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RESEARCH ARTICLE

The contribution of island populations to in situ genetic conservation

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Abstract Genetic variation is often lower within island populations, however islands may also harbor divergent genetic variation. The likelihood that insular populations are genetically diverse or divergent should be influenced by island size and isolation. We tested this assumption by comparing patterns of genetic variation across all major island song sparrow populations along the Pacific North American coast. Allelic richness was moderately lowered even on islands which are close to large, potential sources. The most significant differences in allelic richness occurred on very small or highly remote islands. Gene diversity was significantly lower only on remote or very small islands. We found that island populations contribute to regional genetic variation through both the amount of genetic variation and the uniqueness of that variation. The partitioning of this contribution was associated with the size and isolation of the island populations.

Keywords Allelic richness · Island · Reserve design · Song sparrow

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Introduction

The importance of genetic variation for the fitness, viability and evolutionary responsiveness of populations is a central tenet within conservation genetics (Frankel 1974; Lande and Barrowclough 1987). Although there are cases where populations have recovered despite low genetic variation (Frankham et al. 2002), data from natural populations often supports the benefits of high genetic variation (Reed and Frankham 2003; Spielman et al. 2004; O'Grady et al. 2006; Leimu et al. 2006). Consequently, genetic criteria are increasingly incorporated into conservation plans. An important caveat is that patterns of neutral variation, as measured by molecular markers, may not reflect levels of adaptive variation for all traits across all populations. However, given the difficulty in measuring adaptive variation for wild species, molecular markers are valuable surrogates and in some cases may be conservative estimates of the expectations of loss and recovery of quantitative genetic variation (Lynch et al. 1999).

Although the conservation of both adaptive and neutral variation is justifiable, these two types of genetic variation are not always positively correlated, such that careful consideration of program objectives needs to be made when assigning genetic value to particular populations. A particular population may be designated as being genetically valuable if it is differentiated from other populations, or if it contains high levels of allelic diversity (Petit et al. 1998; Moritz 2002). Island populations have the potential to be genetically

valuable, since for many species, open-water barriers reduce migration rates. This isolation allows island populations to diverge from their mainland relatives, potentially into insular endemics which if diagnosable, will warrant separate management (Crandall et al. 2000). Although high levels of endemicity and genetic divergence make island populations obvious candidates for conservation, genetic diversity can be considerably lower on islands (Frankham 1997; Eldridge et al. 1999). Even island populations located within 5 km from mainland populations have shown lower genetic variation (Dibblers, *Parantechinus apicalis*, Mills et al. 2004; South Island robin, *Petroica australis*, Boessenkool et al. 2007). Lower genetic variation on islands is generally attributed to higher levels of inbreeding (Frankham 1998), founder events (Clegg et al. 2002; Pruett and Winker 2005) and increasingly strong genetic drift due to low immigration rates and smaller population sizes. Yet, drift is a stochastic process, such that alleles that are rare or absent from the mainland may occur at higher frequencies within island populations (Eldridge et al. 2004; Burg et al. 2005), increasing the genetic value of islands. In cases where endemics occur on islands, it is clear that these island populations are harboring divergent genetic variation. In the absence of diagnosable differences, the contribution of island populations to the differentiation or richness components of intraspecific genetic diversity is less clear.

We address this issue by comparing patterns of genetic diversity among islands varying in size and isolation by several orders of magnitude. This comparison was made using a large genetic data set for song sparrow (*Melospiza melodia*) populations obtained along the Pacific Coast of North America, ranging from Alaska to California. Several of the subspecies included in this study are of considerable conservation concern, particularly *M.m.pusillula* and *M.m.graminea* (Shuford and Gardali 2008). Across these populations we first determine patterns of allelic richness and gene diversity (equivalent to expected heterozygosity (H_S)) across mainland and island populations. We focused on patterns of allelic richness and gene diversity as they are central diversity measures in genetic conservation (Schoen and Brown 1991; Petit et al. 1998; Kalinowski 2004). We next evaluate the contribution of the sampled populations to intraspecific genetic diversity, by partitioning genetic variation into differentiation and richness components. We discuss the implications of these results for the expected role of islands in the conservation of intraspecific genetic diversity.

Methods

Field protocol

This study is based on 1,020 song sparrows sampled across 26 sites and 15 subspecies in Alaska, British Columbia (BC) and California (Fig. 1). Most sampling areas occurred in the range of a single subspecies, but San Francisco Bay and the Salton Sea occur at junctions between multiple subspecies (Table 1). In each region samples were collected from island and mainland populations (Table 1, Fig. 1). The samples from the Northern Pacific Coast (Attu, Adak and Kodiak Islands, Alaskan Peninsula, Copper River Delta, Alexander Archipelago, Haida Gwaii and Hyder, BC), San Francisco Bay and the Salton Sea regions have been included in previous studies ($n = 478$; sampling details given in Chan and Arcese 2002; Patten et al. 2004; Pruett and Winker 2005).

