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Molecular status of the dusky Canada goose (*Branta canadensis occidentalis*): A genetic assessment of a translocation effort

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Abstract

Until recently, the dusky Canada goose (*Branta canadensis occidentalis*) was managed as one breeding population from the Copper River Delta (CRD), Alaska. Population numbers on the CRD have declined precipitously over the last three decades, due in part to changes in habitat. In 1981, a pair of Canada geese, presumably *B.c. occidentalis*, was reported nesting on Middleton Island (MID), in the Gulf of Alaska. Numbers of Canada geese on the island increased in the decade subsequent to a translocation of geese from CRD to MID, but it is unclear whether the increase is attributable to the translocation effort. We used genetic data derived from three classes of genetic markers to clarify relationships of Canada geese breeding in south-coastal Alaska. Geese were sampled from 5 populations: CRD, MID, Anchorage (ANC), Admiralty Island (ADM) in southeastern Alaska, and Green Island (GRN) in Prince William Sound (PWS). Mitochondrial DNA analyses demonstrate Canada geese from MID are nearly monomorphic for a unique haplotype fixed on GRN but not found in CRD or any other breeding population. Furthermore, nuclear markers consistently cluster MID with GRN to the exclusion of CRD. We suggest the current population on MID is not derived from birds translocated from CRD, but rather that MID was most likely colonised by birds inhabiting other island habitats within the PWS. Furthermore, since geese from the CRD share mtDNA haplotypes with geese from other breeding locales, they apparently share recent common ancestry and/or gene flow with populations representing other subspecies. Our genetic data raise questions about the validity of current management units of Canada geese.

Introduction

Many conservation and management agencies promote translocation of individuals within their species' range. Translocation is most often used to bolster local population sizes, sometimes intending to increase hunting or fishing opportunities, food supply and economic gain, but also to reestablish or preserve a species or type locality, increase local heterozygosity, or introduce "desirable" genetic traits into a region (Griffith et al. 1989; Leberg 1993; Wolf et al. 1996). Thus, there is an implicit assumption that recipient populations will derive benefit from an artificial boost in population size. However, despite beneficial consequences that may arise from augmentations, undesirable consequences may also arise, particularly if the systematic relationships of the donor and recipient populations are not well understood. Undesirable consequences include disruption of coadapted gene complexes (Templeton et al. 1976; Waser and Price 1989; Parker 1992), disease or spread of parasites (Johnson and Jensen 1986), increased competition in fragmented or altered habitats (NRC 1995), and irretrievable loss of rich historic genetical populations and erosion of genetic diversity within a species (Avise and Hamrick 1996; Westemeier et al. 1998). Thus, the NRC (1995) recommended that augmentation of wild populations be performed only when no alternative methods will ensure short-term population viability, or when there is strong evidence of historical gene flow.

When translocation is intended to augment local population sizes, the genetic consequences are difficult to assess (Scott and Carpenter 1987; Scott et al. 1994). Because large financial resources are usually required for translocations, often at the expense of alternative management strategies, it is desirable to have multiple indicators (or predictors) of population responses subsequent to translocation. Monitoring the genetic characteristics of the translocated populations would provide valuable sources of inference. This is particularly true when the translocations involve a threatened or endangered species, and when the translocation occurs in sites that are remote and difficult to access (Bodkin et al. 2000). Here we examine the genetic consequences of a translocation effort intended to augment a declining population of a waterfowl subspecies, the dusky Canada goose (*Branta canadensis occidentalis*).

Canada geese (*B. canadensis*) have evolved into numerous subspecies that breed in discrete geographic locales during the summer months and mix in moulting, staging and wintering grounds during the non-breeding season. Management of Canada geese of the Pacific Flyway in western North America is based on subspecific status, determined primarily by morphological characteristics (Hansen and Nelson 1964; Bellrose 1978; Johnson et al. 1979). Among the seven recognized subspecies of Canada Goose in the Pacific Flyway, there is considerable variation in population demographic trends. Populations of the western Canada goose (*B. c. moffitti*) have increased dramatically during past decades. Concomitantly, populations of the Aleutian Canada goose (*B. c. leucopareia*) and the dusky Canada goose (*B. c. occidentalis*) are recovering from, or have recently undergone, decreases in population number (Cornely et al. 1985; USFWS 1991; Pacific Flyway Council 1999).

The dusky Canada goose is a large-bodied, dark-plumaged Canada goose that nests primarily on the Copper River Delta (CRD) in coastal south-central Alaska (Figure 1). While population sizes of other large-bodied Canada geese of the Pacific Flyway have burgeoned during the past few decades, the population size of the dusky Canada goose breeding on the CRD has declined precipitously. This decline is attributed in part to modifications of the breeding habitat in the wake of the Great Alaskan Earthquake of 1964 (Campbell 1990). Despite efforts to improve overwinter survival of dusky Canada geese through restriction in harvest, numbers have declined steadily since annual quantitative assessments of goose production on the CRD began in 1971. Recent mid-winter estimates place the population size of dusky Canada geese at about 21,000 (Drut et al. 1998).

Changes have also occurred in the distribution of breeding Canada geese elsewhere in southcoastal Alaska. Recently, Canada geese of unknown subspecies status have begun breeding in the south-central (Anchorage) area, in sites ostensibly within the breeding range of lesser Canada geese (*B. c. parvipes*; Johnson et al. 1979). In addition, large, dark-plumaged ("dusky-like") Canada geese were recently observed nesting on islands within the Prince William Sound (PWS). We have uncovered no records of Canada geese nesting on Middleton Island (MID; Figure 1) in the Gulf of Alaska prior to 1981 (Rausch 1958; O'Farrell and Sheets 1962), when a single nesting pair (and 3 goslings) of large-bodied, "dusky-like" Canada geese was reported on the island (Gould and Zabloudil 1981). Two pairs were observed on MID in 1982 (P. Gould, U.S. Geological Survey, pers. comm.), and 84 adults and 11 young were observed in 1987 (Rosenberg et al. 1996). Researchers propose MID may have been colonised by Canada geese sometime between 1978 and 1981, approximately 40 years after the removal of foxes from the island (Campbell et al. 1988; Campbell and Rothe 1989). To augment this recently established population, and to support the declining populations on the CRD in accordance with the goals of cooperative inter-agency management of the dusky Canada goose, 179 juvenile (84 male, 95 female) and 13 flightless, adult dusky Canada geese (1 male, 12 females) were moved from the CRD to MID in 1987 and 1988 (Rosenberg et al. 1996). A dramatic increase in population numbers of Canada geese on the island occurred in the decade subsequent to this relocation effort, and by 1998, over 2000 geese inhabited MID. However, it is not clear whether the increase is a direct result of the translocation effort, or the result of ongoing colonisation and/or high breeding success of birds already established on MID.

