

Population genetic structure and conservation of marbled murrelets (*Brachyramphus marmoratus*)

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Abstract

Marbled murrelets (*Brachyramphus marmoratus*) are coastal seabirds that nest from California to the Aleutian Islands. They are declining and considered threatened in several regions. We compared variation in the mitochondrial control region, four nuclear introns and three microsatellite loci among 194 murrelets from throughout their range except Washington and Oregon. Significant population genetic structure was found: nine private control region haplotypes and three private intron alleles occurred at high frequency in the Aleutians and California; global estimates of F_{ST} or Φ_{ST} and most pairwise estimates involving the Aleutians and/or California were significant; and marked isolation-by-distance was found. Given the available samples, murrelets appear to comprise five genetic management units: (1) western Aleutian Islands, (2) central Aleutian Islands, (3) mainland Alaska and British Columbia, (4) northern California, and (5) central California.

Introduction

Marbled murrelets (*Brachyramphus marmoratus*; Charadriiformes: Alcidae) are coastal seabirds that nest primarily in large trees in old growth forest from central California to the Aleutians (McShane et al. 2004), and are highly vulnerable to deforestation, forest fragmentation, marine oil pollution and gill netting. They are declining in most of their range (McShane et al. 2004), and are considered threatened in California, Oregon, Washington and British Columbia (U.S. Fish and Wildlife Service 1992; COSEWIC 2003). Although a recovery plan was developed in 1997 (U.S. Fish and Wildlife

Service 1997), little was known about genetic relationships among local populations. Subsequently, Congdon et al. (2000) reported significant population structure in nuclear introns among murrelets from the Aleutians to British Columbia, with the greatest differentiation involving the Aleutians. However, no analyses involving either hypervariable markers or California populations have been published. Given that California represents the southern periphery of the species' range, that populations on the northwestern periphery differ genetically from central populations, and that feeding and nesting conditions differ between peripheral and central regions, California

murrelets may differ genetically from those elsewhere. Furthermore, a significant disjunction in suitable nesting habitat exists between northern and central California (Miller et al. 2002), potentially isolating these populations. We therefore compared variation in the mitochondrial control region, microsatellites and introns among murrelets from throughout their range to determine the extent to which local populations differ genetically and should be managed separately.

Methods

Population screening

Sequence variation in nine nuclear introns among 120 marbled murrelets from the Aleutians to British Columbia was described previously (Congdon et al. 2000). Tissue samples were obtained from an additional 74 marbled murrelets, including 36 from northern California (Humboldt County), 30 from central California (San Mateo County) and eight from Alaska (Figure 1). DNA was extracted using a standard protease-K phenol/chloroform technique (Friesen et al. 1997).

Sequence variation in a 547 base pair (bp) fragment of mitochondrial DNA (mtDNA), including the gene for tRNA^{glu}, all of Domain I (329 bp) of the control region and 218 bp of

Domain II, was analyzed in 146 murrelets from throughout the range. DNA was amplified using PCR primers BmaH600 (5'-CAAAAGTGCCAA AAAGGTCGGATGTCG-3') and ND6 (5'-CCT AGAAAAAGCACAAAATAAGTCAT-3'; Kidd and Friesen 1998a) under standard conditions (Veit et al. 2005) with annealing at 50 °C. Variation was screened initially using single-stranded conformational polymorphisms (SSCPs; Hayashi 1991; Friesen et al. 1997), and individuals were assigned tentative haplotypes. Two or more representatives of each haplotype (one for each unique haplotype) plus all ambiguous samples were re-amplified and gel-purified using Gel Extraction Spin Columns (Qiagen), and sequenced directly using either ThermosequenaseTM cycle sequencing kits (Amersham Pharmacia) or an ABI PrismTM 373 Automated Sequencer (Mobix Labs, McMaster University).

