The Condor 104:84–91

MITOCHONDRIAL DNA SUGGESTS HIGH GENE FLOW IN ANCIENT MURRELETS

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Abstract. Ancient Murrelets (*Synthliboramphus antiquus*) are subarctic seabirds that breed on islands from British Columbia through Alaska to China. In this study, we used sequence variation in the mitochondrial control region and cytochrome *b* gene to estimate the extent of genetic differentiation and gene flow among populations both within British Columbia and across the North Pacific. Results suggest that genetic differentiation is low and female-mediated gene flow is high among colonies within British Columbia, in agreement with banding studies. Surprisingly, genetic differentiation appears to be low and gene flow high between British Columbia and Asia. The effective female population size appears to be stable, but the species may have undergone a range expansion. These results suggest that Ancient Murrelets from throughout the North Pacific may represent a single management unit for conservation.

Key words: Ancient Murrelet, gene flow, management unit, mitochondrial DNA, population genetic differentiation, Synthliboramphus antiquus.

El ADN Mitocondrial Sugiere Alto Flujo Génico en *Synthliboramphus antiquus*

Resumen. Synthliboramphus antiquus es una especie de ave marina subártica que se reproduce en islas desde British Columbia a través de Alaska hasta China. En este estudio estimamos el grado de diferenciación genética y de flujo génico entre poblaciones localizadas dentro de British Columbia y a través del Pacífico Norte. Nos basamos en la variación en secuencias de la región control y el gen citocromo *b* del ADN mitocondrial. Los resultados sugieren baja diferenciación genética y alto flujo génico mediado por las hembras entre las colonias de British Columbia, lo que es consistente con estudios de aves anilladas. Sorprendentemente, la diferenciación genética parece ser baja y el flujo génico alto entre British Columbia y Asia. El tamaño efectivo de la población de hembras parece estar estable, pero la especie podría haber expandido su rango de distribución. Estos resultados sugieren que los *S. antiquus* de todo el Pacífico Norte pueden representar una sola unidad de manejo en términos de conservación.

INTRODUCTION

Ancient Murrelets (*Synthliboramphus antiquus*) are small, migratory seabirds that breed on islands in a 9000-km arc around the northern rim of the Pacific Ocean, becoming increasingly abundant from China to British Columbia, Canada (Gaston 1992). British Columbia supports approximately half of the world's breeding population, while most of the rest nest in Alaska. Over the past several decades, Ancient Murrelets have declined dramatically throughout their range, and the species has been designated as ''vulnerable'' by the Committee on the Status of Endangered Wildlife in Canada (Gaston 1994). Much of the species' decline has been attributed to introduced mammalian predators, including rats (*Rattus rattus* and *R. norvegicus*) and raccoons (*Procyon lotor*; Gaston 1994).

Information about gene flow and the distribution of genetic variation within and among populations is needed for effective management of declining species (Moritz 1994, Haig 1998). However, little is known about the movements of Ancient Murrelets among colonies, and nothing is known about their population genetic structure. In banding studies, several chicks have been recovered breeding away from their colony of origin (Gaston and Adkins 1998), and Gaston

Manuscript received 12 February 2001; accepted 17 October 2001.

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(1990) argued that the colony on Reef Island in the Queen Charlotte Islands may exchange recruits with colonies in Juan Perez Sound, 30 km away (Gaston 1992). Thus gene flow within British Columbia may be high. Gaston (1990) speculated further that colonies such as those on the Limestone Islands (Queen Charlotte Islands) may act as population sinks, being maintained by immigration despite high predation rates. Gaston and Adkins (1998) also suggested that dispersal of murrelets among colonies may not be symmetrical. In contrast, North American and Asian populations are geographically disjunct and may be genetically isolated from each other, since few Ancient Murrelets nest in the Aleutian Islands, Canadian murrelets appear to winter off North America (Gaston 1992), and Asian murrelets appear to winter off the coast of Hokkaido (Piatt and Gould 1994). Furthermore, studies of other seabird and shorebird species have found genetic differences between North American and Asian populations (e.g., Dunlins [*Calidris alpina*], Wenink et al. 1993; Common Terns [*Sterna hirundo*], Pelagic Cormorants [*Phalacrocorax pelagicus*], Zink et al. 1995), and in some species North American and Asian populations probably represent distinct species (e.g., Mew Gulls [*Larus canus*], Zink et al. 1995).