An additional 542 samples are new to this study and were obtained in 1996, 2005 and 2006 from the Channel Islands and southern British Columbia. These samples were obtained during the breeding season (March to July) where adult birds were captured in mist nets using playbacks of male song. After capture, we banded birds with a uniquely numbered aluminum band, collected a blood sample and then released the bird. Blood samples were obtained by puncturing the brachial vein with a 30 gauge needle and collecting 20–50 µl of blood in plain glass capillary tubes. The blood sample was immediately placed in 1 ml of Queen's Lysis buffer (Seutin et al. 1991). Gentle pressure was used to stop bleeding before birds were released back within their territories. DNA was extracted using GenElute^{TM} Blood Genomic DNA Miniprep Kit (Sigma-Aldrich) according to manufacturer's instructions.

In the Channel Islands, we sampled the three extant populations on San Miguel, Santa Rosa and Santa Cruz Islands. In southern BC, three populations were sampled on the BC lower mainland (Delta, Sechelt and Powell River) and four populations were sampled on Vancouver Island (Campbell River, Qualicum, Duncan and Sooke). Within the southern BC region, samples were also obtained from three islands (Triangle, Texada and Sidney Islands) and eight islets (Dock Islands, Shell Islands, Sidney and Mandarte Islands). For comparative purposes, we classified islands as 'islets' if the area was less than 10 ha (Table 1). Patterns of genetic differentiation for the BC and Channel Island populations are provided in Wilson (2008).

DNA extraction and microsatellite amplification

Birds were genotyped at seven polymorphic microsatellite markers: Mme1, Mme2, Mme3, Mme7, Mme12 (Jeffery et al. 2001), ESCU1 (Hanotte et al. 1994), and GF5 (Petren 1998). The loci Mme3 and Mme7 are linked to the z-chromosome, such that females appear as homozygotes. In order to include Mme3 and Mme7, we coded the second allele as 'missing data' for all females. Each polymerase chain reaction (PCR) contained 100 ng genomic DNA,

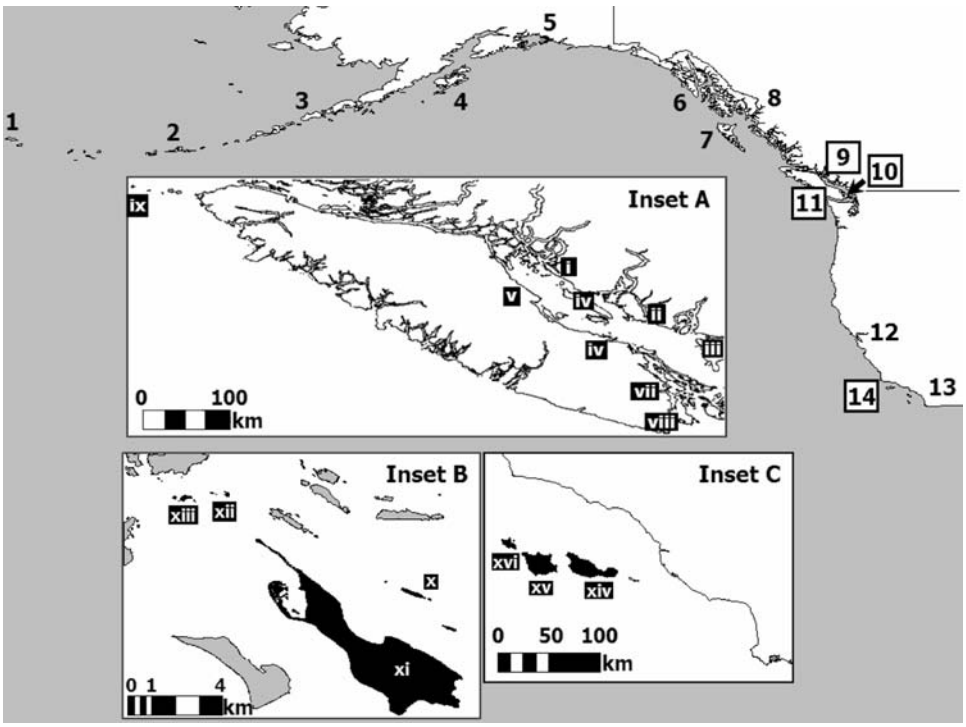

Fig. 1 Map of sampling sites of song sparrow populations. Populations sampled in the Alaskan/Northern BC region are: (1) Attu, (2) Adak, (3) Alaskan Peninsula, (4) Kodiak, (5) Copper River Delta, (6) Alexander Archipelago, (7) Haida Gwaii and (8) Hyder. Sampled areas within southern BC are: (9) BC mainland, (10) Southern Gulf Islands and (11) Vancouver Island; Inset A shows the locations of the populations sampled on the BC Mainland: (i) Powell River, (ii) Sechelt and (iii) Delta. Also shown in inset A are the populations sampled on Vancouver Island: (v) Campbell River, (iv) Qualicum, (vii) Duncan, (viii) Sooke, (ix) Triangle Island and (iv) Texada Island. Within inset B, the Southern Gulf Islands are shown: (x) Mandarte, (xi) Sidney, (xii) Docks, and (xiii) Shell Islands. Populations sampled in southern California were (12) San Francisco Bay, (13) Salton Sea and (14) Channel Islands. Inset map C shows the location of the Channel Islands: (xiv) Santa Cruz, (xv) Santa Rosa and (xvi) San Miguel Islands

10 mM Tris–HCl (pH 8.3), 50 mM KCl, 1.5–2 mM $MgCl_2$, 0.2 mM dNTPs (Invitrogen), 0.16 ug/ul BSA (Bovine serum albumin), 0.1% Triton X-100 (Sigma), 1 pmol of forward and reverse primers, 0.3 pmol of M13 infrared label (LI-COR) and 0.5 U of Taq polymerase (Roche). PCR reactions used standard cycling conditions, based on the locus-specific annealing temperatures and $MgCl_2$ concentrations provided in Chan and Arcese (2002).