Sequence variation in four nuclear introns (α -Enolase, Gpd, Ldh and RP40; Congdon et al. 2000) was screened in the 74 new samples using a combination of SSCP and direct sequencing (Friesen et al. 1997, 1999; Congdon et al. 2000), and combined with data from Congdon et al. (2000). All 194 samples were assayed for length variation in three microsatellite loci (Uaa5-8, Ibarguchi et al. 2000; Bma10-18 [forward: 5'-GGTAGGAGCGGAGTAGGAGG-3'; reverse: 5'-GCAAA ATAAGGGTGAAGGCA-3'] and Cco5-21 [forward:

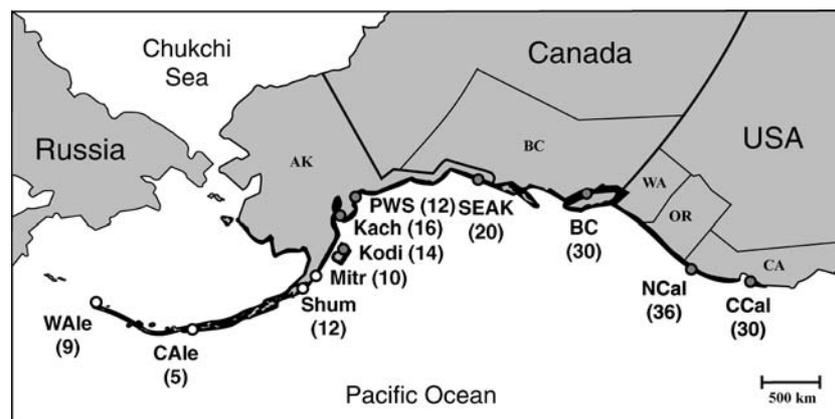


Figure 1. Breeding distribution of marbled murrelets (heavy black lines; from Udvardy 1963), and sampling sites (circles) and numbers. Grey circles represent sites where murrelets nest in trees; white circles represent sites where murrelets nest on the ground. WAle = western Aleutian Islands (Attu Island); CAle = central Aleutian Islands (Adak Island); EAle = eastern Aleutian Islands (Dutch Harbor); Shum = Shumigan Islands (including Belkofski Bay and Koniuji Strait); Mitr = Mitrofanina Bay; Kach = Kodiak Island; PWS = Prince William Sound (Unakwik Fjord); SEAK = Southeastern Alaska (Alexander Archipelago); BC = British Columbia (Desolation Sound); NCal = northern California (Humboldt County); CCal = central California (Santa Cruz).

5'-TCAAGATGATGAAGACCCTAAT-3'; reverse: 5'-AGAGTTGCACAGGTTAAATACC-3'], V.L.F. unpubl.) using standard protocols (Ibarguchi et al. 2000) with annealing at 50, 60 and 52 °C, respectively.

Data analyses

Haplotypic and nucleotide (Nei 1987) diversities (for control regions) and expected heterozygosities (for nuclear loci) were calculated using Arlequin (version 2.0, Schneider et al. 2000). Control region variation was tested for deviations from neutrality using Ewens-Watterson's and Chakraborty's tests (Ewens 1972; Watterson 1978; Chakraborty 1990); for nuclear loci, consistency with Hardy-Weinberg equilibrium expectations was tested using an exact test (Guo and Thomson 1992), and linkage equilibrium was tested using a likelihood ratio test (Slatkin and Excoffier 1996) using Arlequin.

ARLEQUIN was used to estimate Wright's (1931) F_{ST} both for the entire sample and for population

pairs using AMOVA (Excoffier et al. 1992). Hierarchical F -statistics were then calculated to find the population grouping that maximized F_{CT} and minimized F_{SC} (Stanley et al. 1992). For control region sequences, Φ -statistics were calculated using Kimura's 2-parameter mutation model (Kimura 1980). To test for isolation by distance, the shortest geographic distance between populations was calculated using Earth (Byers 1999; Table 1), and Slatkin's linearized estimates of F_{ST} or Φ_{ST} for population pairs were tested for correlation with distance using Mantel's tests (Smouse et al. 1986) in Arlequin. Corrected percent sequence divergence between populations (δ ; Wilson et al. 1985) also was calculated for control region data. For all analyses, statistical significance was tested by randomization using 10,000 permutations of the data, and sequential Bonferroni corrections were applied (Rice 1989).

