

ORIGINAL ARTICLE

The effects of contemporary processes in maintaining the genetic structure of western song sparrows (*Melospiza melodia*)

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Historic events and contemporary processes work in concert to create and maintain geographically partitioned variation and are instrumental in the generation of biodiversity. We sought to gain a better understanding of how contemporary processes such as movement and isolation influence the genetic structure of widely distributed vagile species such as birds. Song sparrows (*Melospiza melodia*) in western North America provide a natural system for examining the genetics of populations that have different patterns of geographic isolation and migratory behavior. We examined the population genetics of 576 song sparrows from 23 populations using seven microsatellite loci to assess genetic differentiation among populations and to estimate the effects of drift and immigration (gene flow) on each population. Sedentary,

isolated populations were characterized by low levels of immigration and high levels of genetic drift, whereas those populations less isolated displayed signals of high gene flow and little differentiation from other populations. Contemporary dispersal rates from migratory populations, estimated by assignment test, were higher and occurred over larger distances than dispersal from sedentary populations but were also probably too low to counter the effects of drift in most populations. We suggest that geographic isolation and limited gene flow facilitated by migratory behavior are responsible for maintaining observed levels of differentiation among Pacific coastal song sparrow populations.

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Introduction

Genetic variation within species provides the raw material for speciation, but many questions remain about the traits of organisms and the environment that facilitate biological diversification, including the role of historic and current processes such as vicariance and gene flow (Coyne and Orr, 2004). In vagile species, such as birds, it is often not known how genetic differentiation between populations is maintained in the absence of barriers to dispersal, particularly among migrants (Paradis *et al.*, 1998; Arguedas and Parker, 2000). Here, we ask how migratory behavior and the distribution of song sparrow populations influences genetic structure along the Pacific coast of western North America where this species occurs in sedentary and partially migratory populations (Table 1; Arcese *et al.*, 2002).

In a partially migratory population, some members of a population perform seasonal longer-distance movements, while other individuals remain in an area

throughout the year. In sedentary populations, most or all adults remain on or near their breeding territories year-round (Arcese, 1989; Wilson and Arcese, 2008). This provides a unique system for comparing the genetic structure and gene flow among populations that exhibit differing migratory propensities. We can examine movement from sedentary into other sedentary populations, sedentary into migratory populations, migratory into sedentary and migratory into other migratory populations. We expect a genetic signal of low immigration and high drift among sedentary populations, but the opposite pattern of high immigration rates and low drift among migratory populations should exist, if migration facilitates dispersal.

Previous work on song sparrows suggests that historic links among populations have shaped population genetic structure, but to different degrees. Analyses of mitochondrial (mt) DNA markers revealed little genetic structure across much of North America but did suggest that song sparrows expanded postglacially into much of their current distribution (Hare and Shields, 1992; Zink and Dittmann, 1993; Fry and Zink, 1998). More recent studies using microsatellite markers report modest to marked population differentiation as a result of sequential founding events in Alaska (Pruett and Winker, 2005) and microgeographic effects in California (Chan and

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Table 1 Locations, migratory behavior and sample sizes among 23 populations for the 576 song sparrows analyzed in this study (see Figure 1)

Location	Migration status	n
AK		
AT	Sedentary	30
AD	Sedentary	30
PN	Sedentary	21
KO	Partially migratory	22
CD	Partially migratory	30
HY	Partially migratory	18
AA	Partially migratory	30
BC		
QC	Partially migratory	24
MD	Partially migratory	30
BB	Partially migratory	25
AK	Partially migratory	24
RF	Partially migratory	25
SB, CA		
MM	Sedentary	21
LG	Sedentary	18
PB	Sedentary	27
DM	Sedentary	27
PM	Sedentary	20
SC	Sedentary	28
GS	Sedentary	21
RR	Sedentary	30
CO	Partially migratory	22
Southern CA		
WR	Partially migratory	24
SS	Sedentary	29

Abbreviations: AA, Alexander Archipelago; AD, Adak Island; AK, Alaksen, Westham Island; AT, Attu Island; BB, Burns Bog; BC, British Columbia; CA, California; CD, Copper River Delta; CO, Cosumnes River; DM, Dumbarton Marsh; GS, Goodyear Slough; HY, Hyder; KO, Kodiak Island; LG, Los Gatos Creek; MD, Mandarte Island; MM, Mark's Marsh; PB, Palo Alto Baylands; PM, Petaluma River Mouth; PN, Alaska Peninsula; QC, Queen Charlotte Islands; RF, Reifel, Westham Island; RR, Rush Ranch Open Space; SB, San Francisco Bay; SC, Sonoma Creek; WR, Western Riverside County.