The fate of the majority of the geese translocated to MID is not known. However, data from band recoveries, collar observations and recaptures of the translocated geese suggest most of the geese, including those translocated as goslings, returned to the CRD the following spring after wintering in Sauvie Island, Oregon (Crowley et al. 1997). Forty-three of the collared geese translocated to MID were observed on the CRD during the summers of 1988–1991. Nineteen of the 184 translocated geese that were banded

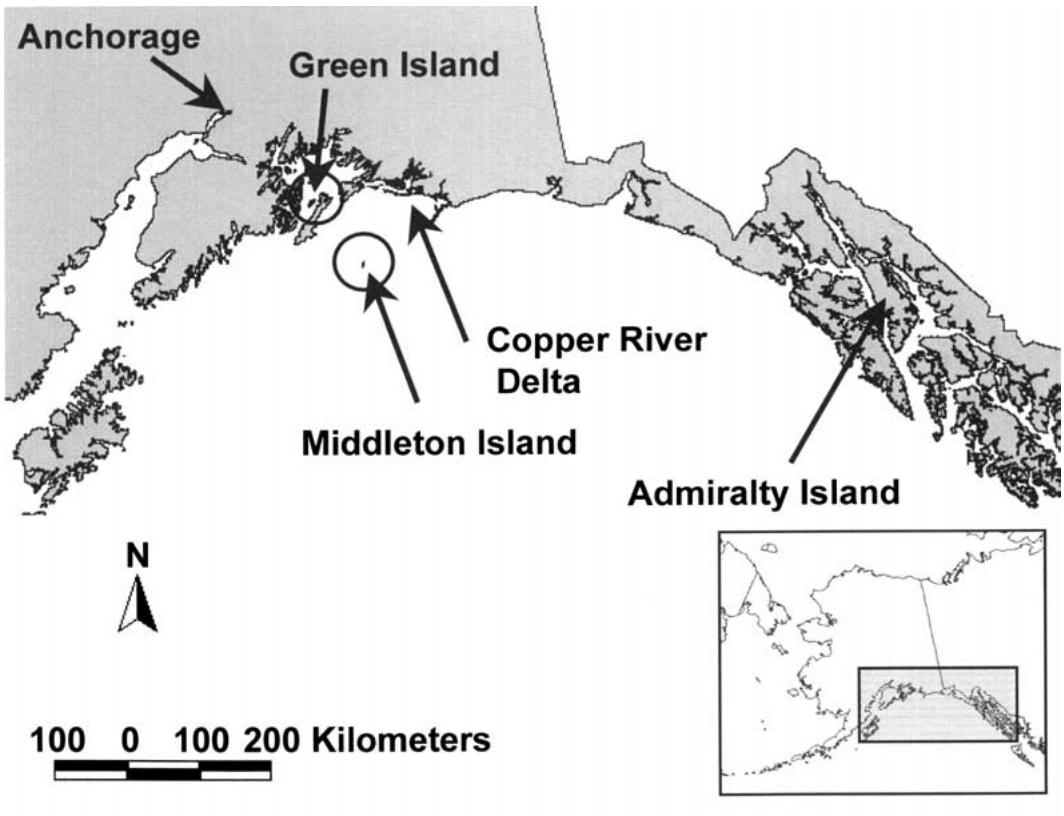

Figure 1. Locations of the 5 populations of Canada geese in southcoastal mainland and island Alaska sampled in this study.

were subsequently recaptured on the CRD between 1988 and 1992; 17 of these were transplanted to MID as goslings (Crowley et al. 1997). Thus, the return of the transplants to MID was poor and as a result a third translocation effort was cancelled (Campbell and Rothe 1990). Despite these observations, MID was considered to contribute an increasingly significant portion of the production for the entire dusky goose population (Pacific Flyway Council 1997).

This study examines the genetic characteristics of Canada geese currently breeding on the CRD, MID, the islands of the PWS, and elsewhere on southcoastal Alaska. We gathered these data using genetic markers with three different modes of inheritance, including nucleotide sequence information from the maternally-inherited mitochondrial DNA (mtDNA) and nuclear genotypic information from 6 autosomally-inherited microsatellite loci and one sex-linked (z-specific) microsatellite locus. Specifically, we address the questions of whether (1) the population currently inhabiting MID are descended from birds translocated from the CRD in 1987 and 1988; and (2) the large, dark plumaged Canada geese breeding on the islands of the PWS and in the Anchorage area (ANC) are genetically distinguishable from Canada geese breeding on the CRD.

Methods

Study area

Study areas included sites along the marine coastal and island habitats in the PWS, south-central, and the southeast panhandle of Alaska (Figure 1). Within these general areas, we collected samples at breeding locales of Canada geese (Van Horn et al. 1979; King and Derksen 1986) from CRD, sites in and around Anchorage, Green Island (GRN) in PWS, MID in the Gulf of Alaska, and Admiralty Island (ADM) of the Alexander Archipelago of Alaska. Herein, we use samples collected from these breeding locales to represent populations.

Sample collection and DNA extraction

Samples collected for genetic analyses included nest materials (flight or contour feathers, eggshell membranes; Pearce et al. 1997), blood, or feather quills from flightless moulting juveniles and adults captured on the breeding ground during brood drives. Nest materials were stored dry, and blood and quill samples were preserved in non-refrigerated buffer (Longmire et al. 1988). From 20–50 samples were collected from each breeding locale. Extraction procedures followed those reported in Pearce et al. (2000) and Pierson et al. (2000).

Laboratory analyses

The gender of each sampled bird was verified using DNA-based sex identification techniques described in Griffiths et al. (1998), and females were used for all analyses. Mitochondrial DNA (mtDNA) and nuclear microsatellite loci were used to determine the genetic characteristics of individuals breeding in each locale. MtDNA was analysed by direct sequencing of PCR-amplified DNA, using primers C1 and C1R (Sorensen and Fleischer 1996), which were determined by screening cesium-chloride purified samples of mtDNA and nuclear DNA to preferentially amplify a relatively rapidly mutating portion of the mtDNA control region (3' end of domain I, Baker and Marshall 1997) of Canada geese subspecies included in this study.