PCR products were fractionated on 7% polyacrylamide gels using a LI-COR 4200 DNA analyzer. Allele sizes were determined by running samples alongside a 50–350 bp standard size ladder (LI-COR) and were calibrated against allele ladders that were repeated across gels and across studies (Chan and Arcese 2002; Patten et al. 2004; Pruett and Winker 2005). In addition, we re-ran a subset of samples from Chan and Arcese (2002), which shared alleles with the newly genotyped populations to ensure that allele sizing was congruent between studies. These standards limited any sizing differences among the different studies. Gel results were visualized using Base ImagIR (LI-COR, Lincoln, NB, USA) and loci were scored manually using RFLP scan (Scanalytics, CSP Inc., Fairfax, VA, USA).

Data analysis

We used GENEPOP v 3.4 (Raymond and Rousset 1995) to test for departures from Hardy–Weinberg (HWE) and linkage equilibrium in both individual populations and within pooled groups. For the diversity contribution analyses (Petit et al. 1998), populations in San Francisco Bay, Salton Sea, BC mainland, Vancouver Island and the Southern Gulf Islands were pooled into five respective groups. All other populations were considered individually. To test for HWE we used 400 batches and 3,000 iterations and 800 batches and 10,000 iterations to examine linkage equilibrium. We corrected for multiple comparisons within these tests using a sequential Bonferroni procedure (Holm 1979). The presence of null alleles was examined using the program ML-Null (Kalinowski and Taper 2006).

Patterns of allelic richness

Estimating allelic richness is dependent on the sample size since a larger sample will contain more alleles than a smaller sample despite equal allelic richness. Similarly, the number of populations sampled also inflates the number of

Table 1 Sampling locations, regions, subspecific membership, allelic richness (AR) and private allelic richness (PAR)

(a) Population level allelic richness

Location	Region	Subspecies	AR ± SE	PAR ± SE
Mainland populations				
Marin County	S.CA	*M.m.gouldii*	7.34 ± 0.76	0.27 ± 0.13
Santa Clara County	S.CA	*M.m.gouldii*	8.07 ± 0.85	0.45 ± 0.15
Sacramento County	S.CA	*M.m.heermanni*	8.44 ± 0.99	0.23 ± 0.13
Solano County	S.CA	*M.m.maxillaris*	7.73 ± 0.81	0.12 ± 0.09
Solano County	S.CA	*M.m.maxillaris*	7.87 ± 0.95	0.26 ± 0.14
Alameda County	S.CA	*M.m.pusillula*	6.80 ± 0.80	0.18 ± 0.12
San Mateo County	S.CA	*M.m.pusillula*	7.46 ± 1.14	0.24 ± 0.13
Sonoma County	S.CA	*M.m.samuelis*	7.97 ± 0.93	0.08 ± 0.06
Solano County	S.CA	*M.m.samuelis*	7.81 ± 1.08	0.11 ± 0.05
Salton Sea	S.CA	*M.m.fallax*	7.97 ± 0.76	0.55 ± 0.13
Salton Sea	S.CA	*M.m.heermanni*	8.27 ± 0.93	0.32 ± 0.15
Alaska Peninsula	NPC	*M.m.sanaka*	4.22 ± 0.64	0.18 ± 0.10
Copper River Delta	NPC	*M.m.caurina*	6.53 ± 0.73	0.11 ± 0.05
Hyder	NPC	*M.m.inexspectata*	7.63 ± 0.85	0.15 ± 0.06
Delta	BCML	*M.m.morphna*	7.94 ± 0.85	0.21 ± 0.08
Powell River	BCML	*M.m.morphna*	9.19 ± 0.95	0.16 ± 0.12
Sechelt	BCML	*M.m.morphna*	8.66 ± 1.21	0.39 ± 0.17
Sechelt	BCML	*M.m.morphna*	8.66 ± 1.21	0.39 ± 0.17
Campbell River	BCML	*M.m.morphna*	8.20 ± 0.87	0.22 ± 0.16
Island populations				
Santa Cruz Island	CHIS	*M.m.graminea*[a]	6.54 ± 0.59	0.42 ± 0.34
San Miguel Island	CHIS	*M.m.graminea*[a]	4.79 ± 0.93	0.007 ± 0.01
Santa Rosa Island	CHIS	*M.m.graminea*[a]	6.06 ± 0.98	0.30 ± 0.21
Alexander Archipelago	NPC Islands	*M.m.rufina*	7.79 ± 0.98	0.28 ± 0.06
Attu Island	NPC Islands	*M.m.maxima*	2.10 ± 0.44	0.31 ± 0.27
Adak Island	NPC Islands	*M.m.maxima*	3.55 ± 0.51	0.06 ± 0.06
Kodiak Island	NPC Islands	*M.m.insignis*	4.69 ± 0.84	0.03 ± 0.02
Haida Gwaii	NPC Islands	*M.m.rufina*	6.87 ± 0.51	0.37 ± 0.11
Duncan	VANCI	*M.m.morphna*	7.71 ± 0.92	0.16 ± 0.11
Qualicum	VANCI	*M.m.morphna*	7.98 ± 0.62	0.21 ± 0.21
Sooke	VANCI	*M.m.morphna*	7.92 ± 1.10	0.22 ± 0.10
Texada Island	S.BC Islands	*M.m.morphna*	7.35 ± 1.18	0.08 ± 0.04
Triangle Island	S.BC Islands	*M.m.morphna*	6.03 ± 0.82	0.16 ± 0.12
Islet populations				
Dock Islands	S.BC Islands	*M.m.morphna*	6.35 ± 0.69	0.02 ± 0.02
Shell Islands	S.BC Islands	*M.m.morphna*	6.69 ± 0.45	0.10 ± 0.08
Sidney Island	S.BC Islands	*M.m.morphna*	7.80 ± 0.89	0.12 ± 0.08
Mandarte Island	S.BC Islands	*M.m.morphna*	5.90 ± 0.61	0.08 ± 0.05

