaviour 53:151–170.

COOKE, F., P. J. MIRSKY, AND M. B. SINGER. 1972. Colour preferences in the Lesser Snow Goose and their possible role in mate selection. Can. J. Zool. 50:529–536.

COOKE, F., D. T. PARKIN, AND R. F. ROCKWELL. 1988. Evidence of former allopatry of the two color phases of lesser snow geese (Chen caerulescens caerulescens). Auk 105:467–479.

DESJARDINS, P., AND R. MORAIS. 1990. Sequence and gene organization of the chicken mitochondrial genome. J. Mol. Biol. 212:599–634.

DZUBIN, A. 1979. Recent increases of Blue Geese in western North America, pp. 141–175. In R. L. Jarvis and J. C. Bartonek (eds.), Management and Biology of Pacific Flyway Geese. Oregon State Press, Corvallis OR USA.

GERAMITA, J. M., AND F. COOKE. 1982. Evidence that fidelity to natal breeding colony is not absolute in female snow geese. Can. J. Zool. 60:2051–2056.

GREENWOOD, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Anim. Behav. 28:1140–1162.

GREENWOOD, P. J., AND P. H. HARVEY. 1982. The natal and breeding dispersal of birds. Annu. Rev. Ecol. Syst. 13:1–21.

GREGORIUS, H.-R., AND M. D. ROSS. 1984. Selection with gene-cytoplasm interactions. 1. Maintenance of cytoplasm polymorphisms. Genetics 197:165–178.

HANSON, H. C., H. G. LUMSDEN, J. J. LYNCH, AND H. W. NORTON. 1972. Population characteristics of three mainland colonies of the Blue and Lesser Snow Geese nesting in the southern Hudson Bay region. Res. Rept. (Wildl.) 93, Ontario Min. Nat. Resources.

KERBES, R. H., P. M. KOTANEN, AND R. L. JEFFERIES. 1990. Destruction of wetland habitats by lesser snow geese: A keystone species on the west coast of Hudson Bay. J. Appl. Ecol. 27:242–258.

KERBES, R. H., M. R. McLANDRESS, G. E. J. SMITH, G. W. BEYERSBERGEN, AND B. GODWIN. 1983. Ross' goose and lesser snow goose colonies in the central Canadian arctic. Can. J. Zool. 61:168–173.

LANSMAN, R. A., R. O. SHADE, J. F. SHAPIRA, AND J. C. AVISE. 1981. The use of restriction endonucleases to measure mitochondrial DNA sequence relatedness in natural populations III. Techniques

and potential applications. J. Mol. Evol. 17:214–226.

LARSON, A., D. B. WAKE, AND K. P. YANEV. 1984. Measuring gene flow among populations having high levels of genetic fragmentation. Genetics 106:293–308.

MACINNES, C. D., AND R. H. KERBES. 1987. Growth of the Snow Goose, Chen caerulescens, colony at McConnell River, Northwest Territories: 1940–1980. Can. Field Nat. 101:33–39.

MANIATIS, T., E. F. FRITSCH, AND J. SAMBROOK. 1982. Molecular Cloning. Cold Spring Harbor Lab., NY USA.

McLANDRESS, M. R., AND I. McLANDRESS. 1979. Blue-phase Ross' geese and other blue-phase geese in western North America. The Auk 96:544–550.

MEYLAN, A. B., B. W. BOWEN, AND J. C. AVISE. 1990. A genetic test of "natal homing" versus "social facilitation" in green turtle migration. Science 248:724–727.

MORITZ, C., T. E. DOWLING, AND W. M. BROWN. 1987. Evolution of animal mitochondrial DNA: Relevance for population biology and systematics. Annu. Rev. Ecol. Syst. 18:269–292.

NEI, M. 1972. Genetic distance between populations. Am. Nat. 106:283–292.

———. 1987. Molecular Evolutionary Genetics. Columbia Univ. Press, N.Y., USA.

NEI, M., AND W.-H. LI. 1979. Mathematical model for studying genetic variation in terms of restriction endonucleases. Proc. Natl. Acad. Sci. 76:5269–5273.

NEI, M., AND F. TAJIMA. 1981. DNA polymorphism detectable by restriction endonucleases. Genetics 97:145–163.

PALMER, R. S. (Ed.). 1976. Handbook of North American Birds (Vol. 2). Yale Univ. Press, New Haven, CT USA.

PATTON, J. C., AND J. C. AVISE. 1985. Evolutionary genetics of birds IV. Rates of protein divergence in waterfowl (Anatidae). Genetica 68:129–143.

QUINN, T. W. 1988. DNA sequence variation in the Lesser Snow Goose, Anser caerulescens caerulescens. Ph.D. Diss. Queen's University, Kingston, Ontario, Canada.

QUINN, T. W., AND B. N. WHITE. 1987. Identification of restriction-fragment-length polymorphisms in genomic DNA of the lesser snow goose (Anser caerulescens caerulescens). Mol. Biol. Evol. 4:126–143.

RABENOLD, P. P., W. H. PIPER, M. D. DECKER, AND D. J. MINCHELLA. 1991. Polymorphic minisatellite amplified on avian W chromosome. Genome 34:489–493.

SCHALLER, G. B. 1972. The Serengeti Lion. University of Chicago Press, Chicago, IL USA.

SHIELDS, G. F., AND A. C. WILSON. 1987. Calibration of mitochondrial DNA evolution in geese. J. Mol. Evol. 24:212–217.

SIBLEY, C. L. 1938. Hybrids of and with North American Anatidae. Proc. 9th Intern. Ornithol. Congr. (1938):327–335.

SLATKIN, M. 1985. Gene flow in natural populations. Annu. Rev. Ecol. Syst. 16:393–430.

———. 1987. Gene flow and the geographic structure of natural populations. Science 236:787–792.

SNEATH, P. H. A., AND R. R. SOKAL. 1973. Numerical

Taxonomy. W. H. Freeman, San Francisco, CA USA.

SOKAL, R. R., AND F. J. ROHLF. 1969. Biometry. W. H. Freeman and Co., San Francisco, CA USA.

TRAUGER, D. L., A. DZUBIN, AND J. P. RYDER. 1971. White geese intermediate between Ross' Geese and Lesser Snow Geese. The Auk 88:856–875.

WAYNE, R. K., A. MEYER, N. LEHMAN, B. VAN VAL-KENBURGH, P. W. KAT, T. K. FULLER, D. GIRMAN, AND S. J. O'BRIEN. 1990. Large sequence divergence among mitochondrial DNA genotypes within populations of eastern African black-backed jackals. Proc. Natl. Acad. Sci. 87:1772–1776.

WELLER, M. W. 1965. Chronology of pair formation in some Nearctic *Aythya* (Anatidae). Auk 82:227–235.

WILSON, A. C., R. L. CANN, S. M. CARR, M. GEORGE, JR., U. B. GYLLENSTEN, K. M. HELM-BYCHOWSKI, R. G. HIGUCHI, S. R. PALUMBI, E. M. PRAGER, R. D. SAGE, AND M. STONEKING. 1985. Mitochondrial DNA and two perspectives on evolutionary genetics. Biol. J. Linn. Soc. 26:375–400.

WOOLFENDEN, G. E., AND J. W. FITZPATRICK. 1984. The Florida Scrub Jay. Princeton University Press, Princeton, NJ USA.

Corresponding Editor: R. Honeycutt