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Rapid divergence and postglacial colonization in western North American Steller's jays (*Cyanocitta stelleri*)

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Abstract

Post-Pleistocene avian colonization of deglaciated North America occurred from multiple refugia, including a coastal refugium in the northwest. The location of a Pacific Coastal refugium is controversial; however, multiple lines of evidence suggest that it was located near the Queen Charlotte Islands (also known as Haida Gwaii). The Queen Charlotte Islands contain a disproportionately large number of endemic plants and animals including the Steller's jay *Cyanocitta stelleri carlottae*. Using five highly variable microsatellite markers, we studied population structure among eight populations of Steller's jay (*N* = 150) from geographical areas representing three subspecies in western North America: *C. s. carlottae*, *C. s. stelleri* and *C. s. annectens*. Microsatellite analyses revealed genetic differentiation between each of the three subspecies, although more extensive sampling of additional *C. s. annectens* populations is needed to clarify the level of subspecies differentiation. High levels of population structure were found among *C. s. stelleri* populations with significant differences in all but two pairwise comparisons. A significant isolation by distance pattern was observed amongst populations in the Pacific Northwest and Alaska. In the *C. s. carlottae* population, there was evidence of reduced genetic variation, higher number of private alleles than northern *C. s. stelleri* populations and higher levels of divergence between Queen Charlotte Island and other populations. We were unable to reject the hypothesis that the Queen Charlotte Islands served as a refugium during the Pleistocene. Steller's jay may have colonized the Queen Charlotte Islands near the end of the last glaciation or persisted throughout the Pleistocene, and this subspecies may thus represent a glacial relic. The larger number of private alleles, despite reduced genetic variation, morphological distinctiveness and high divergence from other populations suggests that the Queen Charlotte Island colonization pre-dates that of the mainland. Furthermore, our results show rapid divergence in Steller's jay populations on the mainland following the retreat of the ice sheets.

Keywords: *Cyanocitta stelleri*, historical biogeography, microsatellite, Pleistocene glaciation, Queen Charlotte Islands, refugia

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Introduction

The Pleistocene glaciations dramatically altered the landscape of temperate North America and profoundly influenced the distribution of many plants and animals. The Pleistocene was characterized by a series of glaciations, each cycle lasting ~100 000 years including a 10 000-year interglacial period (Pielou 1991). At its maximum extent during the Wisconsin, the Cordilleran ice sheet covered most of Alaska and British Columbia and extended into parts of northern Washington and Idaho. In the eastern North Pacific, the last glacial maximum occurred 21–18 kya (thousand years ago), compared to 14 kya in southern British Columbia (Clague 1989; Mandryk *et al.* 2001; Clague & James 2002). These glaciers retreated rapidly from coastal and interior areas, and forests were present on Vancouver Island 13.5 kya and in southeast Alaska 10 kya

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(Mann & Hamilton 1995). The dynamic interaction between these ice sheets and the affected landscape created an environment that caused genetic differentiation and speciation among multiple organismal lineages as a result of habitat fragmentation and changing environments (Soltis *et al.* 1997; Avise & Walker 1998; Weir & Schluter 2004).

Several studies have examined the role of the Pleistocene glaciations in speciation and contemporary population structure of North American songbirds (Zink 1996; Avise & Walker 1998; Milot *et al.* 2000; Ruegg & Smith 2002; Clegg *et al.* 2003; Johnson & Cicero 2004; Lovette *et al.* 2004; Weir & Schluter 2004; Lovette 2005). Most molecular studies found two main divergent lineages corresponding to lineages west and east of the Rocky Mountains (Milot *et al.* 2000; Ruegg & Smith 2002; Clegg *et al.* 2003; Lovette *et al.* 2004). However, few studies have examined fine-scale genetic structure in northwestern North America (Zink & Dittmann 1993; Pruett & Winker 2005). The origin of the main lineages known thus far is believed to be postglacial expansion from multiple refugia: large refugia south of the Laurentide ice sheet in the east and Cordilleran ice sheet in the west, and a smaller coastal refugium along the Pacific coast.

In addition to the large, ice-free areas south of the glaciers, smaller, northerly refugia were present both on nunataks high in the mountains and along the Pacific coast (Warner *et al.* 1982; Heusser 1989; Pielou 1991). Although the existence of a coastal refugium is generally accepted, its location has been controversial (see Byun *et al.* 1999; Demboski *et al.* 1999). Several lines of geological and biological evidence show that one such refugium may have existed in the vicinity of the Queen Charlotte Islands (also known as Haida Gwaii) off the west coast of British Columbia (Warner *et al.* 1982; Mandryk *et al.* 2001). Non-arboreal vegetation was present 16–12 kya on a large sea cliff in Hecate Strait (Clague 1989; Mandryk *et al.* 2001), and subalpine vegetation was present on the islands 45 kya (Mathewes 1989). The glacial history of the Queen Charlotte Islands is distinct from that of the adjacent mainland, as the Cordilleran ice sheet did not extend onto the Queen Charlotte Islands (Barrie & Conway 1999; Clague & James 2002). The Wisconsin glaciation on the Queen Charlotte Islands was characterized by two major glaciations > 52 kya and 27.5–16 kya. This last glacial episode reached its maximum extent and ended earlier than glaciation in southern British Columbia (Mann & Hamilton 1995; Clague & James 2002). In addition to the geological evidence for a refugium, the Queen Charlotte Islands are home to a disproportionately large number of endemic flora and fauna, including bryophytes, lichen, insects, fish, birds and mammals (McTaggart Cowan 1989; Scudder 1989). One such endemic is the Steller's jay subspecies, *Cyanocitta stelleri carlottae*.