Arcese, 2002, 2003; Patten *et al.*, 2004). Overall, these observations suggest that processes, such as geographic isolation and restricted gene flow, may affect population-level diversity and be discernible at larger spatial scales.

Song sparrow populations along the Pacific Coast inhabit two rather different distributional patterns, which for heuristic value we call 'linear' and 'planar'. From western Alaska to British Columbia, most populations are distributed almost linearly, and they are isolated from all other populations except for their nearest coastal neighbors (Figure 1). Populations from coastal British Columbia to California are found on the western edge of the species' continental distribution; but, relative to Alaska populations, they are not isolated from inland populations, being more planar in this distributional dimension (Figure 1). We expected that linear distribution of populations would facilitate isolation and drift, leading these populations to be more structured than planar populations. By combining distribution and migratory behavior, we further categorized song sparrow populations as linear sedentary, linear migratory, planar sedentary, or planar migratory to evaluate the effects of migratory behavior and geographic distribution on

population structure. We expected to observe a gradient in population structure, from highly structured linear sedentary populations to undifferentiated planar migratory populations, with other populations falling between these two extremes.

We used nuclear microsatellite loci to test our predictions in 23 populations of song sparrows studied previously by Chan and Arcese (2003); Patten *et al.* (2004); Pruett and Winker (2005), spanning both the linear and planar distributional and sedentary and migratory behavior patterns represented in the Pacific coastal range of this species (Figure 1, Table 1). Specifically, we asked (1) Is gene flow greater among migratory than sedentary populations? (2) Does genetic structure differ between linear and planar song sparrow populations? And, (3) do linear sedentary populations show a stronger signal of genetic drift and divergence than planar and migratory populations?

Materials and methods

Sampling and microsatellite data acquisition

We examined 576 song sparrows from 23 western North American breeding locations (Figure 1, Table 1). Individuals were sampled during the breeding season, making it unlikely that non-breeding transients were included in any samples. Individuals were collected or bled and released, and DNA was extracted following the methods described in Keller *et al.* (2001); Chan and Arcese (2002, 2003); Patten *et al.* (2004); Pruett and Winker (2005). Seven microsatellite loci were amplified for all individuals using fluorescent, dye-labeled primers developed for song sparrows (*Mme 1, 2, 3, 7, 12*; Jeffery *et al.*, 2001) and for two other bird species (*Escμ1*, Hanotte *et al.*, 1994; *GF2.35*, Petren, 1998). These loci were genotyped as described in Keller *et al.* (2001); Chan and Arcese (2002, 2003); Patten *et al.* (2004); Pruett and Winker (2005). As two of the loci are sex linked (*Mme3* and *Mme7*), in analyses we treated females as having missing data for these two loci. Song sparrows with known size fragments (representing scored alleles) were run among studies to ensure that data were concordant. This was carried out by amplifying individuals that had known allele sizes, running these individuals with each run, and scoring alleles based on these known size fragments.

Genetic structure

Tests for Hardy-Weinberg equilibrium and linkage disequilibrium were performed using ARLEQUIN (ver 2.000, Schneider *et al.*, 2000). Genetic differences between populations (pairwise F_{ST}) and whether these values differed significantly from zero ($\alpha = 0.05$; 10 000 permutations) were determined using ARLEQUIN (ver 2.000, Schneider *et al.*, 2000). As F_{ST} for sex-linked loci may differ from that of autosomal loci (Wang, 1999), we calculated the F_{ST} separately for autosomal and z-linked loci. These values were then weighted based on the proportion of base pairs found on the sex (1.5%; ~1.5 million base pairs) and autosomal chromosomes in relation to the size of the chicken (*Gallus gallus*) genome (~1 billion base pairs, <http://genomeold.wustl.edu/projects/chicken/index.php>). Values for autosomal and sex-linked loci were combined for an overall pairwise F_{ST} value. These values were very similar to the unweighted