In the present study, we compared variation in mitochondrial DNA (mtDNA) among North American and Asian Ancient Murrelets. Based on indirect evidence (above), we predicted that (1) gene flow among British Columbian colonies would be high, but (2) gene flow between Asian and British Columbian populations would be restricted. Because populations may have subdivided only recently (e.g., due to Pleistocene glaciations), we focused on genetic markers with relatively high mutation rates: the mitochondrial control region and cytochrome *b* gene.

METHODS

Samples of blood or solid tissue were collected from 39 adult Ancient Murrelets caught in drift nets off the Kamchatka Peninsula and Kurile Islands in May–July of 1995 and 1996. Birds were in breeding condition, so probably were near their breeding sites, but could not be associated with any particular colony. Tissue also was sampled from 13 adult Ancient Murrelets killed by rats and raccoons on East Limestone Island in the Queen Charlotte Islands (~1150 breeding pairs; Gaston 1992), and from seven eggs and predator-killed adults on George Island, 70 km away (~11 600 breeding pairs; Gaston 1992). Tissue samples are archived at −70°C at Queen's University. DNA was prepared using standard protease digestion and phenol/chloroform extraction protocols (Friesen et al. 1997).

Nuclear copies of mitochondrial genes have been detected in numerous organisms, including other species of alcids (Kidd and Friesen 1998); PCR primers specific to the mitochondrial control region of Ancient Murrelets therefore were developed prior to population screening. Control region sequences for another species of alcid, the Pigeon Guillemot (*Cepphus columba*; Kidd and Friesen 1998) were used to design general primers within the conserved central domain (SaH560, 5′-CGGTCGGATGTCCGCGATCACGGG-3′; and SaL580, 5′-GGGCGTCTTCAGGCAGCCCCTCC-3′). These primers then were used in conjunction with two previously developed general primers, ND6 (TPB, unpubl. data) and SgH1247 (Quinn and Wilson 1993), to amplify and sequence the 5′ and 3′ ends respectively of the control region from a representative Ancient Murrelet (sequencing details below). Finally, the sequence from these fragments was aligned with the corresponding sequence from the guillemot to design two murrelet-specific primers near the 5′ and 3′ ends of the control region (SaL30, 5′-GAGCGGGCGCCTAAATGTTCG-3′; and SaH900, 5′-AATATACGAACGCAAATCGTGAATGG-3′, respectively).

Three fragments of mtDNA were amplified from each of the 58 DNA samples: a 494-bp section of the 5′ end of the control region (using primers SaL30 and SaH560); a 332-bp section of the 3′ end of the control region (using primers SaL580 and SaH900); and a 306-bp fragment of the cytochrome *b* gene (using primers L14841 and H15149 from Kocher et al. 1989). Amplifications were performed in a PTC-100-60™ thermal cycler with a Hot Bonnet™ heated lid (MJ Research, Waltham, Massachusetts) as described in Friesen et al. (1997) but with the inclusion of 0.01% gelatin and 1.6 μM BSA, and annealing at 55°C (control region fragments) or 50°C (cytochrome *b*). Sequence variation was screened initially using single-stranded conformational polymorphisms (SSCPs; Hayashi 1991, Friesen et al. 1997), then representatives of each haplotype were re-amplified and sequenced directly: PCR products were subjected to electro-

phoresis through low-melting agarose gels, isolated by digestion with Agarase™ (Roche Molecular Biochemicals, Laval, Quebec), then sequenced manually using ThermoSequenase™ Radiolabeled Terminator Cycle Sequencing kits (USB Corporation, Cleveland, Ohio) according to the manufacturer's instructions using the L-strand primer. Autoradiograms were scored by hand, and sequences from the three fragments were combined for each individual.

To explore the substitutional relationships among haplotypes, a minimum spanning tree was generated using TCS (version 1.13, Clement et al. 2000); ambiguous loops were resolved by minimizing the number of inferred haplotypes, the total tree length, or both. Haplotypic diversity (H_S; Nei 1987) and nucleotide diversity (π Nei and Tajima 1983) were estimated using ARLEQUIN (version 2.0; Schneider et al. 2000). The assumptions of most subsequent analyses that variation is neutral to selection and that populations are at equilibrium between mutation and genetic drift were tested by using ARLEQUIN to derive mismatch distributions (Rogers and Harpending 1992) and Tajima's *D* (Tajima 1989).