The Steller's jay is an ideal study species for elucidating patterns of regional refugia and the subsequent colonization of previously glaciated areas. Within northern North America there are three subspecies with subtle plumage differences (Fisher 1902; Stevenson 1934; Wiebe 1995). The Steller's jay inhabits a wide range of habitats, including coniferous and mixed coniferous–deciduous forests as well as highly fragmented landscapes (Marzluff *et al.* 2004). Steller's jay is a year-round resident, with some altitudinal migration at higher elevations (Fisher 1902; Stevenson 1934; Campbell *et al.* 1997), and recoveries of banded birds show that it is more philopatric than any other New World corvid at these latitudes (Brewer *et al.* 2000). Although irruptive dispersals of > 50 km occur frequently (Brewer *et al.* 2000), the average breeding dispersal distance is < 4 km (Bird Banding Laboratory, Marzluff *et al.* 2004). These ecological characteristics suggest that Steller's jay could have colonized northern parts of its range shortly after the ice sheet retreated and during the early stages of succession.

The colonization of northwestern North America by Steller's jay could have occurred from a single southern refugium, either once or more than once. If the latter, then the initial expansion could have colonized the Queen Charlotte Islands, which were ice free earlier than the mainland (Barrie & Conway 1999), followed by a gradual expansion eastwards and northwards. Alternatively, a population might have persisted in the Queen Charlotte refugium, in which case that population could have contributed to the colonization of the mainland, along with birds expanding from the southern refugium.

In this study, we examine populations of Steller's jay from a wide portion of their northern range using microsatellite markers. Microsatellites are better able to detect contemporary patterns than other markers because of their high mutation rates (Jarne & Lagoda 1996). We focus on three central questions: (i) Are populations corresponding to the three recognized subspecies of Steller's jay in the Pacific Northwest genetically distinct? (ii) Is there evidence of genetic structure among populations of *C. stelleri*? We predict limited levels of structure will be present in Steller's jay as they have only recently (15–10 kya) colonized the previously glaciated regions of British Columbia and Alaska and show some evidence of philopatry. (iii) Is there evidence that the Queen Charlotte Islands served as a refugium for Steller's jay during the Pleistocene? If populations were present on the Queen Charlotte Islands during the Pleistocene, then they should harbour an unusually high proportion of private alleles that are not present in mainland populations, including populations in southern refugia.

Materials and methods

Description of subspecies

The Steller's jay, *Cyanocitta stelleri*, inhabits western parts of North and Central America from Alaska to Nicaragua.

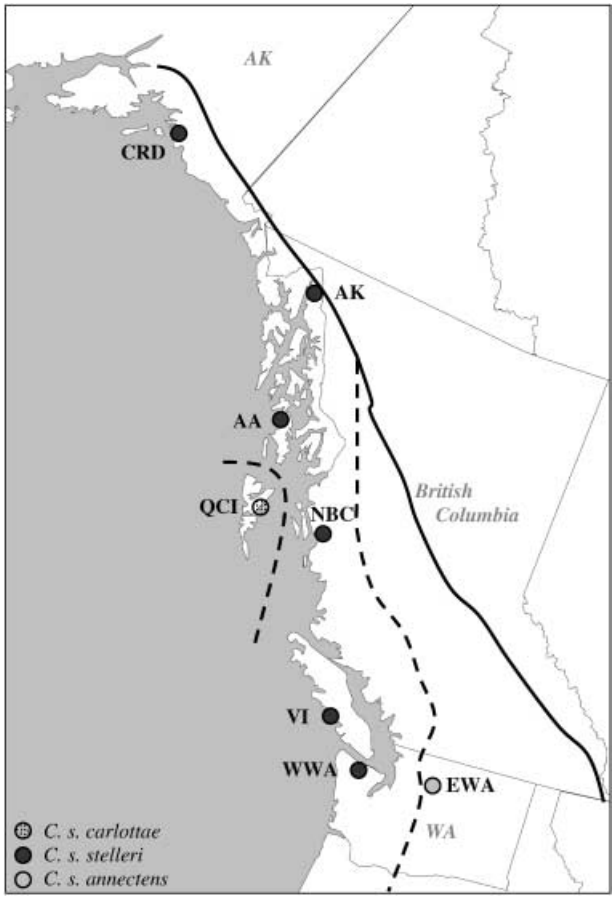

Fig. 1 Map of sampling sites for Steller's jay in western North America. Samples were obtained from *Cyanocitta stelleri stelleri*: Copper River Delta (CRD, $n = 10$), Alaska (AK, $n = 20$), Alexander Archipelago (AA, $n = 33$); northern British Columbia (NBC, $n = 27$); Vancouver Island (VI, $n = 7$) and western Washington (WWA, $n = 10$); *Cyanocitta stelleri carlottae*: Queen Charlotte Islands (QCI, $n = 23$); and *Cyanocitta stelleri annectens*: eastern Washington (EWA, $n = 20$). Species' range limit is indicated by a solid line and subspecies' limits by dashed lines.