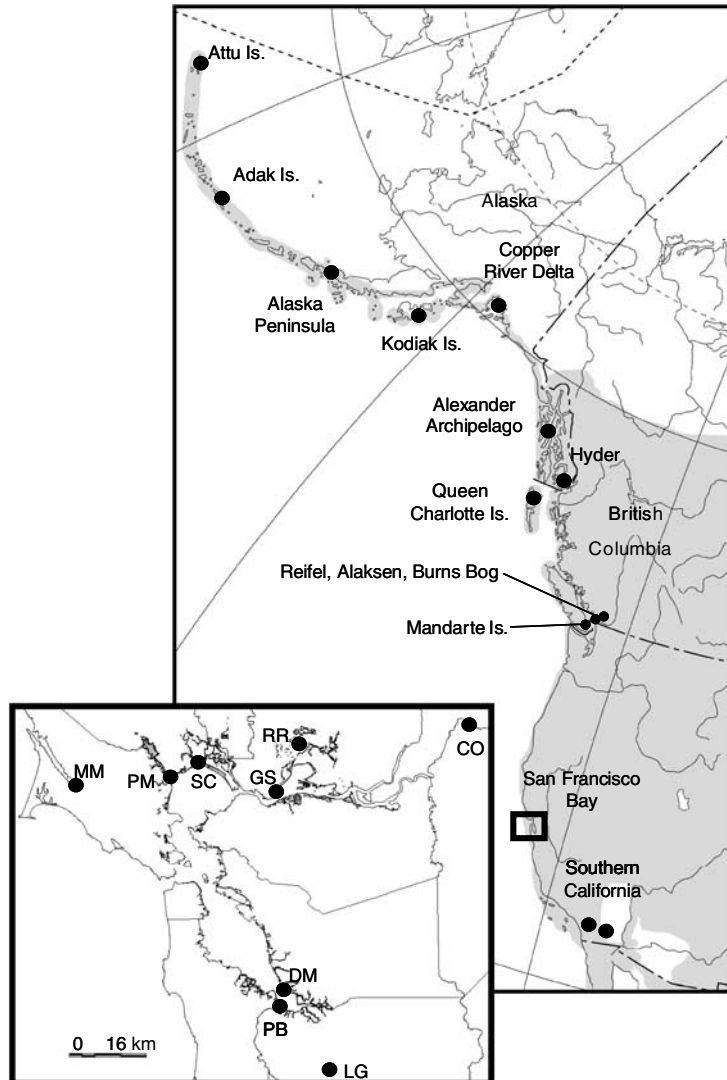


Figure 1 Map of the western distribution of song sparrows (*Melospiza melodia*) in North America shaded in gray. Dots represent sampling locations. Inset map is of San Francisco Bay, California. Attu Island, Adak Island, Alaska Peninsula, Kodiak Island and Copper River Delta locations are in the species' linear distribution. The remaining locations are part of the species' planar distribution.

F_{ST} estimates. We constructed a principle coordinates analysis graph using pairwise F_{ST} estimates (GenAIEx6; Peakall and Smouse, 2006).

Population structure models and assignment tests

We assessed the relative strengths of drift versus immigration in song sparrow populations using a coalescent-based Markov Chain Monte Carlo method as implemented in the program 2MOD (Ciofi *et al.*, 1999). Two models were evaluated: (1) the gene flow model, which assumes that gene frequencies within populations are caused by a balance between immigration and genetic drift, and (2) the drift model, which assumes that populations diverge solely through genetic drift. The relative likelihood of each model was calculated given the data. Where the gene flow model was judged as most likely, Nm (where N is population size and m is immigration rate) was calculated as an estimate of gene flow over time. Where the drift model was chosen, we calculated t/N (where t is the time of divergence; Ciofi

et al., 1999). The Markov Chain Monte Carlo search was performed twice for 500 000 iterations, with 200 000 discarded as burn in. Posterior distributions were checked to ensure convergence.