To test for phylogeographic structure, relationships among control region haplotypes were re-constructed using statistical parsimony

Table 1. Pairwise estimates of geographic distance (km, upper number above diagonal), δ (for control regions, lower number above diagonal), Φ_{ST} (for control regions, upper number below diagonal), F_{ST} (for nuclear loci, lower number below diagonal), and proportion of birds assigned to Population 1 by Structure (diagonal) for murrelet populations

	Wale	CAle	Shum	Mitr	Kodi	Kach	PWS	SEAK	BC	NCal	CCal
Wale	0.04	755	1730	1860	2250	2330	2570	3210	4320	4840	5280
		–	0.73	–	0.94	–	–	0.58	–	0.61	1.11
CAle	–	0.06	1080	1220	1680	1790	2040	2630	3650	4110	4550
	0.03	–	–	–	–	–	–	–	–	–	–
Shum	0.17	–	0.36	140	650	780	1030	1560	2590	3130	3600
	0.13	0.15	–	–	0.27	–	–	0.03	–	0.07	0.46
Mitr	–	–	–	0.46	520	660	900	1420	2460	3010	3490
	0.13	0.16	0.00	–	–	–	–	–	–	–	–
Kodi	0.19	–	0.06	–	0.27	150	380	960	2130	2800	3300
	0.13	0.14	0.00	0.00	–	–	–	0.07	–	0.12	0.45
Kach	–	–	–	–	–	0.31	240	870	2100	2810	3310
	0.17	0.17	0.02	0.00	0.01	–	–	–	–	–	–
PWS	–	–	–	–	–	–	0.31	660	1930	2690	3200
	0.17	0.17	0.02	0.00	0.01	–0.04	–	–	–	–	–
SEAK	0.13	–	0.01	–	0.02	–	–	0.33	1300	2120	2630
	0.17	0.18	0.01	0.00	0.00	–0.01	–0.01	–	–	–0.05	0.32
BC	–	–	–	–	–	–	–	–	0.26	910	1400
	0.15	0.21	0.03	0.00	0.01	0.01	0.01	0.00	–	–	–
NCal	0.18	–	0.02	–	0.03	–	–	0.00	–	0.74	510
	0.17	–	0.06	–	0.04	0.02	0.02	0.03	0.04	–	0.05
CCal	0.18	–	0.08	–	0.08	–	–	0.05	–	0.07	0.29
	0.22	0.25	0.06	0.04	0.06	0.05	0.05	0.06	0.06	0.03	–

Estimates in bold are significant at $\alpha=0.05$ after sequential Bonferroni corrections. Population abbreviations as in Figure 1. Samples for control regions are pooled as described in text.

(Templeton et al. 1992) with the program TCS (version 1.13; Clement et al. 2000). Ambiguous connections were resolved according to Crandall and Templeton (1993), and the tree was nested following the rules of Templeton et al. (1987). Clades with non-random distributions were identified using GeoDis (Posada et al. 2000) with 10,000 randomizations of the data.

Variation in the seven nuclear loci also was analyzed using Structure (Pritchard et al. 2000). The program was run under the no-admixture model with a burn-in of 10,000 iterations, and 100,000 replications after the burn-in; sampling location was not used as *a priori* information, and α was allowed to vary. Each value of k (number of populations) between 1 and 12 was run 10 times, and significance was calculated from the posterior probabilities (Pritchard and Wen 2003).

Results

Control regions

Seventy-six control region haplotypes were found among 146 murrelets (Genbank Accession Numbers AY839310-AY839336). Whereas nuclear copies of mitochondrial genes have been reported in other seabirds, murrelet sequences did not differ from the patterns expected for true mtDNA (Quinn and Wilson 1993; Baker and Marshall 1997; Kidd and Friesen 1998a): the tRNA^{glu} sequence could be folded into a clover-leaf structure appropriate for a functional tRNA for glutamic acid (Desjardins and Morais 1990); sequences of the F, D and C boxes differed little from other alcids (pigeon guillemot *Cephus columba*, Kidd and Friesen 1998a; common murre *Uria aalge*, V.L.F. unpubl. data); a poly-C repeat occurred at the 5' end of the control region, and a poly-T repeat occurred in Domain II; base composition was biased against Gs (25% A, 29% C, 16% G, 29% T); sequences were highly variable, with the greatest variability in Domain I (83% [54] of 65 variable sites); and most (50 of 65) variable sites involved transitions. Haplotypes differed by one to 15 substitutions (0.2–2.7%), with no insertions/deletions. With the exception of Prince William Sound, haplotypic and nucleotide diversities were high (Table S1), and averaged 0.99 and 0.81%

respectively. No significant deviations from neutrality were found (all $P > 0.25$).