As many as 16 subspecies are recognized (Browning 1993), and three subspecies inhabit previously glaciated regions of northwestern North America (Fig. 1). *Cyanocitta stelleri stelleri* is found along the Pacific coast from southeast Alaska to Oregon to the west of the Cascades and Coast Mountains. *Cyanocitta stelleri annectens* is found in the interior to the east of *C. s. stelleri* between the Rocky Mountains and the Coast and Cascade mountain ranges. *Cyanocitta stelleri carlottae* has the most restricted distribution and is endemic to the Queen Charlotte Islands. Differences between these three subspecies consist of subtle plumage variation (Fisher 1902; Stevenson 1934; Browning 1993; Wiebe 1995) and size differences (Fisher 1902; Stevenson 1934; Wiebe 1995; T.M.B., personal observation).

Sample collection and genotyping

The sampling area (Fig. 1) was distributed among populations within the ranges of three recognized subspecies: *C. s. stelleri* (Alaska, Vancouver Island, mainland British Columbia and western Washington), *C. s. annectens* (eastern Washington) and *C. s. carlottae* (Queen Charlotte Islands). The two sites in Washington are from areas believed to be unglaciated during the Pleistocene glaciations (Pielou 1991; Mann & Hamilton 1995; Clague & James 2002) and are therefore considered to be representative of southern refugial populations. Blood and tissue samples were obtained from 150 individual Steller's jays from eight populations in Alaska, British Columbia and Washington (Fig. 1). Blood samples were collected from the Queen Charlotte Islands in 2002, from northern British Columbia in both 2002 and 2003 and from all others sites in 2003. Birds were caught using mist nets. Blood was taken from the brachial vein, dried on filter paper and stored in individual bags. Samples from the Alexander Archipelago, Copper River Delta, and additional samples from the Queen Charlotte Islands and Alaska, collected between 1996 and 2002, were obtained from the University of Alaska Museum.

DNA was extracted using standard proteinase K/phenol–chloroform extraction followed by ethanol precipitation (Sambrook *et al.* 1989). Primers for five microsatellite markers isolated from other species of jays were used to genotype Steller's jay (Table 1). One microsatellite marker was originally isolated from Mexican jay (*Aphelocoma ultramarina*, MJG, Li *et al.* 1997) and four loci were from Florida scrub jay (*Aphelocoma coerulescens*, ApCo, Stenzler & Fitzpatrick 2002). The forward primers were modified by the addition of M13 sequence to the 5′ end to allow for direct incorporation of a fluorescently-labelled M13 primer. All loci were amplified using a two-step annealing procedure: one cycle for 2 min at 94 °C, 45 s at T_{A1}, 60 s at 72 °C; seven cycles of 60 s at 94 °C, 30 s at T_{A1}, 45 s at 72 °C; 30 cycles of 30 s at 89 °C, 30 s at T_{A2}, 45 s at 72 °C; and one final cycle of 5 min at 72 °C. For Florida scrub jay loci ApCo2, 29 and 41, T_{A1} and T_{A2} were 48 °C and 50 °C, respectively. For locus MJG1, $T_{A1} = 50$ °C and $T_{A2} = 52$ °C and for locus ApCo40 $T_{A1} = 55$ °C and $T_{A2} = 57$ °C. Polymerase chain reaction (PCR) products were run on a 6% acrylamide gel on a LI-COR 4200 IR2. Known allele standards were run on each gel to ensure that alleles were sized consistently between gels. Alleles were scored using GENEIMAGIR (LI-COR), and sizing was confirmed by visual inspection.

Statistical analyses

All populations/subspecies and loci were tested for departure from Hardy–Weinberg equilibrium and linkage disequilibrium using GENEPOP (Raymond & Rousset 1995). As the number of detected alleles is highly dependent

Table 1 Total number of alleles (*A*), allelic richness (*AR*), expected heterozygosities (H_E) and percentage of private alleles (*PA*) for eight populations and three subspecies of Steller's jay at five microsatellite loci