We used an assignment test to infer movement among populations (GeneClass 2; Piry *et al.*, 2004). When used conservatively, assignment tests have been shown to effectively measure dispersal among populations (Berry *et al.*, 2004). We used the very conservative method outlined by Underwood *et al.* (2007) to exclude or assign individuals as immigrants using the methods of Rannala and Mountain (1997) and Paetkau *et al.* (2004). Individuals were excluded from their location of origin when the probability of exclusion was greater than 95% ($\alpha = 0.05$). Individuals excluded from their population of origin were marginally assigned to another sampled population when $P > 0.33$. This probability was chosen based on the lowest mean Bayesian probability for the populations examined and thus represents a very conservative method of identifying immigrants. Individuals not assigned to any population with a

probability of $P > 0.33$ were assumed to be from an unsampled population, because we did not sample the entire distribution of song sparrows. We also attempted to use the program BayesAss (Wilson and Rannala, 2003) to infer gene flow among populations. However, our analyses failed to yield reliable results (see Faubet *et al.*, 2007).

Matrix correlations

Associations between $F_{ST}/(1-F_{ST})$ and log-transformed geographic distance and between these two variables controlling for the effect of angular direction (log-transformed bearing) were assessed using simple and partial Mantel tests. We constructed matrices of great-circle distances (<http://mathworld.wolfram.com/Great-Circle.html>) in kilometer and rhumb line bearings (straight-line routes that cross all of the meridians at the same angle based on a Mercator projection) between collection locations. We performed two comparisons for each association (six comparisons total): the entire matrix, the five linear populations (Attu Island to Copper River Delta; Figure 1), and the remaining 18 planar populations (Figure 1). All Mantel tests were performed using the program zt (Bonnet and Van de Peer, 2002), with significance of correlations assessed with 10 000 random permutations of the dependent matrix.

Results

Genetic structure

Tests for Hardy–Weinberg equilibrium showed that two loci (*Mme1* from Attu Island and *Mme2* from Kodiak island, Alexander Archipelago, Alaksen and Reifel) were

deficient in heterozygotes after adjustments for multiple comparisons. All loci were in linkage equilibrium.

Most pairwise F_{ST} estimates (Table 2) were significantly different from zero after Bonferroni correction ($\alpha = 0.0002$, 253 tests). The highest pairwise estimates of F_{ST} were found between all locations and Attu (0.14–0.40) and Adak (0.09–0.26) islands. Comparisons among some populations in British Columbia and most populations in California did not differ significantly from zero (Table 2). A principle coordinates analysis plot showed that most populations with planar distributions clustered together, with the exception of two in San Francisco Bay (Figures 1 and 2), Palo Alto Baylands and Dumbarton

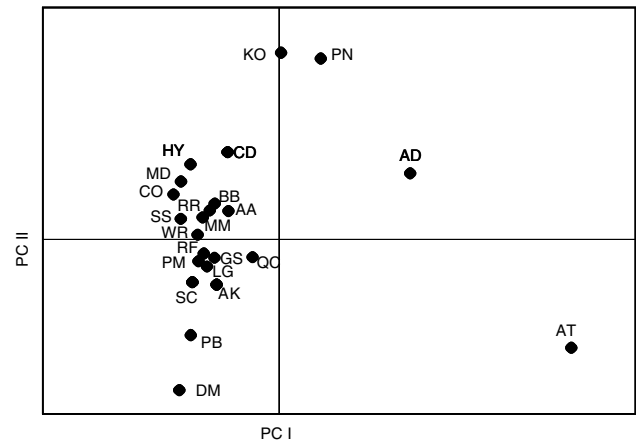


Figure 2 Principal coordinates analysis calculated using pairwise F_{ST} estimates between sites using the program GenAIEx (Peakall and Smouse, 2006). The first two axes explain 92.3% of variation.

Table 2 Pairwise estimates between song sparrow populations of genetic differentiation (F_{ST})