Each population was characterised at 7 polymorphic microsatellite loci. These included the biparentally-inherited microsatellite loci TTUCG-1, TTUCG-4 and TTUCG-5 (Cathey et al. 1998), Bcaμ1, Bcaμ9 and Bcaμ11 (Buchholz et al. 1998), and one sex-linked (z-specific) microsatellite locus (Bcaμ4; Buchholz et al. 1998). All microsatellite loci contained dinucleotide repeats, with the exception of TTUCG-5, which contains a pentanucleotide repeat. Laboratory protocols for PCR amplification, sample purificiation, genotyping and sequencing followed those described elsewhere (Pierson et al. 2000; Pearce et al. 2000).

Statistical analyses

MtDNA sequences. Sequences were manually aligned and sequence data examined for suitability for analyses using parsimony and distance methods. We could not generate hypotheses of phylogenetic relationships among haplotypes using maximum parsimony methods due to an insufficient number of informative sites. As an alternative, we generated pairwise gamma distances ($\Gamma_{\alpha=0.3}$) using the Tamura-Nei (1993) model of DNA sequence evolution, as implemented by MEGA (Ver. 1.01, Kumar et al. 1993) and used the neighbour-joining algorithm of Saitou and Nei (1987) to examine phylogenetic relationships among haplotypes. We used sequences from a small-bodied Canada goose (GenBank Accession # AF175483, Pierson et al. 2000) as an outgroup.

We tested the hypothesis of selective neutrality for mtDNA control region sequence data using the statistical method of Tajima (1989) implemented by ARLEQUIN (Ver. 2.0, Schneider et al. 1997). We used Chakraborty's (1990) population amalgamation test, as implemented by ARLEQUIN, to evaluate population homogeneity.

Estimation of levels of genetic variation. For all locales, we performed analyses of heterozygosity and exact tests for deviations from Hardy-Weinberg equilibrium for each microsatellite locus and across loci, using the computer program ARLEQUIN (Schneider et al. 1997). Fisher's exact p-values were calculated using the Markov chain random walk algorithm described by Guo and Thompson (1992). We verified locus independence by testing for genotypic linkage disequilibrium for all pairs of loci within each population, using the Markov chain method implemented in the computer program GENEPOP (Raymond and Rousset 1995). Inbreeding coefficients (F) were estimated as $1 - H_O/H_E$ and tested for significance as described by Li and Horovitz (1953).

Genetic heterogeneity of mtDNA within samples was estimated using 2 indices of intrapopulation genetic diversity: (1) the nucleon (haplotypic) diversity index (h) for nonselfing populations from pairwise haplotype divergences calculated using Tamura-Nei distance algorithm (Tamura and Nei 1993) and (2) the nucleotide diversity (π) (estimated using equations 8.4 and 10.6 of Nei 1987, respectively). We calculated both using ARLEQUIN (Ver. 1.5, Schneider et al. 1997). We tested for significance in heterogeneity of haplotype distribution among populations, using the MONTE function in the program REAP (Ver. 4.0, McElroy et al. 1991) and 1000 replicates based on the Monte Carlo χ^2 test of Roff and Bentzen (1989).

Estimation of degree of population subdivision. Gene frequencies were estimated for each microsatellite locus and for mtDNA for all populations. Levels

of population differentiation, based on distribution of alleles across populations, were examined using Fisher's exact test, based on a Markov chain adaptation of row-by-column contingency tables, as generated by GENEPOP (Raymond and Rousset 1995). Distribution of genotypes across populations was examined using a log-likelihood (G) based exact test (Goudet et al. 1996), implemented by GENEPOP. Multiple test significance was judged using Fisher's exact test method (GENEPOP) and/or by applying sequential Bonferroni procedures (Rice 1989).

Significance of spatial variation in gene frequency for each microsatellite locus was also assessed using *F*-statistics (Cockerham 1969, 1973; Weir and Cockerham 1984), which describe the apportionment of allelic variance among individuals within populations (F_{IS}) and among populations (F_{ST}), using the program FSTAT (Goudet 1994). Significance of F_{ST} values was based on random permutation tests (N = 1000). We also estimated R_{ST} values (Slatkin 1995) using the program RSTCALC (Ver 2.2, Goodman 1997).

Analyses of molecular variance (AMOVA) based on F_{ST} and R_{ST} values between and within populations were performed for microsatellite data using ARLEQUIN (Schneider et al. 1997). Similarly, interpopulation estimates of variance in mtDNA haplotype frequency (ϕ_{ST}) were obtained using the program ARLEQUIN (Schneider et al. 1997).

We quantified genetic divergence for the 6 biparentally inherited microsatellite loci among populations by using 2 distance measures: $(\delta\upsilon)^2$ (Goldstein et al. 1995) and Cavalli-Sforza and Edwards' (1967) chord distance (D_{CE}). The 2 distance matrices were used independently to generate consensus neighbour-joining trees. We examined the stability of tree topology by generating 2000 replicate microsatellite distance trees and obtaining bootstrap estimates on topology using a program written by J. Cornuet (INRA, Laboratoire de Neurobiologie comparee des invertebres, Bures-surYvette, France). We generated a final population tree using a combined method whereby topology and branch-lengths were estimated from D_{CE} and $(\delta\upsilon)^2$, respectively, with the user-tree option in FITCH/PHYLIP (Felsenstein 1997). Cavalli-Sforza and Edwards' (1967) least-squares method was used to estimate branch lengths from $(\delta\upsilon)^2$.

We estimated genetic distance among the 5 populations for mtDNA and the z-linked microsatellite locus Bcaμ4 separately using the coancestry coefficient [$\ln(1 - \theta)$; Reynolds et al. 1983], where θ represents pairwise variance in haplotype or allele frequency between populations. This distance measure assumes divergence among populations is strictly a function of genetic drift. Graphic representations of interpopulational distances were made using the NEIGHBOR program in PHYLIP. Data from a population of small-bodied Canada geese from the Yukon-Kuskokwim Delta (YKD) (*B. c. minima*, see Pierson et al. 2000) were included for comparison. Significance of each interpopulational distance estimate was based on pairwise estimates of interpopulational variance in haplotype or allele frequency and tested using random permutation tests.