Sampling Site	MJG1	ApCo2	ApCo29	ApCo40	ApCo41	Average
C. s. stelleri						
Copper River Delta (n = 10)						
A	1	6	4	7	2	4.0
AR	1.0	5.5	3.6	6.0	2.0	3.6
H_E	0.00	0.73	0.57	0.82	0.46	0.51
PA						0%
Alaska (n = 20)						
A	4	12	5	7	4	6.4
AR	2.9	8.6	3.5	5.7	2.7	4.7
H_E	0.33	0.90	0.61	0.80	0.54	0.64
PA						0%
Alexander Archipelago (n = 33)						
A	4	14	8	9	3	7.6
AR	3.1	8.4	4.0	6.5	2.2	4.8
H_E	0.49	0.89	0.49	0.83	0.52	0.64
PA						5%
Northern British Columbia (n = 27)						
A	3	12	7	7	2	6.2
AR	2.9	7.6	4.4	6.2	2.0	4.6
H_E	0.60	0.86	0.63	0.81	0.44	0.67
PA						0%
Vancouver Island (n = 7)						
A	3	9	4	6	2	4.8
AR	3.0	9.0	4.0	6.0	2.0	4.8
H_E	0.50	0.84	0.64	0.80	0.49	0.65
PA						4%
Western Washington (n = 10)						
A	5	5	4	7	5	5.2
AR	4.4	4.1	4.1	5.5	4.4	4.5
H_E	0.69	0.50	0.57	0.65	0.73	0.63
PA						8%
C. s. stelleri						
Total (n = 107)						
A	6	16	12	11	5	10
H_E	0.53	0.90	0.63	0.85	0.54	0.69
C. s. annectens						
Eastern Washington (n = 20)						
A	4	14	7	10	5	8.8
*AR**	3.0	9.3	5.0	6.2	4.1	5.5
H_E	0.56	0.91	0.74	0.80	0.69	0.74
PA						10%
C. s. carlottae						
Queen Charlotte Islands (n = 23)						
A	2	13	2	7	4	5.6
*AR**	1.9	7.8	2.0	5.8	2.9	4.1
H_E	0.27	0.88	0.39	0.81	0.56	0.58
PA						11%

*Values are population estimates not subspecies estimates.

on the number of individuals sampled, allelic richness was calculated in FSTAT (Goudet 2001) by estimating the expected number of alleles for a given locus in a subsample of $2n$ genes, where n is fixed at the smallest number of individuals typed for a sample. We also plotted the number of alleles in each population against the number of individuals sampled to determine if a sampling bias was present.

Two standard indices of population differentiation were calculated: F_{ST} and allelic goodness of fit. Goudet *et al.* (1996) found that F_{ST} estimators and allelic goodness of fit

tests were more powerful than genotypic goodness-of-fit tests and, when sample sizes are unequal, that allelic goodness-of-fit tests were the most powerful. Two commonly used distance-based estimators of population differentiation are F_{ST} and R_{ST}. R_{ST} was developed specifically for microsatellites and incorporates microsatellite specific mutation models, yet simulation studies have shown that F_{ST} performs better when sample sizes (< 50/population) and/or number of loci (< 20) are small (Gaggiotti *et al.* 1999). Weir and Cockerham's estimator of F_{ST} (1984) was used to summarize population variation. Both global and pairwise F_{ST} estimates were calculated in GENETIX 4.02 (Belkhir *et al.* 2000), significance was tested using 50 000 permutations, and sequential Bonferroni corrections for multiple tests were applied (Rice 1989).

F_{ST} was originally developed for bi-allelic markers, and an F_{ST} of 1 corresponds to maximum divergence between two populations each being monomorphic for a different allele. However, microsatellites are highly variable and contain multiple alleles, so the maximum F_{ST} is less than one, even for populations with non-overlapping alleles (see Hedrick 1999). Therefore, the maximum F_{ST} value that could be obtained using these five loci was calculated following Hedrick (1999).

In addition to F_{ST}, tests for homogeneity of allele frequencies were performed. TFPGA version 1.3 was used to test for differences in allele frequencies among populations/subspecies (1000 dememorization steps, 20 batches and 20 000 permutations/batch, Miller 1997), and significance values were combined across all loci. TFPGA uses a Markov chain Monte Carlo (MCMC) approximation of Fisher's exact test to test for significant differences in allele frequencies between pairs of populations.

The program STRUCTURE version 2.1 (Pritchard *et al.* 2000) was used to determine the level of population structure in the data set independent of the individual's geographical origin. Three independent runs of 10^6 MCMC iterations were performed using the admixture model to estimate the number of populations (K) for K = 1–10. Results from runs at each value of K were averaged.

Tests for isolation by distance allow us to evaluate the relative historical roles of gene flow and drift on population structure by comparing expected pairwise genetic and geographical distances with those expected under a stepping-stone model of population structure (Hutchison & Templeton 1999). If gene flow is affected by geographical distance, we would expect a larger number of migrants to be exchanged between adjacent populations. The correlation between geographical distance and genetic distance was examined in GENEPOP (Raymond & Rousset 1995) and significance was determined using a Mantel test with 500 000 permutations.

To describe the geographical clustering of populations, we carried out a principal component analysis (PCA) using the program PCA-GEN version 1.2 (Goudet 1999). This analysis uses allele frequencies to define new variables (components) that summarize the variance among populations and then performs permutation tests to evaluate the significance of each component (5000 randomizations).