	AT	AD	PN	KO	CD	HY	AA	QC	MD	BB	AK	RF	MM	LG	PB	DM	PM	SC	GS	RR	CO	WR	
AD	0.14	—																					
PN	0.29	0.09	—																				
KO	0.37	0.18	0.09	—																			
CD	0.34	0.21	0.17	0.09	—																		
HY	0.37	0.21	0.17	0.11	0.05	—																	
AA	0.32	0.20	0.16	0.11	0.05	0.03	—																
QC	0.34	0.21	0.18	0.11	0.07	0.04	0.03	—															
MD	0.37	0.25	0.20	0.10	0.12	0.10	0.08	0.09	—														
BB	0.38	0.22	0.17	0.11	0.10	0.04	0.05	0.04	0.05	—													
AK	0.37	0.23	0.20	0.14	0.10	0.06	0.03	0.06	0.07	0.00	—												
RF	0.38	0.24	0.19	0.14	0.09	0.06	0.03	0.06	0.06	0.02	0.01	—											
MM	0.38	0.22	0.15	0.10	0.10	0.06	0.06	0.09	0.11	0.04	0.04	0.04	—										
LG	0.39	0.23	0.18	0.13	0.09	0.07	0.05	0.08	0.09	0.04	0.04	0.04	0.02	—									
PB	0.39	0.24	0.20	0.16	0.11	0.07	0.04	0.09	0.13	0.03	0.04	0.03	0.05	0.03	—								
DM	0.40	0.26	0.23	0.19	0.12	0.09	0.06	0.10	0.15	0.07	0.06	0.04	0.07	0.04	0.02	—							
PM	0.35	0.20	0.14	0.11	0.08	0.05	0.04	0.07	0.08	0.03	0.02	0.02	0.01	0.01	0.04	0.04	—						
SC	0.35	0.22	0.16	0.10	0.09	0.06	0.04	0.07	0.09	0.02	0.02	0.02	0.01	0.00	0.02	0.03	0.00	—					
GS	0.36	0.22	0.17	0.16	0.09	0.07	0.04	0.07	0.09	0.02	0.02	0.01	0.02	0.01	0.03	0.04	0.00	0.00	—				
RR	0.36	0.21	0.16	0.11	0.10	0.06	0.04	0.08	0.08	0.02	0.02	0.02	0.02	0.00	0.03	0.05	0.00	0.00	0.00	—			
CO	0.38	0.22	0.15	0.11	0.10	0.05	0.05	0.08	0.09	0.03	0.04	0.03	0.02	0.01	0.04	0.05	0.00	0.01	0.03	0.00	—		
WR	0.36	0.21	0.16	0.11	0.10	0.06	0.05	0.08	0.08	0.02	0.02	0.02	0.01	0.01	0.03	0.04	0.01	0.01	0.01	0.01	0.01	0.03	—
SS	0.39	0.24	0.17	0.13	0.11	0.07	0.07	0.10	0.11	0.05	0.05	0.04	0.02	0.03	0.05	0.05	0.02	0.02	0.03	0.03	0.02	0.02	0.02

Abbreviations: AA, Alexander Archipelago; AD, Adak Island; AK, Alaksen, Westham Island; AT, Attu Island; BB, Burns Bog; CD, Copper River Delta; CO, Cosumnes River; DM, Dumbarton Marsh; GS, Goodyear Slough; HY, Hyder; KO, Kodiak Island; LG, Los Gatos Creek; MD, Mandarte Island; MM, Mark's Marsh; PB, Palo Alto Baylands; PM, Petaluma River Mouth; PN, Alaska Peninsula; QC, Queen Charlotte Islands; RF, Reifel, Westham Island; RR, Rush Ranch Open Space; SC, Sonoma Creek; WR, Western Riverside County.

F_{ST} estimates in italics are not significantly different from zero after Bonferroni correction ($P = 0.0002$, 253 tests). Seventy-nine percent (201) of pairwise comparisons exhibited significant genetic differentiation after Bonferroni correction.

Marsh. Populations in the linear distribution were the most genetically differentiated (Figures 1 and 2).

Population structure models and assignment tests

The genetic structure of all song sparrow populations is best explained by the gene flow model ($P=1.00$). The relative effects of gene flow and genetic drift were evaluated using F (the probability of identical alleles by descent) and M (the number of migrants per generation; Ciofi *et al.*, 1999). Low levels of immigration over time relative to drift were inferred in the linear populations (Table 3), with Attu Island showing the strongest signal of drift ($F=0.65$, 90% highest posterior density range: 0.52–0.69; $M=0.14$). In contrast, high levels of immigration relative to drift were found in most of the planar populations ($F=0.02$ –0.18; $M=1.16$ –12.9). Using information available from long-term studies of song sparrows (Arcese *et al.*, 2002), we used the formula by Sæther *et al.* (2005) to estimate a generation time of 2.56 years for the species. On the basis of this estimate, one migrant per 18.6 years has reached Attu Island and less than one migrant per year has reached the other linear populations (Table 3). In contrast, planar populations were estimated to have several immigrants annually into both migratory and sedentary populations (Table 3).