Detection of bottleneck. We used 2 statistical tests, the sign test and the Wilcoxon test, to detect excess heterozygosity for polymorphic microsatellite loci as an indicator of recent bottlenecks in each population (Cornuet and Luikart 1996). The sign test determines if the proportion of loci with heterozygosity excess is significantly larger (or smaller) than expected at equilibrium, and the Wilcoxon test determines if the average of standardized differences between observed and expected heterozygosities is significantly different from zero. These two statistical tests detect recent bottlenecks using heterozygosity and allele frequency data for each of several loci, and require no data on historical population sizes or levels of genetic variation. Tests were conducted using the program BOTTLENECK (Cornuet and Luikart 1996; Luikart and Cornuet 1998), under 3 models thought to represent the range of possible mutation modes generating polymorphism at microsatellite loci (Chakraborty and Jin 1992). These include the stepwise mutation model (SMM, Ohta and Kimura 1973), the infinite-alleles model (IAM, Kimura and Crow 1964), and the two-phase model (TPM, see Di Rienzo et al. 1994) of microsatellite mutation. One thousand simulations were performed for each population.

Results

MtDNA sequence variation

Sequence data were obtained from 144 bp of domain I of the mtDNA control region of 154 Canada geese from all populations. Eight haplotypes, characterised by 9 variable sites (5 parsimony sites), were found among all geese sampled. Sequence information for each haplotype is given in GenBank (accession

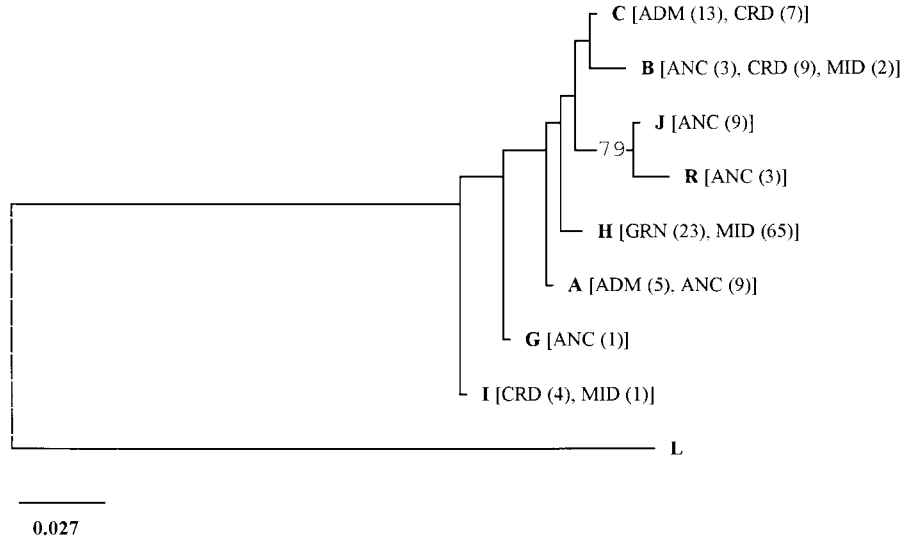

Figure 2. Mitochondrial DNA neighbour-joining tree showing evolutionary relationships among 8 haplotypes found among 154 Canada geese nesting in 5 populations in south-central Alaska. Haplotypes are identified from nucleotide sequences obtained from domain I of the mtDNA control region. Pairwise distances are based on gamma distribution (α = 0.3), under the Tamura-Nei (1993) model of nucleotide substitution. Bootstrap values (>50%) are based on 1000 replications and are listed at nodes. Haplotype L, found in small-bodied Canada geese, is used to root the tree.

Table 1. Frequencies and distribution of 8 mtDNA haplotypes found among 154 Canada geese sampled from southcoastal mainland and island breeding populations. Analyses are based on sequence information obtained from 144 bp of domain I of the Canada goose mtDNA control region

	n per locality						*Sequence position*
	ADM[a]	ANC[b]	CRD[c]	GRN	MID[d]	TOTAL	
Haplotype							
A	5	9	—	—	—	14	00001111
B	—	3	9	—	2	14	33880222
C	13	—	7	—	—	20	38236123
G	—	1	—	—	—	1	CTCATTAA
H	—	—	—	23	65	88	T.T.....
I	—	—	4		1	5	..T.....
J	—	9	—	—	—	9	..T.C...
R	—	3	—	—	—	3	.......G
							.CT.....
Haplotypes/	2	5	3	1	3		...G.C..
population							...G.CG.

[a]*B. c. fulva* (Johnson et al. 1979).
[b]*B. c. parvipes* (Johnson et al. 1979).
[c,d]*B. c. occidentalis* ([c]Johnson et al. 1979, [d]Pacific Flyway Council 1997).

numbers AF175473, AF175476 – AF175479, AF17494 and AF17546).

Figure 2 displays the relationships among the haplotypes and associated sampling localities. Bootstrap support for all but one node is small (<50%) and expected, due to the small number of nucleotide substitutions among haplotypes.

Five of the 8 haplotypes found were present in more than one population (Table 1, Figure 2). Haplotype B was found in the largest number of populations (60%), and Haplotypes G, J and R were detected only in ANC. Populations of Canada geese breeding on the islands of PWS and Gulf of Alaska were found to be fixed (GRN) or nearly so (MID, 96%)

Table 2. Measures of genetic diversity estimated for large-bodied Canada geese breeding in 5 populations in southcoastal mainland and island Alaska

Varibale	ADM	ANC	CRD	GRN	MID
	Autosomal microsatellite loci				
H_O[a]	0.659	0.650	0.648	0.722	0.720
H_E[a]	0.716	0.708	0.735	0.724	0.742
A[b]	7.670	7.500	8.170	6.670	7.830
F	0.079	0.082	0.118	0.003	0.027
(N)	(25)	(42)	(51)	(34)	(30)
	z-specific microsatellite locus				
D[c]	0.851	0.608	0.854	0.588	0.658
(# alleles)	(8)	(7)	(13)	(6)	(7)
	mtDNA control region sequence				
h[d]	0.425	0.740	0.668	0.000	0.114
π[e]	0.003	0.015	0.006	0.000	0.003
(# haplotypes)	(2)	(5)	(3)	(1)	(3)

[a] H_O and H_E = observed and expected heterozygosity.
[b] A = mean number of alleles.
[c] *D* = Genetic diversity (Nei 1987, eq. 8.3).
[d] *h* = haplotypic diversity (Nei 1987, eq. 8.4).
[e] π = nucleotide diversity (Nei 1987, eq. 10.6).

for a single mtDNA haplotype (Haplotype H, Table 1 and Figure 2). This haplotype differs by at least one site transition from all other haplotypes characterizing geese sampled from populations of Canada geese in coastal Alaska (Table 1). This unique haplotype has not been found in samples representing the other 3 breeding populations of large-bodied Canada geese, and is thus considered a diagnostic marker for Canada geese breeding on these islands.