(b) Regional level allelic richness

Region	AR ± SE	PAR ± SE
S. California	12.00 ± 1.62	0.87 ± 0.18
Channel Islands	9.77 ± 1.52	1.02 ± 0.64
Northern Pacific Coast (NPC)	10.62 ± 1.43	0.43 ± 0.15
N. Pacific Coast Islands	9.33 ± 0.89	0.71 ± 0.23
BC mainland	12.65 ± 1.72	0.81 ± 0.26

Table 1 continued

(b) Regional level allelic richness		
Region	AR ± SE	PAR ± SE
Vancouver Island	12.26 ± 1.43	0.85 ± 0.47
S. BC Islands	10.55 ± 1.43	0.29 ± 0.08

Rarefied samples are reported at: (a) population level and (b) group level, based on a rarefaction sample of 22 genes with three populations taken from each group. Abbreviations for regions are: Southern California (S.CA), Northern Pacific Coast (NPC), BC mainland (BCML), Channel Islands (CHIS), Northern Pacific Coast Islands (NPC Islands), Vancouver Island (VANCI) and S.BC Islands

[a] Taxonomy as per Patten (2001)

alleles detected relative to a region with fewer sampled populations. A method called rarefaction corrects for this sampling artifact, making it possible to compare diversity across samples differing in sample size. Hierarchical rarefaction is a newer method, which allows comparison among regions where different numbers of populations have been sampled (Kalinowski 2004). Rarefaction calculates the expected allelic richness of a sample taken from each population if g genes (alleles) had been sampled. The value of g equals the smallest number of genotypes for any loci from any of the sampled populations. In the case of diploids, g is twice the number of individuals sampled. Hierarchical rarefaction calculates the expected allelic richness for a region (or population group), if S_k populations had been sampled in each region, where S_k is fewest populations sampled in any of the k regions (Kalinowski 2004).

We used the hierarchical rarefaction method available in HP-RARE (Kalinowski 2005), to calculate allelic and private allelic richness (alleles which are unique to a particular population) at both the population and group level. We grouped the populations into seven groups: Channel Islands, California Mainland, Northern Islands, Northern Pacific Coast, BC mainland, Vancouver Island and the southern BC Islands (Table 1). We rarefied to the minimal size of 22 genes with three population samples taken from each group. The units of the allelic and private allelic richness are the standardized mean number of alleles per locus, averaged across loci. Allelic retention was calculated for each island population by dividing the allelic richness on the island by the allelic richness from the closest mainland population with genetic data. We tested for statistically significant differences between island and mainland groups using 1,000 random permutations of populations among group classes.

Patterns of gene diversity

FSTAT v 2.9.3.2 (Goudet 2001) was used for a between-group comparison in gene diversity (H_S) between islet, island and mainland populations. Gene diversity calculations are equivalent to rarefying to two genes, so reflect the probability that the two sampled genes are different alleles (Nei 1973). Statistical significance was estimated by 1,000 random permutations of populations among groups.

Contribution of islands to overall diversity

The contribution of a particular population to overall genetic diversity (C_T, Nei's diversity) or allelic richness (C_{TR}) can be partitioned into the contributions made by within-population variability (C_S) and differentiation from other populations (C_D) (Petit et al. 1998).

The joint summation of the diversity (C_S) and the differentiation (C_D) components determines if the overall contribution of a particular population (C_T) to the reference population group is positive or negative. A positive contribution for a population indicates that the group diversity would be lower if that particular population was absent. For example, positive contributions in diversity (C_S) would arise if a population had high within-population variability, whereas positive differentiation contributions (C_D) occur when allelic frequencies are divergent from those in the other populations. Genetically depauperate populations would have negative diversity components (C_S) while undifferentiated populations would have negative differentiation contributions (C_D).

Using the program CONTRIB program v1.02 (Petit et al. 1998), we calculated the contribution of populations and population groups to intraspecific levels of genetic diversity (C_T) and allelic richness (C_{TR}). Population groupings were made for regions which were intensively sampled such as: Vancouver Island, BC mainland, Southern Gulf Islands, San Francisco Bay and Salton Sea.