Founder effects can cause a reduction in the number of alleles in new populations. Similar decreases in allelic variation can also result from population bottlenecks. To test for recent population bottlenecks, we used the program BOTTLENECK version 1.2.02 (Cornuet & Luikart 1996; Piry *et al.* 1999). During a bottleneck, alleles will be lost from the population and levels of heterozygosity will temporarily be higher than expected under mutation–drift equilibrium. The one-tailed Wilcoxon signed rank test is the most powerful and robust of the three tests in BOTTLENECK for studies using less than 20 loci (Piry *et al.* 1999). We therefore used this test with a two-phase mutation model (TPM) with 95% stepwise mutations, a variance of 12 and 1000 iterations, as recommended by Piry *et al.* (1999), to determine whether a bottleneck occurred in the last $2N_e$–$4N_e$ generations.

Results

High levels of genetic variation were found in Steller's jays. Populations contained 1–14 alleles per locus with an overall total of 6–21 alleles at each locus (Table 1). Levels of allelic richness based on the smallest sample size (n = 7) ranged from 1.0 to 9.3. Only locus ApCo2 showed a significant correlation between number of alleles and number of samples (P = 0.01) with the three less extensively sampled populations having fewer alleles (Table 1). Thirteen of the 57 alleles were restricted to a single population and all but eight of the alleles were present in one of the two putative southern refugia. The proportion of private alleles in the populations ranged from 0% (Copper River Delta, Alaska and northern British Columbia) to 11% in the Queen Charlotte Islands (Table 1). The distribution of private alleles was not significantly heterogeneous (G_{adj} = 11.01, P = 0.14). However, pairwise tests showed significant differences between the Queen Charlotte Islands and Copper River Delta, Alaska and northern British Columbia (all $P < 0.05$). Similar differences were found between the southern refugia population in eastern Washington and Copper River Delta, Alaska and northern British Columbia (all $P < 0.05$).

Differentiation among subspecies

Deviations from Hardy–Weinberg equilibrium were found when samples were grouped by subspecies: *Cyanocitta stelleri annectens* at locus ApCo40 and *Cyanocitta stelleri stelleri* at locus ApCo29. However, these were not significant after corrections for multiple tests. Significant differentiation among the three subspecies was found

($P < 0.01$). Given a theoretical maximum F_{ST} value of 0.326, pairwise F_{ST} values between subspecies were relatively high: *Cyanocitta stelleri carlottae*–*C. s. annectens* = 0.076, *C. s. carlottae*–*C. s. stelleri* = 0.090 and *C. s. annectens*–*C. s. stelleri* = 0.018. Levels of genetic variation within the three subspecies varied considerably. *Cyanocitta stelleri carlottae* on the Queen Charlotte Islands had significantly lower levels of allelic diversity (average 5.6 alleles/locus) compared with *C. s. annectens* (8.8 alleles/locus) and *C. s. stelleri* (10 alleles/locus) ($F = 10.28$, $P = 0.03$). The reduced level of genetic variation in *C. s. carlottae* is also evident in measures of allelic richness that account for differences in sample sizes (*C. s. carlottae* = 5.39 alleles/locus, *C. s. stelleri* = 6.99 alleles/locus, and *C. s. annectens* = 7.95 alleles/locus; $F = 8.09$, $P = 0.01$). Pairwise tests show significantly lower levels of allelic richness between *C. s. carlottae* and *C. s. stelleri* ($F = 14.46$, $P = 0.02$), and *C. s. carlottae* and *C. s. annectens* ($F = 9.47$, $P = 0.04$), but not between *C. s. stelleri* and *C. s. annectens* ($F = 3.70$, $P = 0.13$).

Differentiation among populations

Deviations from Hardy–Weinberg equilibrium were detected at locus ApCo40 in eastern Washington and at locus ApCo29 in northern British Columbia. However, after Bonferroni corrections neither was significant. None of the tests for linkage disequilibrium were significant.

Prior to testing for differences among populations, tests were performed on samples collected in different years from the same site (i.e. Queen Charlotte Islands, northern British Columbia and Alaska). No significant differences were found between years; therefore all samples collected at the same site were combined for further analyses.

The global F_{ST} estimate was 0.075, indicating a relatively high level of divergence (23% of the maximum possible value). Pairwise estimates of F_{ST} ranged from 0.021 (Copper River Delta and Alaska) to 0.252 (Copper River Delta and Queen Charlotte Islands) and showed statistically significant population differentiation between all but six population comparisons (Table 2). The exceptions were pairwise comparisons involving the less extensively sampled populations.

Highly significant differences in allele frequencies were found using Fisher's exact test (Table 2). All but three pairwise tests (Copper River Delta vs. Alaska, Vancouver Island vs. northern British Columbia, and eastern Washington vs. Vancouver Island) were significant, and one of the nonsignificant estimates (Vancouver Island vs. northern British Columbia) was only slightly higher than the critical P value (corrected critical $P = 0.007$).