Forty-seven of 576 birds (8.16%) were excluded as having originated in the location where they were sampled with a probability of $\geq 95\%$ (Table 3). Of these 47 birds, 17 were assigned to another location and 15 of

those 17 assigned best to partially migratory populations. Thirty individuals were not assignable with a high probability to any site (Table 3). The percentage of individuals excluded from their location of origin ranged between 3 and 22% (Table 3). Similar numbers of individuals from migratory ($N=16$) and sedentary ($N=14$) populations did not assign strongly to any population. Individuals from migratory populations appeared to move greater distances when dispersing to another location, with average distances moved from migratory to migratory ($N=10$; 1 409 km \pm 369) and migratory to sedentary ($N=5$; 772 km \pm 216) being much larger than from sedentary to sedentary ($N=2$; 65 km \pm 39) and from sedentary into migratory populations ($N=0$).

Matrix correlations

We found several strong correlations between genetic and geographic matrices including a significant correlation between F_{ST} and geographic distance ($r=0.538$; $P=0.0001$), even after controlling for the effect of angular direction in the entire dataset ($r=0.502$; $P=0.0001$). When submatrices were examined, both distributional patterns showed a signal of isolation by distance (linear $r=0.809$, $P=0.0083$; planar $r=0.500$, $P=0.0001$), even after accounting for a possible interaction between distance and angle of direction (linear $r=0.825$, $P=0.017$; planar $r=0.505$, $P=0.0001$). However, there

Table 3 2MOD and GENECLASS test results for western song sparrow populations

Location	n	2MOD			GENECLASS			
		F (90% HPD)	M	Years/migrant	MBP	Unassigned	Assigned	Likely origin
AT	30	0.65 (0.52–0.69)	0.14	18.6	0.70	1	0	—
AD	30	0.50 (0.39–0.52)	0.25	10.1	0.63	2	0	—
PN	21	0.32 (0.26–0.34)	0.53	4.87	0.59	3	2	HY, CD
KO	22	0.21 (0.21–0.29)	0.97	1.52	0.59	3	1	WR
CD	30	0.12 (0.09–0.12)	1.88	1.36	0.52	3	1	BB
HY	18	0.07 (0.06–0.09)	3.10	0.83	0.36	2	2	MD, CO
AA	30	0.05 (0.04–0.07)	5.05	0.51	0.45	0	0	—
QC	24	0.10 (0.10–0.15)	2.32	1.10	0.49	4	0	—
MD	30	0.18 (0.15–0.25)	1.16	2.21	0.53	3	2	BB, WR
BB	24	0.05 (0.04–0.09)	4.67	0.55	0.62	3	1	RF
AK	24	0.06 (0.05–0.08)	3.60	0.71	0.53	2	1	RF
RF	25	0.05 (0.05–0.08)	4.31	0.59	0.57	1	0	—
MM	21	0.04 (0.04–0.07)	5.52	0.46	0.47	2	1	BB
LG	18	0.02 (0.02–0.04)	11.2	0.23	0.33	4	1	PM
PB	27	0.06 (0.05–0.07)	4.04	0.63	0.54	1	0	—
DM	27	0.04 (0.04–0.10)	5.34	0.48	0.56	1	0	—
PM	20	0.02 (0.02–0.04)	11.3	0.23	0.49	1	0	—
SC	28	0.02 (0.02–0.03)	12.9	0.20	0.49	4	3	AK, GS, WR
GS	21	0.03 (0.02–0.04)	8.55	0.30	0.41	3	2	CO, WR
RR	30	0.03 (0.02–0.04)	7.03	0.36	0.61	0	0	—
CO	22	0.02 (0.01–0.04)	10.7	0.24	0.41	1	0	—
WR	24	0.02 (0.02–0.04)	11.8	0.22	0.38	2	0	—
SS	29	0.04 (0.04–0.07)	5.68	0.45	0.58	1	0	—

Abbreviations: AA, Alexander Archipelago; AD, Adak Island; AK, Alaksen, Westham Island; AT, Attu Island; BB, Burns Bog; CD, Copper River Delta; CO, Cosumnes River; DM, Dumbarton Marsh; GS, Goodyear Slough; HPD, highest posterior density; HY, Hyder; KO, Kodiak Island; LG, Los Gatos Creek; MBP, mean Bayesian probability; MD, Mandarte Island; MM, Mark's Marsh; PB, Palo Alto Baylands; PM, Petaluma River Mouth; PN, Alaska Peninsula; QC, Queen Charlotte Islands; RF, Reifel, Westham Island; RR, Rush Ranch Open Space; SC, Sonoma Creek; WR, Western Riverside County.