STATISTICAL ANALYSES

The extent of population differentiation and gene flow was assessed at two levels: (1) within British Columbia, and (2) between British Columbia and Asia. We estimated γ (the probability that any two individuals chosen at random from different populations will have different haplotypes; Lynch and Baker 1994) using RAND-G_{ST} (A. Lynch, University of Toronto, unpubl. program), and Φ_{ST} (the proportion of sequence variation due to differences among populations; Excoffier et al. 1992) and δ (Nei's [1987] genetic distance between populations) using ARLEQUIN. All indices were tested for statistical significance using 1000 randomizations of the data. Gene flow ($N_f m$, where N_f is effective female population size and m is migration rate) was calculated using MIGRATE (version 0.9.10; Beerli 2000), which uses a maximum likelihood approach based on coalescent theory (Beerli and Felsenstein 1999). Estimators of migration rates based on coalescent theory can accommodate possible asymmetries in migration rates and differences in population sizes, so are thought to be more accurate than traditional estimators (Beerli 1998, Beerli and Felsenstein 1999). Most of the default settings for MIGRATE were used, but the number of trees sampled was increased to 10 000 for the short chains and 100 000 for the long chains to avoid local maxima on the likelihood surface. A trial run was used to generate the input parameters for a second run (P. Beerli, pers. comm.); results of the second run were then reported. Changes to the random number seed, and inclusion of corrections for rate heterogeneity, did not alter the results appreciably.

Most methods for estimating gene flow assume that populations are in equilibrium between mutation, genetic drift, and dispersal, which may not be true for species in recently glaciated areas. Nested clade analysis, which does not make this assumption, therefore was conducted following the method of Templeton (1998). The minimum spanning tree was nested following the rules of Templeton et al. (1987), and the presence of clades with significantly small or significantly large geographic distributions was examined by analysis of variance using GEODIS (Posada et al. 2000) with 10 000 randomizations to assess confidence. Means are presented ± SE.

RESULTS

PATTERNS OF SEQUENCE VARIATION

Several lines of evidence indicate that the DNA fragments amplified in the present study (GenBank accession number AB070632) represent the intended mitochondrial targets rather than nuclear homologues. Cytochrome *b* sequences matched previously published sequences for Ancient Murrelets (GenBank accession number U37303; Friesen, Baker and Piatt 1996), and none of the four variable sites involved insertions, deletions, transversions, or amino acid substitutions. The control region was similar in size (~1050 bp) to those of other species of birds, had a similar base composition (27% A, 26% C, 15% G, and 32% T on the light strand), and contained several conserved structural features, including the F, D, and C boxes, CSB-1, and a 7-bp tandem repeat at the 3′ end (Berg et al. 1995, Baker and Marshall 1997, Kidd and Friesen 1998; contact VLF for alignments).

A total of 20 mtDNA haplotypes, defined by 20 variable sites and one 9-bp insertion/deletion, were found among the 58 samples (Table 1). The mean transition:transversion ratio was 8:1. Se-

TABLE 1. Sequence differences among 20 mtDNA haplotypes in 58 Ancient Murrelets. Numbers (read vertically) refer to position relative to the 3′ end of the relevant light strand primer (see Methods). Dots indicate identity with haplotype A. ? = unresolved base.

	Position			
	Control Region			
	5′ end		3′ end	Cyt*b*
Haplotype	11111122 256767789902 190090696983	23 35 41	11 926 904	111 9467 6427
A	CGTTCATATATC	CG	GCC	AAAC
B	TACCTGC..GC.	.A	...	....
C	TACC..C.....	.A	...	....
D	TACCTGC...C.	.A	...	....
E	T..CT.....C.	.A	...	....
F	TACC..C...C.	..	...	....
G	..CCT..G..C.	T.	...	....
H	T.CC......C.	CCTGAATCC.A	...	....
J	.ACC..C.....	.A	...	....
K	..CCT...C.C.	.A	...	....
L	..CC....C.C.	.A	...	....
M	.ACCTGC.....	.A	..T	....
N	.ACC..C..GC.	?A	...	....
O	TACCTGC..GC.	.A	T..	....
P	TACCTGC..GC.	.A	.T.	....
Q	TACCTGC..GC.	.A	...	.C..
R	TACC..C.....	.A	...	..G.
T	T..CT.....C.	.A	...	G...
U	T..CT.....C.	.A	A..	....
V	TACCTGC..GC.	.A	...	...T

quence divergence among haplotypes averaged 0.47 ± 0.14%, and ranged from 0.09% to 0.97% (counting the 9-bp insertion/deletion as a single mutation). Fourteen of the variable sites and the insertion occurred in a hypervariable region at the 5′ end of the control region, as in other species of birds (Baker and Marshall 1997, Kidd and Friesen 1998). The minimum spanning tree involved a series of ''hubs'' from which other haplotypes radiated, and included several long branches (Fig. 1).