Results

The majority of populations were in HWE and linkage equilibrium, with several exceptions. Following corrections for multiple contrasts, significant deviations from HWE occurred within the pooled Southern Gulf Island group and

Kodiak Island at Mme2, Attu Island at Mme1 and within Triangle Island at Mme2 and Mme12. Departures from linkage equilibrium occurred between Mme1/GF25 within the Southern Gulf Island group. Allelic drop-out has been reported in previous studies for Mme2, Mme12 (Jeffery et al. 2001) and GF25 for the San Francisco Bay populations (Chan and Arcese 2002). Since drift and inbreeding act at the genome level, when these deficits occur disproportionately at a particular locus, we considered the potential influence of null alleles or allelic drop-out. Although not significant after correction for multiple comparisons, there was a heterozygote deficit at Mme12 ($P < 0.001$) on San Miguel and on Adak Island at ESCU1 ($P = 0.04$) and GF25 ($P = 0.001$). Given the absence of heterozygote deficits at these loci within the same subspecies on the nearby islands, it is more probable that these are actual deficits rather than null alleles. Analyses with and without these loci resulted in similar overall patterns, so we retained all loci in the analyses.

Patterns of allelic richness

We found that allelic richness tended to be lower on islands relative to the nearest mainland populations. The mean allelic richness within Vancouver Island populations (12.26 ± 1.43) was marginally lower than within the BC mainland populations (12.65 ± 1.72) (Table 1). Mean allelic richness within the Southern Gulf Island group (10.55 ± 1.43) was lower than the populations on Vancouver Island and the BC mainland (Table 1).

At the group level, allelic richness within the northern Channel Islands was 18% lower than the mainland. Among the individual islands, allelic richness was increasingly lower with each westerly island step along the archipelago. The mean allelic richness was slightly lower on Santa Rosa (6.06 ± 0.98) than on Santa Cruz Island (6.54 ± 0.59), but considerable differences occurred between San Miguel (4.79 ± 0.93) compared to Santa Rosa Island.

When populations were classified as islands or mainland populations, island groups had significantly lower allelic richness (6.35) compared to mainland populations (7.64, $P = 0.006$). Private allelic richness was relatively high on some of the more isolated islands such as Attu and Triangle Island, but it was very low on others such as San Miguel and Kodiak (Table 1a).

Patterns of gene diversity

Gene diversity (H_S) was calculated at the group level for three population types: islands: $H_S = 0.67$, mainland: $H_S = 0.81$ and islets: $H_S = 0.76$. Group-level comparisons between islands and mainland populations were significantly different for gene diversity ($P = 0.05$), where H_S was lower on islands than mainland populations. Islet and mainland populations did not differ significantly in gene diversity ($P = 0.18$).

Contribution of islands to overall diversity

At the regional level, mainland populations typically had higher contributions to total diversity (C_T) and allelic richness (C_{TR}) than island populations. In these cases, contributions were primarily through the diversity component for mainland populations, while contributions from island populations were primarily through the differentiation component. Exceptions to this pattern were the low contributions from the Alaska Peninsula and Copper River Delta compared to the Alexander Archipelago (Figs. 2 and 3). Within southern BC, Vancouver Island and the BC mainland populations had comparable levels of positive contributions, with similar partitioning of contributions. The Southern Gulf Islands, Texada and Triangle Island also had positive contributions, with considerable differentiation components in the latter two.

The southern California region had considerable contributions to intraspecific diversity. Both the San Francisco Bay and Salton Sea populations had positive total contributions, which was mostly due to diversity. The exception was the moderate differentiation component of the allelic richness contribution from the Salton Sea. Unlike the other islands in the data set, the Channel Islands provided positive contributions for both diversity and allelic richness, with the exception of San Miguel. The most notable contribution came from Santa Rosa Island.

Discussion

Allelic richness patterns on islands

Among most of the islands, allelic richness was lower on islands than on the mainland, and allelic richness declined along archipelagoes in a sequential manner. Island isolation and size appear to be important determinants of genetic variation within song sparrow populations, due to the influence of these factors on gene flow and drift respectively. In general, allelic richness tended to be higher on the larger islands, but isolation influenced this pattern. The largest changes in allelic richness occurred along the Aleutian Archipelago and within the Channel Islands. Compared to the Alaskan mainland, the allelic richness was 50% lower on Attu Island, a change which occurred over a distance of more than 1,600 km and multiple island steps. Interestingly, comparable differences were present in the Channel Islands, in particular in the terminal island of San Miguel, which lies only 50 km offshore. Although much