2MOD results are based on the gene flow model with F being the probability that two genes share a common ancestor within a population and M being the number of migrants per generation. Years per migrant (years/migrant) are based on the estimated generation time of song sparrows of 2.56 years. GENECLASS results show the number of individuals excluded from their population of origin (unassigned), when there was less than a 0.05 chance that their genotype occurs at that site. Assigned individuals have a greater than 0.33 likelihood of being the source for an immigrant.

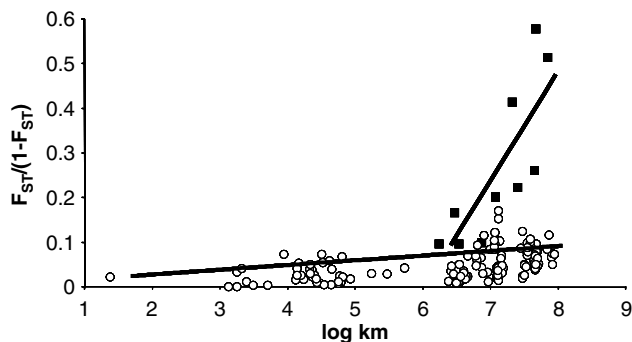


Figure 3 Plot of genetic divergence ($F_{ST}/(1-F_{ST})$) and log-transformed geographic distance in kilometer for linear (black squares) and planar (white circles) populations.

was a much steeper association between F_{ST} and geographic distance for the linear populations (Figure 3).

Discussion

Effects of migration on genetic structure

Migratory behavior appears to facilitate dispersal in Pacific coast song sparrow populations and as suggested by Paradis *et al.* (1998) may act to increase gene flow and reduce genetic structure among populations. In Pacific coast song sparrows, 88% of unassigned birds had likely dispersed from a partially migratory population (assigned strongly to another site), and this dispersal was potentially over large distances (>500 km; Figure 1, Table 3). Long-distance movement of over 1 000 km has been documented in song sparrows based on banding recoveries (Davis and Arcese, 1999). Theory suggests that long-distance dispersal events should reduce population genetic structure (Ibrahim *et al.*, 1996). But in song sparrows, movement among geographically distant populations does not appear to have counteracted the effects of genetic drift, especially in populations that are geographically isolated. For example, the Kodiak Island population had an individual that assigned with high likelihood to southern California (WR). However, song sparrows from Kodiak Island differ genetically from those sampled in California and show a strong signal of genetic drift, less than one immigrant per generation. If outbreeding depression occurs among hybrids from distant populations, natural selection may also influence the genetically effective rate of migration and reduce its influence on population differentiation (Marr *et al.*, 2002). Another possibility is that the misassigned individual from Kodiak Island dispersed from an unsampled interior location that was genetically very similar to the southern California population. Given that genetic structuring is evident at microgeographic scales (Figure 2), the likelihood of a location several hundred kilometers away from southern California exhibiting a similar genetic signature as the WR population seems remote. Regardless, the nearest unsampled populations are greater than 500 km from Kodiak Island (Figure 1) and are migratory. Thus, long-distance dispersal (in this instance) is very likely from a migratory population.

Our results also suggest that most individuals from sedentary populations of song sparrows remain philopatric to their natal population, or when disperse they move relatively short distances to other sedentary

populations (based on assignment tests; Table 3). Apparent immigrants coming from a sedentary location dispersed on average 65 km. In contrast, short-distance dispersal might be linked to ongoing gene flow in some San Francisco Bay populations that cannot be distinguished genetically. Other sedentary populations appeared to be currently isolated with no individuals excluded by assignment test but nevertheless showed fairly high numbers of immigrants per generation (more than four individuals per generation) and a weak signal of genetic drift (Table 3), perhaps as a consequence of high historic gene flow but current isolation. A lack of current gene flow appears sufficient to have isolated song sparrow populations in the Palo Alto Baylands and at Dumbarton Marsh, contributing to their divergence from other populations of song sparrows in San Francisco Bay.