Control region haplotype 05 was found in seven populations, and haplotype 02 was found in five. All other haplotypes occurred in only one or two populations each (usually adjacent), at frequencies between 3.3% and 67% (Table S1); notably, the western Aleutians and the two California populations each had one or more private haplotypes that occurred in >10% of birds from each site. Because sample sizes for some populations were small, samples from British Columbia were excluded and Alaska samples were pooled into four regions for AMOVA: Aleutian Islands, Alaska Peninsula (Shumigan Islands and Mitrofan Bay), Gulf of Alaska (Kodiak Island, Kachemak Bay and Prince William Sound), and Southeastern Alaska. AMOVA indicated significant population structure (global $\Phi_{ST} = 0.084$, $P < 0.0001$); most pairwise estimates of Φ_{ST} and δ involving the Aleutians, and several estimates involving northern and central California were significant (Table 1). In hierarchical AMOVAs, variation was explained best when populations were placed in three groups: (1) Aleutians, (2) Alaska Peninsula to northern California, and (3) central California, although Φ_{CT} did not quite attain statistical significance and significant variation remained within groups ($\Phi_{CT} = 0.10$, $P = 0.06$; $\Phi_{SC} = 0.023$, $P = 0.018$). Estimates of Φ_{ST} tended to increase with geographic distance between populations but Mantel's test was not significant ($r = 0.27$, $P = 0.09$).

Some phylogeographic structure was evident, with haplotypes from the same or adjacent regions (especially California and the Aleutian Islands) tending to cluster on the gene tree (Figure 2, Table S1). Specifically, clades 2–1, 2–3, 2–5, 2–8, 2–10 and 3–2 had significantly small clade distances, and clades 2–2, 2–7, 2–9 and 3–1 had significantly large nested clade distances (all $P < 0.02$).

Nuclear loci

The number of alleles per locus ranged from five to 19 for the introns, and from six to 20 for the microsatellites (Table S2). Bma10-18 contained a complex repeat, and so probably does not follow a simple stepwise mutation model; microsatellite data were therefore combined with introns and analyzed assuming an infinite alleles model. (Analyses of the

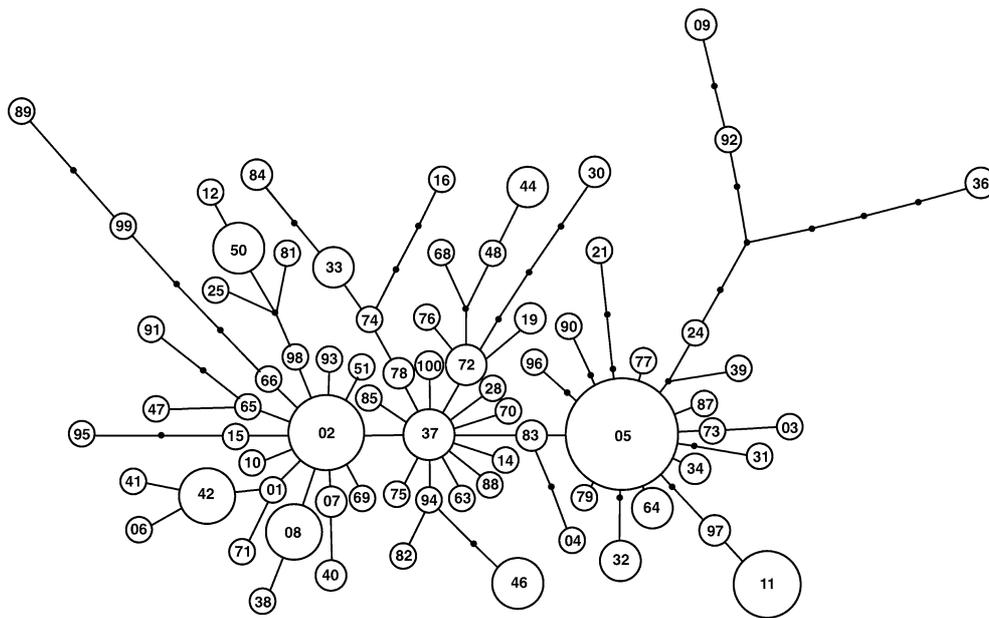


Figure 2. Statistical parsimony tree for mitochondrial control region sequences of 146 marbled murrelets. Black dots represent missing haplotypes (haplotypes that either were not sampled or are extinct). All internode branches represent a single mutational step. Haplotypes are identified to region in Table S1.

other two microsatellite loci assuming a stepwise model produced similar results as for the combined loci [see below], although resolution was poorer [results not shown]. The *Ldh* intron had a significant heterozygote excess in northern California and a heterozygote deficit in central California (both $P < 0.001$), and *Uaa5-8* exhibited a slight heterozygote excess for the total sample ($P = 0.03$); otherwise, no deviations from Hardy–Weinberg or linkage equilibrium were found (all $P > 0.05$). Heterozygosities were high (range of means per locus = 0.46 to 0.86; Table S2), and did not differ among populations (ANOVA, $P > 0.05$).