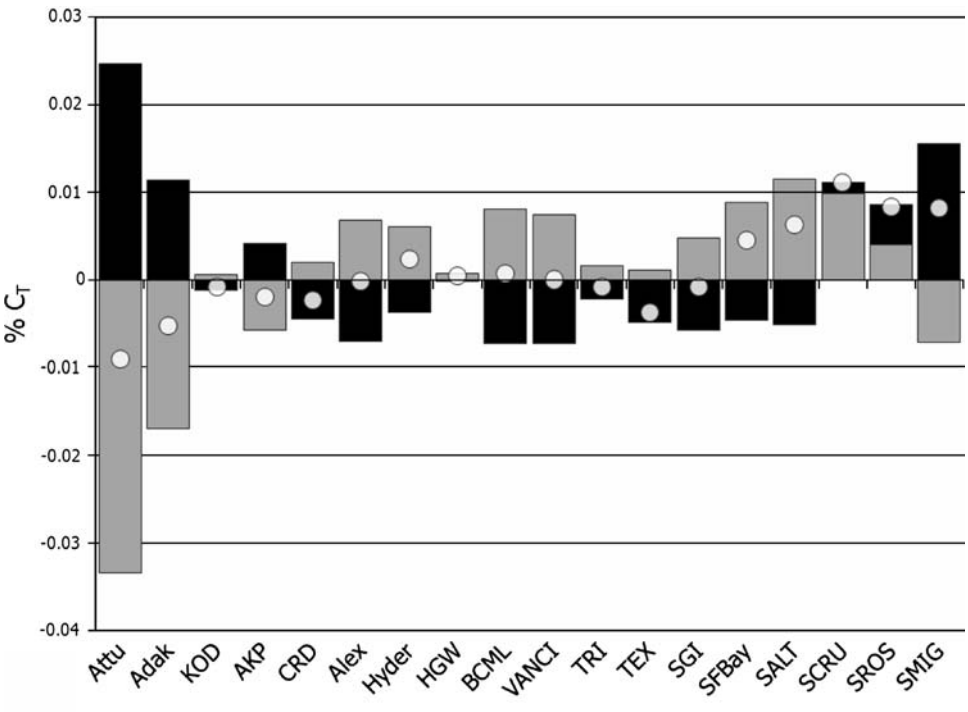

Fig. 2 The contribution of each population to the total diversity (C_T) is shown with open circles. The total contribution (C_T) towards diversity has been subdivided into a diversity component (C_S) shown in grey, and a differentiation component (C_D) shown in black ($C_T = C_S + C_D$). Populations are: Attu (Attu), Adak (Adak), Kodiak (KOD) Islands, Alaska Peninsula (AKP), Copper River Delta (CRD), Alexander Archipelago (Alex), Hyder, BC (Hyder), Haida Gwaii (HGW), BC mainland (BCML), Vancouver Island (VANCI), Triangle (TRI) and Texada Islands (TEX), Southern Gulf Islands (SGI), San Francisco Bay (SFBay), Salton Sea (SALT) and the Channel Islands: Santa Cruz (SCRU), Santa Rosa (SROS) and San Miguel (SMIG)

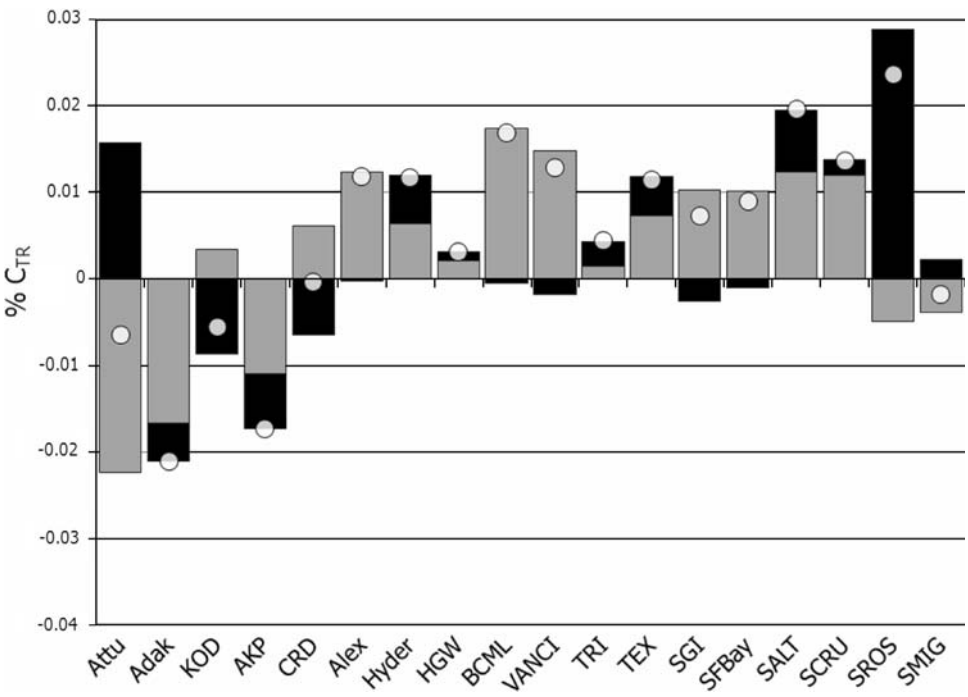

Fig. 3 The contribution of each population to the total allelic richness (C_{TR}) is shown with open circles. The total contribution has been subdivided into a diversity component (C_{RS}) shown in grey, and a differentiation component (C_{RD}) shown in black ($C_{TR} = C_{RS} + C_{RD}$). Population abbreviations are given in caption for Fig. 2

less isolated than Attu Island, San Miguel Island is considerably older and smaller. Attu Island was unglaciated as late as 6–11 kya (Stilwell and Kaufman 1996), but song sparrows have been on the Channel Islands for as long as 39 kyr (Guthrie 1992) and have been isolated on San Miguel Island for an estimated 18 kyr (Bloom 1983).