No significant deviations from the null hypothesis of selective neutrality of mtDNA sequences (Tajima 1989), or population homogeneity (Chakraborty 1990; data not shown) were detected in any population.

Levels of genetic variability

Haplotype diversity (h) within populations ranged from zero (GRN) to 0.740 ± 0.052 (ANC), with mean haplotype diversity 0.380 ± 0.020 (Table 2). Nucleotide diversity (π) values were much lower than haplotype diversity values, as expected since they are corrected for the number of base pairs examined. Nevertheless, the trend in nucleotide diversity corresponded with haplotype diversity; i.e., lowest values were found among geese sampled from GRN (zero) and MID (0.0026 ± 0.003) and highest values among geese sampled from ANC (0.015 ± 0.009), with mean nucleotide diversity 0.0046 ± 0.0017. Haplotype heterogeneity, tested using Monte Carlo simulations, across populations was significant ($\chi^2 = 287.22$, $p < 0.001$).

Table 3. Pairwise ϕ_{ST} and F_{ST} values among 5 southcoastal mainland and island Alaskan Canada goose populations based on mtDNA sequences (above diagonal) and a z-linked microsatellite locus (below diagonal)

	ADM	ANC	CRD	GRN	MID
ADM	—	0.361**	0.275**	0.891**	0.776**
ANC	0.071*	—	0.416**	0.569**	0.625**
CRD	0.015	0.112**	—	0.803**	0.783**
GRN	0.093*	0.019	0.089*	—	0.004
MID	0.133*	0.137*	0.108*	0.128**	—

* = values significantly different from zero ($p < 0.05$).
** = values significantly different from zero ($p < 0.001$).

Analyses of mtDNA haplotype variance, and resulting F_{ST} analog (ϕ_{ST}), indicated the 5 populations were significantly differentiated overall. Analyses of haplotype frequencies among populations showed that over 66% of the overall mtDNA haplotype variance was due to differences between populations. Variation among individuals within populations accounted for 34% of the overall variance. Pairwise population analyses indicated variance in haplotype frequency was significantly distributed between populations ($p < 0.001$) for all pairwise comparisons, with the exception of MID and GRN ($\phi_{ST} = 0.004$, $p > 0.590$) (Table 3).

A neighbour-joining tree constructed using mtDNA haplotype frequency information, based on a matrix of coancestry coefficients ($[-\ln(1 - \phi_{ST})]$; Reynolds et al. 1983) suggests the population on MID is genetically more similar to the population on GRN than it is to the population on CRD (Figure 3). The CRD population is clustered more closely with the population on ADM than on MID (Figure 3).

Microsatellite diversity

Four to 17 alleles were found across all populations at each microsatellite locus. The mean number of alleles per locus was lowest in GRN and highest in CRD (Table 2). Genotype proportions at biparentally-inherited microsatellite loci accord well with Hardy-Weinberg expectations (HWE). Twenty-five of 30 individual tests (84%) revealed no significant departure from HWE proportions. Combining probabilities over populations for the biparentally-inherited

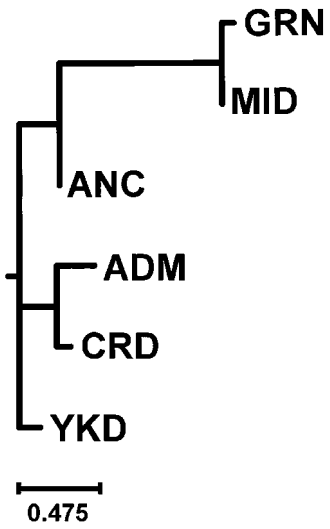

Figure 3. Neighbour-joining tree showing relationships among 5 populations of Canada geese nesting in south-central Alaska. Relationships are based on Reynolds et al. (1983) genetic distances, generated from mtDNA haplotype frequency data. All pairwise distances were statistically significant with the exception of MID and GRN.

Table 4. Pairwise θ_{ST} and R_{ST} values among 5 southcoastal mainland and island Alaskan Canada goose populations based on 6 autosomal microsatellite loci. Values above the diagonal are pairwise q_{ST} values (Weir and Cockerham 1984), values below the diagonal represent R_{ST} values (Goodman 1997)

	ADM	ANC	CRD	GRN	MID
ADM	—	0.057*	0.014	0.027	–0.004
ANC	0.019	—	0.046*	0.075*	0.039*
CRD	–0.027	0.073*	—	0.012	–0.019
GRN	0.020	0.129*	0.017	—	–0.012
MID	0.013	0.151*	–0.031	–0.050	—

*values significantly different from zero ($p < 0.008$).

microsatellite loci shows that 1 locus (TTUCG-5) displays significant departure from HWE, due largely to a deficit of heterozygotes in 4 of the 5 populations. Because no significant heterozygote deficit was detected at this locus for geese sampled from 2 other populations of large-bodied Canada geese nesting in northwestern North America (Scribner et al., unpubl. data), or in small-bodied Canada geese nesting in western Alaska (Pierson et al. 2000), we consider it unlikely the observed deficit is due to the presence of a null allele.

Combining probabilities over loci revealed no significant departures from HWE in the two island populations (GRN and MID), suggesting a general lack of inbreeding or pronounced subdivision within these 2 populations. However, significant departures from HWE in geese sampled from ANC and the CRD were observed, and could be due to inbreeding, pronounced subdivision, or recent admixture within these populations. Since the value of H_o varies from locus to locus among these populations, not all loci within those 2 populations deviated significantly from HWE expectation, and the inbreeding coefficients (F, Wright 1969; see Table 2) were not significant, the deviation from HWE observed within these 2 populations is more likely due to population substructuring (e.g., sampling across extended familial groups) or recent admixture, than to inbreeding *per se*. Tests for genotypic linkage disequilibrium rejected the null hypothesis of independence in only 5 of 75 (7%) population comparisons, with loci TTUCG-1 and TTUCG-4 significantly associated with each other in 3 of the 5 populations (ADM, CRD and GRN).