Most haplotypes occurred in only one or two individuals each; only five had frequencies greater than 5% (Table 2). Nucleotide diversity averaged 0.41 ± 0.23%, and was similar among collection sites (Table 2). The mismatch distribution was distinctly ragged (Fig. 2), and differed significantly from the distribution expected under a sudden population expansion (sum of squares = 0.018, $P > 0.1$). Tajima's D (0.082) did not differ significantly from zero ($P > 0.6$).

POPULATION DIFFERENTIATION AND GENE FLOW

Although sample sizes were small, little evidence was found for genetic differentiation among murrelets from George and East Limestone Islands. Two of eight haplotypes found in British Columbian samples were shared between islands, and only one of six private haplotypes occurred at high frequency (Table 2). None of the indices of population structure differed significantly from zero ($\gamma = 0.34$, $\Phi_{ST} = 0.00$, $\delta = 0.015$; all $P > 0.4$). Estimates of gene flow derived by MIGRATE were high: 11 females per generation from East Limestone Island to George Island (99% CI = 6–18 females per generation), and 8 females per generation from George Island to East Limestone Island (99% CI = 4–13 females per generation).

Since little evidence was found for differentiation of mtDNA among murrelets from George and East Limestone Islands, samples from these sites were pooled for comparison with Asian samples. In this second analysis, 15 of 20 haplotypes occurred at low frequency (in only one or two individuals each) in either British Columbia or Asia, one haplotype (E) occurred at high frequency in Asia but was absent from British Columbia, and four haplotypes were found in both Asia and British Columbia (Table 2). All

TABLE 2. Frequencies of mtDNA haplotypes, and nucleotide diversity indices (π) for Ancient Murrelets from sites in British Columbia and Asia.

Sampling Site	Haplotype																								π
	A	B	C	D	E	F	G	H	J	K	L	M	N	O	P	Q	R	T	U	V	Total	
Within British Columbia																									
George I.	3	4	1	—	—	—	—	—	—	—	—	—	2	1	1	—	—	—	—	—	12	0.44
East Limestone I.	2	—	2	2	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	7	0.45
Between British Columbia and Asia																									
British Columbia	5	4	3	2	—	—	—	—	—	—	—	—	2	1	1	1	—	—	—	—	19	0.44
Asia	3	13	4	1	5	2	1	1	1	2	1	1	—	—	—	—	1	1	1	1	39	0.40
Total	8	17	7	3	5	2	1	1	1	2	1	1	2	1	1	1	1	1	1	1	58	0.41

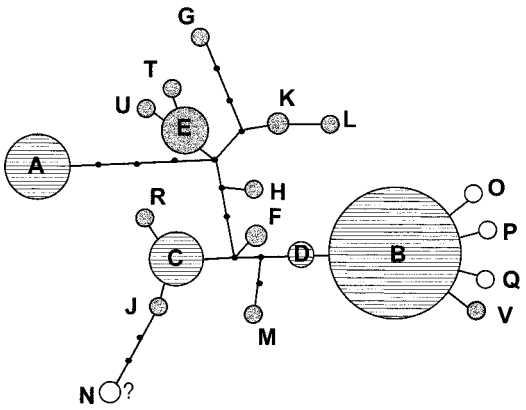

FIGURE 1. Minimum spanning tree for mtDNA haplotypes of Ancient Murrelets. Sizes of circles are proportional to frequencies of haplotypes. Gray circles = haplotypes found only in Asia; white circles = haplotypes found only in British Columbia; hatched circles = haplotypes found in both areas; black dots = missing haplotypes. Three alternative connections (between haplotypes H and L, A and J, and between haplotypes M and J) did not change the final results of the nested clade analysis. N has a question mark because its placement depends on the identity of the unknown base pair (Table 1).

indices of population genetic differentiation were low and none differed significantly from zero ($\gamma = 0.17$, $\Phi_{ST} = 0.02$, $\delta = 0.00$; all $P > 0.3$). Results from MIGRATE suggested that gene flow is high: 103 females per generation from British Columbia to Asia (99% CI = 85–125 females per generation), and 22 females per generation from Asia to British Columbia (99% CI = 19–25 females per generation).