However, island size is likely more influential for the considerable genetic losses on San Miguel, which is almost 20 times smaller than Attu Island. The smaller, older islands populations of silvereyes (*Zosterops lateralis*) also had the largest genetic losses compared to younger populations undergoing sequential founder events (Clegg et al. 2002). Comparable patterns in allelic richness have been reported in other species on Vancouver Island (American marten, *Martes americana*, Small et al. 2003) and the Channel Islands, (Loggerhead Shrike, *Lanius ludovicianus*, Eggert

et al. 2004; Island Scrub Jay, *Aphelocoma insularis*, Delaney and Wayne 2005). In contrast to this study however, several other species of birds and mammals have lower allelic richness on Haida Gwaii (*M. Americana*, Small et al. 2003; Steller's Jay, *Cyanocitta stelleri*, Burg et al. 2005) and in the Alexander archipelago (Northern flying squirrels, *Glaucomys sabrinus*, Bidlack and Cook 2001), compared to mainland populations. The Haida Gwaii was likely a glacial refugia for song sparrows, which could account for the higher allelic richness for this population (Zink and Dittman 1993; Pruett and Winker 2005). Allelic richness is often higher in glacial refugia, since newly colonized areas are effectively a subsample of the refugial gene pool (Hewitt 1996). The high retention of allelic richness within song sparrow populations on Vancouver Island is likely due to a large effective population size (N_e) and the close proximity to the mainland, leading to low drift and high levels of mainland gene flow.

The more substantial loss of allelic richness within the Southern Gulf Islands could be the result of spatially restricted immigration and stronger drift. Within these islets, the immigration rate ranges from 0.7 to 3.8 birds per year, of which more than half originate from nearby islands (Wilson and Arcese 2008), thus restricting the influx of alleles from outside the island group. Frequent extinction leads to eventual genetic homogeneity, particularly when populations are repeatedly reestablished from a single source (Gilpin 1991). This extinction-recolonization cycle is likely operational within the Southern Gulf Islands, given that extinctions and population turnovers (complete replacement of population members) regularly occur among these islands (Wilson and Arcese 2008).

Although components of genetic variation can be quickly restored on these islands (Keller et al. 2001), immigrants arriving to Mandarte Island tend to bring in alleles that are relatively common in the larger gene pool (unpublished data). Therefore, it is unlikely that any rare alleles that may have drifted to higher frequencies within Mandarte will be reintroduced if the population were extirpated.

Private allele richness

Although allelic richness may be lower in isolated populations, the presence of private alleles increases the conservation value of a population (Crozier 1992). As genetic drift increases, alleles which are rare on the mainland may drift to higher frequencies on islands. These rare alleles may be at such a low frequency on the mainland that they are unsampled, and are thus incorrectly interpreted as being private to those island populations. Alternatively, private alleles may have arisen due to mutation or are genetic relicts within the larger and older island populations. Private allelic richness was highest on Haida Gwaii, which is a putative glacial refugia and on two of the Channel Islands (Santa Cruz and Santa Rosa Islands), which based on fossil evidence (Guthrie 1992), and paleohistory (Bloom 1983), likely predate all other island populations.

Within-region comparisons suggested that more isolated islands had increased probability of private alleles. Within the Georgia Basin, the more isolated Triangle Island had private alleles, whereas the less isolated Texada Island did not. Other molecular studies of island population have also reported lowered allelic richness along with increases in private alleles within more remote island populations (Burg et al. 2005; MacAvoy et al. 2007). However, on San Miguel Island, allelic richness was lower and private allelic richness was negligible, which may be due to a very small effective population size (N_e), inbreeding and past bottlenecks. Low allelic richness and the absence or near absence of private alleles was also reported for island populations of Egyptian vulture (*Neophron percnopterus*, Kretzmann et al. 2003) and the Galápagos penguin (*Spheniscus mendiculus*, Akst et al. 2002).

Patterns of gene diversity

Conserving allelic richness requires a much larger N_e than does the maintenance of gene diversity (Lande and Barrowclough 1987). Thus it is not surprising that although allelic richness was lower on islets within the Southern Gulf Islands, genetic diversity was similar to adjacent mainland populations. Because sparrow population sizes are very small on these islets, we would expect inbreeding and drift to reduce gene diversity. However, on several of these islets there is a low incidence of inbreeding among pedigreed individuals (unpublished data) as there is high movement among the islets (Wilson and Arcese 2008). Furthermore, population turnovers and extinctions occasionally occur on these islets (Wilson and Arcese 2008), so divergence due to drift may only accumulate on more isolated islands with persistent populations. For example, gene diversity was only significantly lowered on Mandarte Island, where inbreeding occurs, complete extinctions have yet to be observed, and immigration is rare (Keller et al. 2001). The low gene diversity on Mandarte may be a localized effect, since immigrants arriving there had substantially higher allelic and gene diversity than resident birds (unpublished data). Lower gene diversities only became apparent on the large, remote islands. Extended periods of isolation, drift and population-level inbreeding may explain why these large, remote island populations showed lower gene diversities, compared to the mainland and islet populations. Island populations that are the most isolated (Nichols et al. 2001; Hille et al. 2003) and occupy the smallest area (Wayne et al. 1991; Lucid and Cook 2004; Petren et al. 2005; White and Searle 2007) often show lower levels of gene diversity.