Substantial variation was observed across the breeding populations in terms of both microsatellite allele and mtDNA haplotype frequencies (Table 2). Heterozygosities ranged from 0.467 to 0.914, averaging 0.737 across all 6 loci combined (data not shown). Fisher's combined test of independence across all 6 loci showed significant differentiation for genotypes among all populations overall, (χ^2 = infinity; df = 12, $p < 0.001$), and for 72% of total pairwise comparisons (43 of 60; data not shown). Non-significant pairwise comparisons occurred most often between MID and either ADM or GRN (4 of 6 loci for both). Distribution of alleles across populations was also significantly different overall, (χ^2 = infinity; df = 12, $p < 0.001$), and for 75% of pairwise comparisons (45/60). Unique alleles that occurred at >5% within any one population were found in ANC and CRD (1 unique allele for Bcaμ1 and Bcaμ9, respectively).

Analyses of allelic frequencies among populations showed that 2.5% of the overall microsatellite allelic variance was due to differences between populations. Allelic variance among individuals within populations accounted for 97.5% of the overall variance. F_{ST} and R_{ST} values ranged from –0.019 to 0.075 and –0.050 to 0.151 (Table 4), respectively. Mean F_{ST} and R_{ST} for all 6 loci were 0.026 and 0.031, respectively (data not shown). Pairwise population analyses indicated variance in allelic frequency was significantly distributed between populations ($p < 0.008$) for 4 of 10 pairwise comparisons, all involving ANC (Table 4).

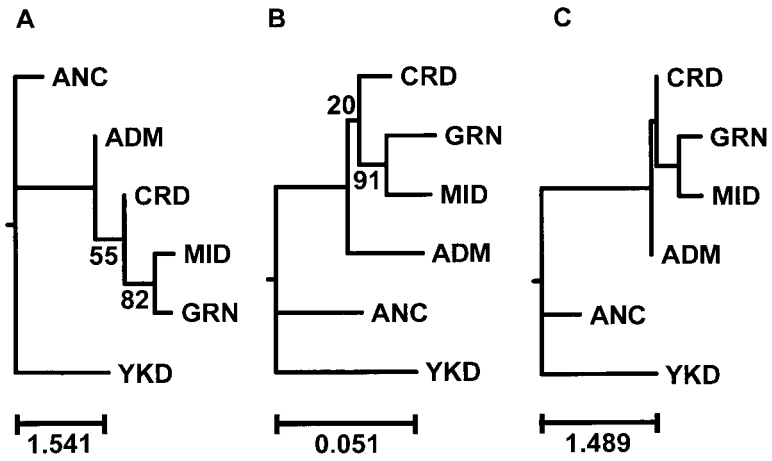

Figure 4. Neighbour-joining tree showing relationships among 5 populations of Canada geese nesting in south-central Alaska, using bi-parentally inherited microsatellite allele frequency data. Relationships are based on: (a) Goldstein et al.'s (1995) ($\delta\mu^2$) distances, (b) Cavalli-Sforza and Edward's (1967) distances (C_{SE}), or (c) ($\delta\mu^2$) distances constrained to a topology generated using C_{SE}. Bootstrap values listed at the nodes are based on 2000 replications. Statistically significant distances occurred between ANC and all other populations. A population of small-bodied Canada geese from YKD is used as an outgroup.

Genetic relationships among populations are indicated in Figure 4a and 4b. For both D_{CE} and $(\delta\upsilon)^2$ distances, the greatest distances between populations were between ANC and GRN(D_{CE}), or MID $(\delta\upsilon)^2$. The smallest distances were observed between GRN and MID (D_{CE}), and between CRD and ADM [$(\delta\upsilon)^2$]. A consensus tree derived from $(\delta\mu)^2$ genetic distance values (Figure 4a), bootstrapped over individuals, gave the same topology as that derived from D_{CE} distance values (Figure 4b); both separated populations on MID and GRN from populations of the CRD, and were supported by high bootstrap values (82 and 91%). Figure 4c shows a population tree generated by FITCH in PHYLIP, with topology constrained to that generated using (D_{CE}) distances, and branch lengths generated using $(\delta\mu)^2$.

Z-specific locus

Fisher exact tests for genic and genotypic differentiation confirm high structuring among all populations overall ($p < 0.001$, data not shown) at the z-specific locus. Pairwise population comparisons indicated distribution of alleles was significantly different for all pairwise comparisions ($p < 0.001$, data not shown), and distribution of genotypes was significantly different for 6 of 10 pairwise comparisons. Significant genotypic differentiation was observed between MID and all other populations ($p < 0.001$), between GRN and ADM ($p < 0.05$) , and between CRD and ANC ($p < 0.001$) (data not shown).

Analyses of allelic frequencies among populations, using AMOVA, showed that 9.3% of the overall microsatellite allelic variance was due to differences between populations at the z-specific locus. Variation among individuals within populations accounted for 90.7% of the overall variance. Analyses of pairwise F_{ST} values indicate most of the populations (8 of 10 pairwise comparisons) are significantly differentiated in terms of variance in allelic frequency. There was no significant difference between GRN and ANC, as well as CRD and ADM (Table 3) for this locus.

A neighbour-joining tree constructed using allele frequency information for Bcaμ4, based on a matrix of coancestry coefficients ([–ln(1 – ϕ_{ST})], Reynolds et al. 1983) and using a population of small-bodied Canada geese (*B. c. minima*) from the YKD to root the tree, again demonstrates the presence of structuring between populations (Figure 5). Unlike analyses of haplotype or allele frequencies conducted using mtDNA or biparentally-inherited microsatellites, that indicated the population on MID was genetically most similar to birds nesting on GRN, analyses of the z-specific microsatellite locus suggested a closer relationship between ANC and GRN populations.