Nested clade analysis indicated that the geographic range of haplotype A (which was found

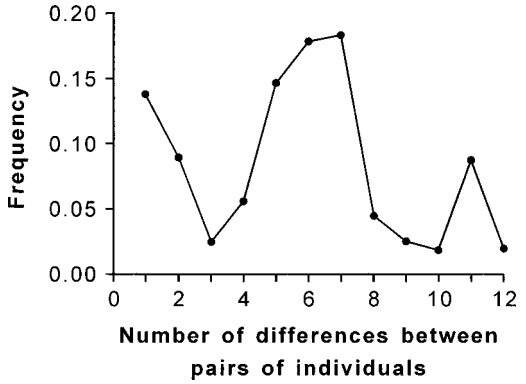

FIGURE 2. Mismatch distribution for mtDNA variation in Ancient Murrelets.

everywhere but occurred within a clade that otherwise was found only in Asia) was significantly larger than expected ($P = 0.002$), and the distribution of the tip clade containing haplotypes E, T, and U (Fig. 1) was significantly smaller than expected ($P < 0.05$). These results are suggestive of a contiguous range expansion (Templeton 1998). Otherwise, none of the clades had geographic distributions either significantly larger or significantly smaller than expected (all $P > 0.1$), providing no evidence of either historical fragmentation or restricted gene flow between any of the sampling sites.

DISCUSSION

DEMOGRAPHIC HISTORY

The present data suggest that Ancient Murrelets are in equilibrium between mutation and genetic drift: Tajima's *D* did not differ significantly from zero, the mismatch distribution was ragged (Fig. 2), and the minimum spanning tree contained many hubs and long branches (Tajima 1989, Slatkin and Hudson 1991, Rogers and Harpending 1992, Rogers 1995). Thus, the genetically effective population size appears to be stable. This finding contrasts with results for other high latitude seabirds, which appear to have increased in numbers since recession of the Pleistocene glaciers (e.g., Thick-billed Murres [*Uria lomvia*], Birt-Friesen et al. 1992), but is similar to results for Red-legged Kittiwakes (*Rissa brevirostris*), which breed in the Bering Sea (Patirana et al. 2002).

POPULATION DIFFERENTIATION AND GENE FLOW

No evidence was found either for differentiation of mtDNA or for restrictions in female-mediated gene flow between Ancient Murrelets breeding on George vs. East Limestone Islands. Although this finding should be treated with caution given the small numbers of samples and loci analyzed, it is consistent with evidence of high intercolony dispersal from banding studies (Gaston 1990, Gaston and Adkins 1998).

Genetic differentiation also appears to be low between Asian and British Columbian Ancient Murrelets, and female-mediated gene flow appears to be high. This finding contrasts with our expectation. However, genetic homogeneity may be due to either historical association or restricted present-day gene flow, depending on whether a species is in equilibrium between mutation, genetic drift, and dispersal. Nested clade analysis, which does not assume equilibrium, suggests that Ancient Murrelets have undergone a range expansion, and that estimates of gene flow may be influenced by historical association. Asian haplotypes occur throughout the gene tree (Fig. 1) in both terminal (tip) and internal (hub) positions, whereas British Columbian haplotypes occur mostly in terminal or subterminal positions, suggesting that contemporary Ancient Murrelets may have originated in Asia and expanded their range to British Columbia (although this expansion was probably not accompanied by a population increase). Several other studies also found little or no genetic differentiation within geographically widespread species of birds, including Thick-billed Murres (Birt-Friesen et al. 1992), Common Murres (*Uria aalge*; Friesen, Montevecchi, et al. 1996), Sooty Terns (*Sterna fuscata*; Avise et al. 2000), Snow Geese (*Chen caerulescens*; Avise et al. 1992), Knots (*Calidris canutus*; Baker et al. 1994), and Red-winged Blackbirds (*Agelaius phoeniceus*; Ball et al. 1988). In most of these studies, lack of population genetic differentiation also was attributed to recent expansion from a single refugium from the Pleistocene glaciations. However, the possibility of a range expansion in Ancient Murrelets needs to be confirmed by analysis of nuclear loci and additional samples from British Columbia, Alaska, and China.

The absence of differentiation in mtDNA among Ancient Murrelets either within British Columbia or between British Columbia and Asia suggests that Ancient Murrelets across the North Pacific may represent a single management unit (Moritz 1994). If this is true, then loss of a local population will not have a large effect on the species' genetic resources; however, additional analyses are needed before firm conservation recommendations can be made.

ACKNOWLEDGMENTS

We thank A. J. Gaston for suggesting this study, and C. French, A. J. Gaston, M. Lemon, J. Smith and the Laskeek Bay Conservation Society for collecting samples from George and East Limestone Islands. The Kamchatka Federal Department for Protection and Reproduction of Fish Resources and Fisheries Regulations provided logistical support for collecting the samples in the Russian Far East. A. Patirana, L. Veit, E. Croteau, G. Ibarguchi, G. Gissing, and R. Kristensen provided help with laboratory work. P. Boag provided helpful comments on earlier versions of the manuscript. Financial support was provided by the Summer

Work Experience Program (Queen's University) and an NSERC Research Grant (to VLF).

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