The Bayesian structure analysis returned the highest probability for five clusters [$\Pr(K = 5) = 0.99$]. However, likelihood estimates of $K = 5$–7 were similar (–2187, –2196 and –2199, respectively), and Pritchard *et al.* (2000) urged caution when estimating K, particularly when differences in likelihood estimates are small. Values of $K > 5$ resulted in further division of existing inferred clusters, and the percentage membership within each cluster decreased. The clusters containing individuals from western Washington, Queen Charlotte Islands and Copper River Delta were the most robust.

Table 2 Results of pairwise tests for population differentiation, including F_{ST} values with P values in parentheses (above diagonal) and P values for tests of allelic differentiation (below diagonal). Bold indicates significance after Bonferroni correction at $P < 0.05$. Refer to Fig. 1 for abbreviations of sampling sites

	CRD	AK	AA	NBC	VI	WWA	EWA	QCI
C. s. stelleri								
CRD		0.021 (0.073)	**0.112 (< 0.001)**	**0.107 (< 0.001)**	**0.143 (0.007)**	**0.196 (< 0.001)**	**0.095 (0.003)**	**0.252 (< 0.001)**
AK	0.030		**0.042 (< 0.001)**	**0.046 (< 0.001)**	**0.088 (0.004)**	**0.105 (< 0.001)**	0.031 (0.018)	**0.159 (< 0.001)**
AA	**< 0.001**	**< 0.001**		**0.028 (0.002)**	**0.086 (0.001)**	**0.090 (0.001)**	**0.037 (0.002)**	**0.099 (< 0.001)**
NBC	**< 0.001**	**< 0.001**	**< 0.001**		**0.052 (0.009)**	**0.086 (< 0.001)**	0.022 (0.019)	**0.070 (< 0.001)**
VI	**0.002**	**< 0.001**	**< 0.001**	0.009		0.117 (0.019)	0.030 (0.103)	**0.059 (0.005)**
WWA	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**		0.064 (0.011)	**0.158 (0.001)**
C. s. annectens								
EWA	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	0.115	**< 0.001**		**0.076 (< 0.001)**
C. s. carlottae								
QCI	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**0.001**	**< 0.001**	**< 0.001**	

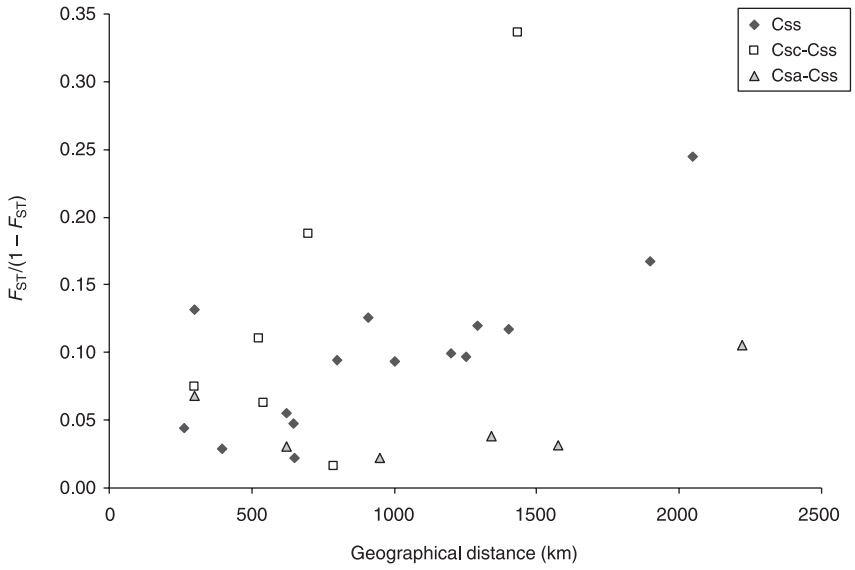

Fig. 2 Relationship between geographical and genetic distance (F_{ST}) in Steller's jay populations from western North America. The comparisons for *Cyanocitta stelleri carlottae*, *Cyanocitta stelleri stelleri* and *Cyanocitta stelleri annectens* (see legend) have been plotted separately.

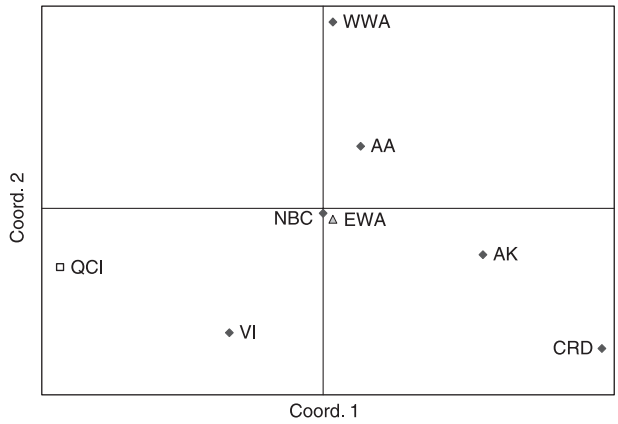

Fig. 3 Principle component analysis of Steller's jay populations. Coordinate 1 accounted for 44.4% of the inertia and coordinate 2 16.7%. Symbols represent different morphologically defined subspecies: *Cyanocitta stelleri annectens* (triangle), *Cyanocitta stelleri carlottae* (square) and *Cyanocitta stelleristelleri* (diamond).