Bottlenecks and population expansions

Microsatellite data. We detected signatures of significant recent bottlenecks in 2 of the 5 Canada goose populations sampled, using the sign test and the

Table 5. Sign and Wilcoxon tests for heterozygosity excess in 6 autosomal microsatellite loci in 5 populations of Canada geese in southcoastal mainland and island Alaska. Heterozygote excess and defiency ratios are listed as *e/d* for the sign test

POP	(N)	Sign Test Mutational Model						Wilcoxon Test Mutational Model					
		IAM		TPM		SMM		IAM		TPM		SMM	
		e/d	(*p*)	*e/d*	(*p*)	e/d	(*p*)	H_e	H_d	H_e	H_d	H_e	H_d
CRD	(51)	6/0	(0.043)*	4/2	(0.530)	2/4	(0.190)	0.007*	1.000	0.039*	0.977	0.945	0.078
MID	(30)	6/0	(0.041)*	4/2	(0.530)	3/3	(0.459)	0.008*	1.000	0.055	0.960	0.781	0.280
GRN	(34)	6/0	(0.037)*	5/1	(0.213)	4/2	(0.535)	0.007*	1.000	0.015*	0.992	0.343	0.710
ANC	(42)	5/1	(0.208)	4/2	(0.529)	3/3	(0.464)	0.078	0.945	0.281	0.781	0.718	0.344
ADM	(25)	5/1	(0.214)	3/3	(0.472)	2/4	(0.189)	0.056	0.961	0.578	0.500	0.922	0.218

*significant deviation ($p < 0.05$) from equilibrium/non-bottleneck expectation.

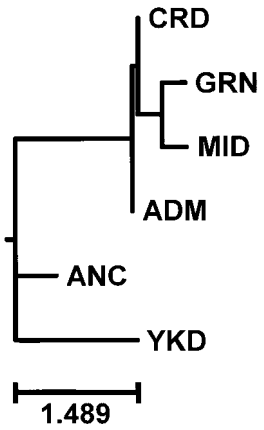

Figure 5. Neighbour-joining tree showing relationships among 5 populations of Canada geese nesting in south-central Alaska. Relationships are based on Reynolds et al. (1983) genetic distances, generated from the z-specific microsatellite allele frequency data. All pairwise distances were statistically significant with the exception of GRN and ANC, and CRD and ADM. A population of small-bodied Canada geese from YKD is used as an outgroup.

most appropriate underlying model of evolution for the marker type (TPM, Wilcoxon one-tailed test for heterozygosity excess, G. Luikart, INRA, pers. comm.), and 3 under the IAM model of evolution (Table 5). Similarly, the Wilcoxon test detected significant recent bottlenecks in the same 3 populations under the IAM, and for 2 under the more conservative TPM model (Table 5). Thus, observed heterozygosity exceeded the average of the corresponding distribution of heterozygosities expected at equilibrium for these tests in populations of the CRD, MID and GRN, suggesting a recent bottleneck in all 3 populations. However, no significant recent bottleneck was detected for the ADM or ANC populations. Under the most conservative model of evolution (SMM), no population sampled demonstrated a signature of a recent bottleneck.

None of the populations showed a significant deficiency of heterozygosity under any model of mutation (Table 5). This implies none of the populations, including MID, have experienced a recent expansion in population size or recent influx of rare alleles from genetically distinct immigrants (Luikart and Cornuet 1998).

Discussion

Our results do not support the hypothesis that the nesting population of Canada geese on MID derived from CRD stock as a result of natural colonisation or a translocation. Expecting homogeneity between the 2 populations, we found instead significant differentiation between them, both in distribution of allelic and genotypic frequencies at all loci, and in the apportionment of variation in allele frequencies for 2 of the 3 marker types. On the other hand, CRD (representing the subspecies *B. c. occidentalis*) is indistinguishable from ADM (representing the subspecies *B. c. fulva*) for the nuclear microsatellite loci, shares mtDNA haplotypes, although at different frequencies, and clusters consistently closer to ADM in consensus population trees derived from analyses of all markers. Using a subset of the same markers, for the same populations, Pearce et al. (2000) found that maximum likelihood estimation (MLE) simulations correctly assign individuals from MID back to their breeding locale over 80% of the time, with the majority of misallocated individuals being assigned to GRN and not to the CRD. Likewise, these simulations suggested geese nesting on the

CRD can be attributed to their correct breeding locale over 95% of the time, with the majority of misallocations to ADM, and not MID (Pearce et al. 2000).

What is the source of the population that expanded on MID, if not from the CRD? The similarity in overall levels of nuclear and mtDNA diversity, coupled with presence of this single, unique, fixed mtDNA haplotype among geese sampled from GRN, and its near-fixation on MID, points to a close relationship between the 2 south-central Alaskan island populations.

Large, dark-plumaged Canada geese breeding in forested habitats on islands of the PWS, adjacent to the CRD on the west and eastward along the Gulf of Alaska, are present in low densities and are highly dispersed (Pacific Flyway Council 1997). Consequently, we were unable to obtain sufficient samples from other islands to include in our analyses. For this study, then, we rely on samples taken from GRN to represent the other islands of the PWS and Gulf of Alaska; this may not be reasonable. Nevertheless, mtDNA data obtained from 4 geese nesting on other islands of the PWS (Hinchenbrook and Hawkins Islands) suggest these populations are also comprised of birds possessing the H haplotype (unpublished data). These island birds' wide dispersion and low population size, and presumably low effective population size, may have aided in the fixation of a single mtDNA haplotype (Haplotype H). Thus, the most parsimonious explanation for our results is that individuals sampled from MID descended from females recruited from other islands of the PWS, and not from CRD. Additionally, the presence of this diagnostic haplotype, and similar private haplotypes in other populations (Table 1) argues strongly for lack of overlap and exchange of females among geographically proximate breeding populations sampled from southcoastal mainland and island habitats in Alaska.

Population numbers on MID have increased rapidly during the past decade (Pacific Flyway Council 1997). Surprisingly, the microsatellite data did not reveal a genetic signature of recent population expansion (within the past 2 to 40 generations, G. Luikart, INRA, Laboratoire de Neurobiologie comparee des invertebres, Bures-surYvette, France, pers. comm.) in MID, although a signature of a bottleneck was detected. If a substantial proportion of the population increase on MID is indeed due to ongoing colonisation by birds from islands of the PWS, we would not necessarily expect to see a genetic signature of a population expansion; the MID population would appear to be just an extension of a larger PWS metapopulation.