Effects of distributional pattern on population structure

Pacific coastal populations of song sparrows are distributed relative to neighboring populations in two different ways, which we have heuristically termed linear and planar on a macrogeographic scale (Figure 1). The genetic structures of populations associated with each distributional pattern were markedly dissimilar. Linearly distributed populations displayed more genetic structure and stronger signal of genetic drift than populations occurring along the continental planar distribution. There was modest genetic structure among populations occurring along the edge of the planar distributional pattern, with southeast Alaska and British Columbia locations having significantly different F_{ST} values from California locations. However, at finer scales, populations within British Columbia or California, were not strongly geographically structured except for two locations in San Francisco Bay (Dumbarton Marsh and Palo Alto Baylands). The marked differentiation of these two populations was noted previously by Chan and Arcese (2002, 2003) and reflects isolation due to adaptive differences in salinity tolerance or cryptic geographic barriers. Whatever the reason, these two populations clearly do not fit the patterns expected with the larger-scale condition among other planar populations where there are no strong geographic isolating barriers to gene flow.

The differences between linear and planar populations were also apparent in the matrix correlations (Figure 3): genetics and geography were correlated significantly across the entire dataset. This association appeared to be primarily due to the strong signal of isolation by distance among linear populations. Although there was genetic structuring within the planar populations, it was not as strongly correlated with geographic distance. Whether or not populations were oriented in a north–south or east–west direction was not correlated with the genetic divergence among populations. Pruett and Winker (2005) found a sequential loss in diversity and an increase in differentiation among the linear populations that was likely caused by the initial founding of Alaska by song sparrows. However, the maintenance of genetic relationships among these populations is most likely the result of restricted gene flow caused by their linear distribution. Although our results may be confounded to some degree by differences in life-history strategy (that

is, sedentariness versus partial seasonal migration), there appear to be pronounced genetic effects to being distributed in a one-dimensional (linear) versus a two-dimensional (planar) macrogeographic pattern.

Synergy of geography and behavior

By sampling across geographically (linear versus planar) and behaviorally (sedentary versus seasonally migratory) varying populations, we can evaluate whether there is a synergistic effect of being linearly distributed and sedentary or planarly distributed and migratory. These complementarily coupled patterns would theoretically represent synergistic extremes in which linear sedentary populations should be strongly differentiated from other populations and planar-migratory populations should be the least differentiated because of differences in gene flow in these coupled patterns. Linear populations do fit this expected pattern. Linear sedentary populations (Aleutian Island and Alaska Peninsula) showed a strong genetic signal of drift and differentiation, and thus it seems likely that geography and behavior are synergistically maintaining differentiation in these populations. Kodiak Island and Copper River Delta song sparrows are linear migratory and have a moderate signal of differentiation with limited gene flow. Thus, migratory behavior does seem to facilitate gene flow to some extent in these linear populations.

Among planar sedentary San Francisco Bay populations, Dumbarton Marsh and Palo Alto Baylands strongly differed from all other populations. Thus, sedentariness does appear to have an effect on the genetic structuring of these populations. However, other San Francisco Bay song sparrows showed little differentiation among themselves and when contrasted with planar migratory populations. In addition, planar sedentary birds from the Salton Sea were similar to other planar populations. We found that planar migratory populations in British Columbia and southern California also were not divergent from other populations. These findings suggest that a planar distribution is more important than migratory behavior in structuring song sparrow populations. However, an equally plausible explanation is that historic signals of high gene flow (high number of migrants per generation in the 2MOD analysis; Table 3) are obscuring contemporary effects of limited gene flow.

Teasing apart the roles of historic and contemporary processes is difficult. However, it is apparent that both processes have played and continue to play a strong role in the genetic structure occurring today in Pacific coastal song sparrows. Limited dispersal among populations, with much of this dispersal apparently occurring over large geographic distances, appears to have little effect on homogenizing the genetics of geographically distant populations. This limited movement should, over time, lead to higher differentiation—and potentially to speciation—especially in isolated, linearly distributed populations.

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