Most intron alleles occurred in all populations, but 17 occurred in only one or two neighbouring populations (Table S2). Notably, the two California populations together possessed 11 private alleles, with frequencies $< 27\%$. Private microsatellite alleles were always at low frequency (Table S2). AMOVA indicated significant population structure (global $F_{ST} = 0.052$, $P < 0.0001$), and pairwise F_{ST} s for most comparisons involving the Aleutian and/or California populations were statistically significant (Table 1). F_{CT} was highest when populations were placed in five groups: (1) western Aleutians, (2) central Aleutians, (3) mainland Alaska and BC, (4) northern California,

and (5) central California ($F_{CT} = 0.069$, $P = 0.002$; $F_{SC} = 0.004$, $P = 0.30$). Mantel's test was highly significant ($r = 0.60$, $P = 0.004$).

Results from Structure provided strong support for two genetic populations ($P [k = 2] = 0.998$). The probability for $k = 1$ (i.e. no structure) was very low ($P < 10^{-13}$). Genetic populations did not correspond exactly to sampling populations, but most (82%) birds from California were assigned to Population 1 and most (95%) birds from the Aleutians were assigned to Population 2 (Table 1).

Discussion

Results of the present study indicate that significant population genetic structure exists in marbled murrelets:

- (1) The Aleutian and California populations each had one or more private control region haplotypes that occurred at high frequency, and the two California populations together had private intron alleles, with three at high frequency.
- (2) Global estimates of F_{ST} and Φ_{ST} were significant, as were many pairwise estimates involving the Aleutian or California populations.

- (3) Hierarchical AMOVAs indicated that 7–10% of variation represents differences among population groups.
- (4) Haplotypes tended to cluster on the control region gene tree.
- (5) Significant isolation-by-distance was found for the nuclear markers.
- (6) Results from Structure provided strong support for two genetic populations, and clearly rejected a single population.

These results support previous studies, which reported significant population genetic structure in murrelets. For example, estimates of F_{ST} and Φ_{CT} based on allozymes and introns respectively were both 0.09 (Friesen et al. 1996a; Congdon et al. 2000). This level of structure is intermediate to values typical for seabirds: e.g. murrelets (*Uria* spp.) exhibit virtually no population genetic structure (Friesen et al. 1996b; Moum and Arnason 2001; V.L.F. unpubl. data), whereas guillemots (*Cephus* spp.) show very strong structure (Kidd and Friesen 1998b, V.L.F. unpubl. data). The genetic affinities of murrelets breeding in Oregon and Washington still need to be explored. Murrelets in these states may group with populations either in British Columbia or California, or may be unique to themselves.

Hierarchical AMOVAs suggested that murrelet populations sampled in the present study constitute five groups: (1) western Aleutians, (2) central Aleutians, (3) mainland Alaska and British Columbia, (4) northern California, and (5) central California. These populations are probably demographically independent and non-exchangeable (Crandall et al. 2000; Moritz 2002). Thus for conservation purposes, given the available samples, murrelets appear to constitute five genetic management units (*sensu* Moritz 1994). Genetic divergence of Aleutian and California populations is consistent with their low densities (McShane et al. 2004), fragmented habitat (Nelson 1997), and peripheral locations. Divergence of central and northern California populations is also consistent with movements of radio-marked murrelets (both nesting and non-nesting) from Redwood Creek, northern California: these murrelets only moved an average 22.3 km north of Redwood Creek ($n=1780$ detections) or 16.7 km south of Redwood Creek ($n=1840$ detections), and were rarely detected over 100 km away (Hébert and Golightly, unpubl. data). Peripheral populations

may be especially vulnerable to extinction due to their generally small size, relative isolation, and often marginal habitat (reviewed in Lesica and Allendorf 1995; Vucetich and Waite 2003). Given that murrelets in California are declining (McShane et al. 2004), and that populations in the Aleutians and California are genetically differentiated from those elsewhere, the Aleutian and California populations especially need protection.

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