Multiple markers and gender bias in population structure

We observed incongruence in levels and distribution of genetic variation assessed using the 3 marker types. Lack of correlation between mtDNA and nuclear DNA data can be attributed to differences in levels of male and female gene flow (Moritz 1994a). However, lack of congruence between the z-specific marker and the biparentally-inherited marker is more difficult to explain. Because females pass on the z-specific locus to the next generation via sons, that locus can provide a single estimate of male-mediated gene flow from the preceding generation, if sampling is conducted using only females, as in this study. Thus, if gene flow accounts for a portion of the lack of differentiation among certain populations, our data suggest that (1) gene flow occurring among these populations is largely mediated by males; (2) only the 2 island populations of MID and GRN demonstrate any significant signature of female mediated gene flow, but (3) recent male-mediated gene flow (assessed using the z-specific marker) may be restricted between the 2 island populations.

Productivity of geese breeding on the CRD is low; consequently, generation time for dusky Canada geese is estimated to be approximately 6.6 years (J. B. Grand, Auburn University, pers. comm). Thus, while we cannot determine the allele frequencies prevailing in either MID or CRD at the time of the translocation, we were able to analyse genetic information from the CRD within only a few generations subsequent to the translocation. Differences between the populations at microsatellite loci were due mostly to frequency differences; there was overlap in allele distribution and few private alleles. On the other hand, the mtDNA sequences appeared more powerful when used for discriminating among populations, due to the presence of private and diagnostic haplotypes as well as significant differences in haplotype frequencies. Thus, we rely heavily upon the identification of the unique mtDNA haplotype in our interpretation of these data. Estoup et al. (1999) recommended the use of juxtaposed microsatellite systems (JMS) to identify recently admixed populations by differentiating between introduced and homoplasious microsatellite alleles, and we suggest JMSs could be appropriate markers to use in this case.

Conservation genetics implications

Augmentation of wild populations, either by translocation from other wild populations or with stock from breeding facilities, is an increasingly common strategy for species considered at risk for decline (NRC 1995). Our data suggest that despite the observed increase subsequent to the translocation effort, it had little or no enhancement effect on the resident populations. The presence of 2 CRD haplotypes in individuals sampled from MID suggests some natural immigration from CRD may occur, but at low levels not sufficient to offset the influx of genes from individuals colonizing from the islands in the PWS.

Translocation of individuals from wild populations is considered an effective way to stimulate growth in a stable but small population, under at least 3 criteria: (1) when the source population is showing positive rates of growth; (2) when suitable unoccupied (or underoccupied) habitat exists, and (3) when the factors leading to the extirpation of the species from that habitat have been identified and reduced, or eliminated (Cade 1990; Scott et al. 1994; NRC 1995). Conditions of the MID translocation failed to meet at least 1 of these criteria. Although MID provided suitable nesting habitat devoid of mammalian predators partially responsible for low productivity on the CRD, the source populations on the CRD were characterised by negative rather than positive rates of growth (Campbell 1990).

The natural colonisation of Middleton Island by large, dusky-like female Canada geese apparently originating from neighbouring islands and subsequent increase in population numbers may have been possible due to the eradication of arctc foxes (*Alopex lagopus*) from the island in the 1940s or 1950s. Similarly, the recent increase in population numbers and subsequent delisting of the endangered Aleutian Canada goose in 2001 has been attributed to the eradication of foxes from a number of Aleutian Islands (J. Martin, Refuge Manager, USFWS, pers. comm), concomitant with restrictions on hunting and protection of wintering habitat. Translocation efforts, unlike those for MID, were eventually effective for the western Aleutian Island populations. In that case, systematic relationships were considered in the augmentation effort: all geese translocated to newly fox-free Aleutian Islands derived from either wild-caught or captive-reared Aleutian Canada geese (Byrd 1998).

Female Canada geese are more likely involved in nest site selection than males (Mickelson 1975; Cooper 1978), and the colonisation of MID may have been by females dispersing from islands in the PWS seeking nesting habitat similar to their natal locale. Due to differences in nesting habitat, the geese translocated to MID from the CRD may have been less successful than females naturally colonizing from nearby islands. These observations have implications for translocation efforts, since, over time, successful populations are expected to become morphologically, behaviourally and physiologically adapted to local environments. Thus, influx of genes from nonnative stock which may have evolved different behavioural phenotypes could disrupt adaptations specific to local habitats (Frankham and Loebel 1992).

Taxonomy

Based on morphological characteristics and the past history of translocation, the MID population is managed as a member of the dusky Canada goose subspecies (Pacific Flyway Council 1997). However, populations of large, dark-plumaged Canada geese breeding on other islands of the PWS – such as GRN, Hawkins and Hinchenbrook islands – are currently unclassified taxonomically and are not managed as dusky Canada geese. This is despite the observation that geese from these islands, and presumably from throughout the PWS, are indistinguishable from either geese from MID or the CRD for the morphological characteristics used to distinguish dusky Canada geese harvested on their wintering grounds (Pearce et al. 2000). Our genetic data indicate that despite morphological similarity of the geese of MID and the islands of the PWS to geese of the CRD, the island birds as a group clearly share a more recent common ancestry with each other than with birds on the CRD. Canada geese breeding on the CRD and nominally classified as *B. c. occidentalis* differ significantly in nuclear allele and mtDNA haplotype frequency, but share haplotypes with geese of other subspecies (*B. c. parvipes* from Anchorage, *B. c. fulva* from Admiralty Island). Thus, they meet the genetic criteria widely used to identify management units (MUs) *sensu* Moritz (1994b). Alternatively, Canada geese from the PWS appear to constitute a monophyletic group with respect to mtDNA, and are significantly differentiated from other populations in terms of nuclear DNA. Thus, they meet the genetic criteria widely used to identify

"evolutionarily significant units" (ESUs) *sensu* Moritz (1994b). Certainly, the contemporary demographic independence of female Canada geese on the islands of the PWS and Gulf of Alaska should be considered in any plan used to manage those populations, since island populations experiencing substantial loss of numbers cannot be expected to recruit females from neighbouring mainland coastal populations. Nevertheless, we caution that, because the mtDNA data used herein are based on a very short segment of the mtDNA (144 bp), additional criteria, such as occupancy of unique and geographically and temporally separate habitats, morphology, and variation in life history traits, should be integrated with phylogeographic and population genetic lines of evidence when targeting these populations for conservation or management purposes.

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