The test for isolation by distance among *C. stelleri* populations was significant ($r = 0.42$, $P = 0.04$, Fig. 2). As the patterns for the three morphologically defined subspecies differed, the test was also performed on *C. s. stelleri* populations only. The result of this test was also highly significant ($r = 0.73$, $P = 0.007$). The significant isolation by distance pattern suggests that levels of gene flow among more geographically distant populations are lower than among nearby populations and that populations are in migration–drift equilibrium (Hutchison & Templeton 1999).

The first two axes of the PCA accounted for 61.1% of the total inertia (44.4% and 16.7% respectively for PC1 and PC2; Fig. 3). However, only PC1 explained a significant proportion of the total inertia ($P = 0.036$). The third axis was similar to the second axis (PC3 = 15.1%) but separated the eastern Washington and northern British Columbia populations (data not shown).

The one-tailed Wilcoxon test in BOTTLENECK did not detect any significant heterozygote excess in any of the populations ($P > 0.11$). This suggests that any reduction in the number of alleles is not the result of a recent bottleneck.

Discussion

A high level of population structure was detected in the Steller's jay throughout the northern portion of its range. Significant genetic differences were found not only among subspecies, but also among *Cyanocitta stelleri stelleri* populations. There is evidence of reduced genetic diversity in *Cyanocitta stelleri carlottae* and high levels of genetic divergence between *C. s. carlottae* and other populations.

Subspecific differences

Significant levels of differentiation were found between each of the three metapopulation samples grouped by subspecies distribution. Levels of divergence, measured by F_{ST}, between *C. s. carlottae* and the other groups were consistently higher than divergence between *C. s. stelleri* and *Cyanocitta stelleri annectens*, which appeared to be less genetically distinct. Reduced gene flow among these morphologically defined groups is likely the result of physical isolation, either in glacial refugia (discussed below) or due to other barriers. While additional sampling of *C.* s. *annectens* is required, the lower levels of divergence between *C. s. stelleri* and *C.* s. *annectens* populations (Table 2; Fig. 3) are no doubt related to the lower levels of isolation these populations experience on or near the mainland.

Coastal refugium

Several lines of evidence suggest that the Queen Charlotte Islands may have served as a refugium for Steller's jay populations during part of the Pleistocene. First, there is the historic recognition of an endemic, morphologically defined subspecies on the Queen Charlotte Islands. Although morphological differences can accumulate over a short period of time or result from founder effects (Clegg *et al*. 2002b), combined with the genetic data (outlined below) it supports prolonged isolation. Second, genetic distances, as measured by F_{ST}, were generally higher for birds from the Queen Charlotte Islands. If there was a single postglacial colonization of the northwestern range and rapid divergence, levels of genetic divergence should be similar to those found in the nearby populations on the Alexander Archipelago and in northern British Columbia. Third, levels of allelic diversity on the Queen Charlotte Islands were lower and are indicative of a reduced historical population size, such as would be found in a small refugium. The increased divergence and decreased variation could also be attributed to a founder event. However, the relatively high proportion of private alleles on the Queen Charlotte Islands suggests that this is unlikely or at least it is not attributable to a founder event occurring during the same wave of colonization that populated the adjacent areas. In addition, the Queen Charlotte Island population shares the private alleles profile of putative refugia (e.g. eastern Washington) and is significantly different from populations that are most likely to have been postglacially colonized (e.g. Copper River Delta, Alaska and northern British Columbia), thus better fitting the concept that it was a refugium for this population. Therefore our findings are consistent with Steller's jays on the Queen Charlotte Islands being glacial relics from a small, ice-free refugium that existed either on the Queen Charlotte Islands or in Hecate Strait between the mainland and the Queen Charlotte Islands (Warner *et al*. 1982; Clague 1989; Mathewes 1989; Mandryk *et al*. 2001) although we cannot exclude the possibility that Steller's jay populations on the Queen Charlotte Islands resulted from a separate, and perhaps earlier, postglacial colonization than the adjacent mainland. Both of these scenarios are consistent with the morphological differences, lower levels of genetic variation, and higher levels of divergence in Queen Charlotte Island populations; however, only the glacial refugium hypothesis is consistent with the distribution of private alleles.

Few molecular studies of western North American species include samples from the Queen Charlotte Islands. Many of these studies suggest that one or more coastal refugia may have existed, but the locations of such refugia are unknown (Deagle *et al*. 1996; Byun *et al*. 1997; Ritland *et al*. 2001; Printzen *et al*. 2003).