Contribution of islands to overall diversity

The assessment of total genetic contributions and the partitioning of this contribution closely reflected patterns of allelic richness. Among the islands in this study, those closer to potential mainland sources with large effective population sizes, had positive diversity components (C_S). The contribution of remote islands to total diversity (C_T) and total allelic richness (C_{TR}) was primarily through the differentiation component (C_D), which for some islands resulted in positive contributions, particularly for total allelic richness. The differentiation component (C_D), increases either with the presence of private alleles, or disparate allelic frequencies (Petit et al. 1998), as was the case for Attu and San Miguel Islands.

At the intraspecific level, BC and particularly southern California, made considerable contributions, which is in accordance with the higher regional levels of allelic richness (Table 1b), geological age of populations and the inclusion of several endemic subspecies within our Californian samples. Although the Alaskan sample also included several subspecies, the overall contribution was lower, demonstrating that genetic contributions as defined by neutral markers may omit adaptive differences in species lacking the strong phenotypic differences which are so obvious among song sparrow subspecies.

Implications for islands as reserves

Island populations are often targeted for conservation, because of high levels of endemism, and islands are often ecologically different from than their mainland counterparts. Islands also have additional conservation value as predator refugia (Anderson 1991; Burbidge 1999), and as tractable management units. In this study we focused on the extent to which intraspecific diversity is partitioned among island and mainland populations, in both the presence and absence of diagnosable subspecies. Our results suggest that the conservation of the differentiation components of genetic variation would typically require the inclusion of large and remote islands. For the song sparrows, these islands were also inhabited by endemic subspecies (Table 1), some of which are threatened. Even in the absence of obvious endemism, the relative conservation value of isolated island populations will be increased due to their genetic divergence, such that their contribution towards total diversity could be high relative to island area (Lesica and Allendorf 1995). Genetic targets usually aim to include alleles that occur at a frequency >0.05, which is based on the rationale that very rare alleles can be prohibitively difficult to sample, are evolutionarily insignificant due to high drift-mediated loss and have negligible contributions to heterozygosity (Marshall and Brown 1975; Brown and Briggs 1991; Holsinger and Gottlieb 1991). However, in programs targeting rarer alleles, it may be productive to include divergent island sites, as despite lower diversity even small samples from these islands could encompass certain frequency classes of alleles that could not be obtained in a mainland sample. However, small islands are prone to extinction, reducing their contribution towards in situ preservation. If these islands were already protected based on other criteria, which is the case for the Southern Gulf Islands, our results suggest these islands could contribute modest levels of genetic variation. For larger-scale genetic conservation, the mainland populations will often encompass the majority of the regional diversity, making mainland reserves essential inclusions for in situ genetic conservation programs (Eldridge et al. 2004). Nevertheless, we show that despite lower allelic richness, island populations still have the potential to contribute towards in situ genetic preservation. The extent to which this contribution is through diversity or differentiation can be predicted to some extent by island size, isolation, and population history.

Our conclusions have several important caveats. First, despite a per annum decline at the species-level, song sparrows remain abundant, but their trans-continental distribution enables them to serve as a model species for surveying geographic patterns in genetic variation. These patterns are relevant for the several song sparrow subspecies which are of conservation concern (*M.m.pusillula* and *M.m.graminea*, Shuford and Gardali 2008), but may also be indicative of potential patterns in other avian species which are undergoing more serious declines. Examples of declining species with both insular and mainland populations within our study range are: sage sparrow (*Amphispiza belli clemente*), Bewick's wren (*Thryomanes bewickii*), spotted towhee (*Pipilo maculates*) and horned lark (*Eremophila alpestris*) (Sauer et al. 2006). However, patterns of genetic variation may not be concordant across co-occurring taxa (O'Meally and Colgan 2005), and will depend on similarities in vagility and local population history.

The second, but most important caveat to our results is that the patterns of neutral genetic variation may not reflect the variation present at adaptive loci (Reed and Frankham 2001). Although the preservation of both neutral and adaptive diversity is justifiable (Crandall et al. 2000; Moritz 2002), the possibility for joint management depends on whether variation at neutral and adaptive loci are positively correlated. Under simulated conditions, the correlation between variation at adaptive and neutral loci depends on patterns of gene flow and selection (Le Corre and Kremer 2003). The discrepancies between variation at adaptive and neutral loci, has prompted suggestions that adaptive variation be directly measured (Reed and Frankham 2001). Within natural populations, current methods for estimating adaptive variation can be difficult and unsuitable for broad-scale surveys. Only

a few adaptive loci such as the major histocompatibility complex (MHC) can be surveyed at the molecular level. Reports of coinciding declines in diversity at both microsatellite and MHC loci have been reported in some island populations (Seddon and Baverstock 1999; Miller and Lambert 2004), however, high MHC variation has also persisted on island populations which are depauperate at neutral loci (Aguilar et al. 2004).

Advancements in population genomics hold the potential to settle this issue, as researchers will be able to screen larger portions of the genome, providing more accurate measures of genome-level variation (Bonin et al. 2007). Broader genomic coverage will increase the potential for detecting adaptive loci and thus the ability to survey adaptive variation at a broad-scale (Luikart et al. 2003). The capability to contrast patterns of variation across neutral and adaptive loci will contribute towards establishing priorities for genetic conservation and to our understanding of evolutionary processes on islands.

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