Levels of population differentiation

The extent of genetic differentiation amongst populations of Steller's jays is extremely high in comparison with recent studies of other temperate passerines. The high levels of population differentiation were detected using both traditional (F_{ST} and allelic tests) and Bayesian (STRUCTURE) analyses. Most of the mainland populations in this study, with the exception of those in Washington, are known to have colonized their current ranges < 15 kya. Limited phylogeographical or population structure has been found in other North American forest birds inhabiting previously glaciated areas. Most studies detected the presence of two distinct lineages: east/west or coastal/continental (Milot *et al*. 2000; Ruegg & Smith 2002; Drovetski *et al*. 2004; Lovette *et al*. 2004); however, several studies revealed multiple western lineages (Zink 1994; Kimura *et al*. 2002). In British Columbia, coastal and Rocky Mountain lineages of fox sparrows (*Passerella iliaca*) were reported by Zink (1994). However, unlike *C. stelleri*, these lineages corresponded to known subspecific differences.

The high level of differentiation in *C. stelleri* could have been created by sociality, habitat fragmentation, founder effects, and geological history. Both sociality and habitat discontinuity have been suggested as sources for differing rates of population differentiation in *Aphelocoma* jays, the sister genus to *Cyanocitta*. Peterson (1992b) hypothesized that differences in mating systems were driving differentiation in scrub jays. Communally breeding species (i.e. gray-breasted jay, *Aphelocoma ultramarina* and Florida scrub jay, *Aphelocoma coerulescens*) accrued genetic differences over smaller geographical scales faster than pair-breeding species (i.e. western scrub jay, *Aphelocoma californica*). However, Steller's jays, like western scrub jays, are not communal breeders. The higher levels of philopatry associated with communal breeding, and not the mating system, could be causing the increased rate of differentiation observed within *Aphelocoma* jays. This is consistent with the higher levels of population structure often observed in highly social species (e.g. Peterson 1992b; McDonald *et al*. 1999; Uimaniemi *et al*. 2000).

Habitat fragmentation has also been suggested as a cause for population differentiation in jays. Genetic structure in the Siberian jay (*Perisoreus infaustus*) is thought to be caused by limited dispersal across highly fragmented habitat in northern Europe (Uimaniemi *et al*. 2000). Similarly, McDonald *et al*. (1999) reported that fragmentation of sand dunes in Florida is responsible for low levels of dispersal of Florida scrub jay between adjacent patches. Recently, Steller's jay's habitat has been affected by fragmentation, most notably by forestry. However, the Steller's jay is positively associated with logged areas (Brand & George 2001; Marzluff *et al*. 2004), and it is unlikely that the moderate levels of modern fragmentation are responsible

for the observed level of population differentiation pattern.

Founder effects are associated with reduced genetic diversity and fixation of alleles. Furthermore, serial colonization, in which new populations are founded from populations that themselves were 'recently' founded, can result in decreased allelic diversity due to loss of rare alleles (Clegg *et al*. 2002a). These effects are more pronounced in species with a linear distribution than in widely distributed species (Kimura & Weiss 1964). To date only one study has found strong evidence of reduced genetic variation due to serial colonization of previously glaciated areas (Pruett & Winker 2005). Steller's jay populations in previously glaciated areas contain a subset of the alleles present in refugia. However, the allelic diversity among populations in glaciated and nonglaciated regions is similar. The exception is the Copper River Delta population near the extreme northern end of species' distribution. This population shows decreased genetic variation that may be attributed to founder effects.

The high level of population differentiation could also be the result of colonization from multiple southern refugia. This is unlikely for several reasons. First, colonization from multiple refugia would involve long-distance dispersal. In the contemporary populations, a significant isolation by distance pattern is present indicating that dispersal is limited by geographical distance. Second, with the exception of the Queen Charlotte Islands and the Alexander Archipelago, none of the more northerly populations contain private alleles suggesting a common ancestral population.

Patterns of dispersal

Genetic differentiation among many Steller's jay populations is consistent with it being a sedentary species, and this is supported by behavioural and banding data (J.M. Marzluff, personal communication). Estimates of F_{ST} suggested that dispersal in *C. s. stelleri* is restricted by geographical distance. Populations of *C. s. stelleri* form an almost linear distribution along the western coast of North America and gene flow conforms to a stepping-stone model. Similar patterns have been found in other North American corvids (Peterson 1992a; McDonald *et al*. 1999). Peterson (1992a) suggested that the differences in the scale of spatial structuring reflected the level of sociality in the species. Cooperatively breeding species are more philopatric thus facilitating differentiation at small spatial scales. Our results show that pair-breeding species can also exhibit genetic differences over small geographical scales (< 300 km), suggesting that factors other than the degree of sociality may influence dispersal.

Steller's jays in previously glaciated regions of western North America show very high levels of population structure, the highest observed yet for a corvid species (Peterson 1992a; McDonald *et al*. 1999; Uimaniemi *et al*. 2000; Fok *et al*. 2002). Each of the three morphologically defined subspecies is genetically distinct, and the population on the Queen Charlotte Islands is highly divergent. Our data are consistent with the possibility of a Pleistocene refugium on the Queen Charlotte Islands. Considering the ecological reconstructions of the region indicate that *C. s. stelleri* colonized the northern portions of its range in the last < 15 000 years, after the retreat of the Cordilleran ice sheet, remarkable levels of genetic differentiation have been achieved in a comparatively short period of time.

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