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FINE-SCALE POPULATION STRUCTURE AND ASYMMETRICAL DISPERSAL IN AN OBLIGATE SALT-MARSH PASSERINE, THE SALTMARSH SPARROW (*AMMODRAMUS CAUDACUTUS*)

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ABSTRACT.—Understanding the spatial scale of gene flow can yield valuable insight into the ecology of an organism and guide conservation strategies. Fine-scale genetic structure is uncommon in migratory passerines because of their high vagility and presumed high dispersal abilities. Aspects of the behavior and ecology of some migratory species, however, may promote structure on a finer scale in comparison to their mobility. We investigated population genetic structure in the Saltmarsh Sparrow (*Ammodramus caudacutus*), a migratory passerine that breeds along the northeastern coast of the United States, where it is restricted exclusively to a narrow strip of patchily distributed tidal marsh habitat. Using genotyping with 10 microsatellite loci, we detected weak but significant population structure among Saltmarsh Sparrows from nine marshes on the breeding grounds between Scarborough, Maine, and Oceanside, New York. Genetic variation among marshes was largely consistent with a pattern of isolation by distance, with some exceptions. One inland marsh was genetically divergent despite its proximity to other sampled marshes, which suggests that mechanisms besides geographic distance influence population genetic structure. Bayesian clustering, multivariate analyses, and assignment tests supported a population structure consisting of five groups. Estimates of migration rates indicated variation in gene flow among marshes, which suggests asymmetrical dispersal and possible source–sink population dynamics. The genetic structure that we found in Saltmarsh Sparrows may result from natal philopatry and breeding-site fidelity, combined with restricted dispersal due to obligate dependence on a patchy habitat. Our findings suggest that fine-scale population structure may be important in some migratory passerines. Received 12 July 2011, accepted 1 February 2012.

Key words: *Ammodramus caudacutus*, dispersal, genetic structure, microsatellites, migratory passerine, Saltmarsh Sparrow, source–sink dynamics.

Estructura Poblacional a Escala Fina y Dispersión Asimétrica en *Ammodramus caudacutus*, un Paserino Habitante de Marismas

RESUMEN.—El entendimiento de la escala espacial del flujo genético puede brindar información valiosa sobre la ecología de un organismo y guiar las estrategias para su conservación. La estructura genética a escala fina es poco común en aves migratorias por su alta capacidad de movimiento y su presuntamente alta capacidad de dispersión. Sin embargo, algunos aspectos del comportamiento y la ecología de algunas especies migratorias podrían promover la aparición de estructura en una escala más fina en comparación con su movilidad. Investigamos la estructura genética de *Ammodramus caudacutus*, un paserino migratorio que se reproduce a lo largo de la costa noreste de Estados Unidos, donde se restringe a una franja estrecha de marismas con distribución discontinua. Usando genotipificación basada en 10 loci de microsatélites detectamos estructura poblacional débil pero significativa entre poblaciones de *A. caudacutus* de nueve marismas en las áreas de reproducción entre Scarborough, Maine y Oceanside, Nueva York. La variación genética entre marismas fue ampliamente consistente con un patrón de aislamiento por distancia, con algunas excepciones. Una de las zonas de marisma del interior fue genéticamente divergente a pesar de su proximidad a otras zonas muestreadas, lo que sugiere que otros mecanismos aparte de la distancia geográfica afectan la estructura genética poblacional. Nuestros análisis de agrupamiento bayesiano, análisis multivariados y pruebas de asignación sustentaron una estructura poblacional compuesta por cinco grupos. Los estimados de las tasas de migración indicaron flujo genético diferencial entre marismas, lo que sugiere dispersión asimétrica y posiblemente una dinámica de poblaciones fuente–sumidero. La estructura genética que encontramos en *A. caudacutus* puede ser el resultado de filopatría natal y fidelidad al sitio de reproducción, junto con dispersión restringida debida a la dependencia obligatoria de un hábitat distribuido en parches. Nuestros resultados sugieren que la estructura poblacional a escala fina puede ser importante en algunas aves migratorias.

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IDENTIFYING PATTERNS OF population genetic structure, including the scale of dispersal and connectivity, is essential if we are to understand the complexities that underlie the dynamics of natural populations. The scale at which populations are connected by gene flow can indicate the approximate scale of demographic independence and provide insight into the designation of management units (Scribner et al. 2005, González-Suárez et al. 2009), thereby having important implications for effective conservation.

High mobility is commonly invoked to explain genetic homogeneity of avian populations (Crochet 2000). Despite their high vagility, many avian species exhibit behaviors and occupy habitats that promote population genetic structure. Even some of the most mobile migratory species have been found to exhibit population structure associated with oceanographic barriers, variation in foraging patterns, and breeding-season philopatry (e.g., Friesen et al. 2007, Milot et al. 2008, Gómez-Díaz et al. 2009, Barlow et al. 2011). Strong population structure has been documented in species that display natal philopatry (Temple et al. 2006, Coulon et al. 2008), cooperative breeding (Bouzat and Johnson 2004, Double et al. 2005, Woxvold et al. 2006), and sex-biased dispersal (Hall et al. 2009, Sonsthagen et al. 2009). Discontinuous or patchily distributed core habitats (resulting from natural or anthropogenic fragmentation) also influence population structure of both migratory and nonmigratory avian species (Johnson et al. 2003, Segelbacher et al. 2003, Fazio et al. 2004, Barr et al. 2008, Lindsay et al. 2008, Bruggeman et al. 2010). Fragmentation of breeding habitat may pose a barrier to dispersal on a much finer scale in comparison to the movement abilities of a species during migration (Lindsay et al. 2008). Finally, landscape heterogeneity can affect the spatial distribution of a species, and the emergence of marginal edge habitats can lead to asymmetrical dispersal between patches of varying quality (Kawecki 2008). These demographic effects may be manifested in source–sink population dynamics, in which self-sustaining source populations produce surplus emigrants that sustain sink populations in lower-quality habitats (Pulliam 1988).

Few studies have documented genetic structure in migratory passerines on small spatial scales within the breeding grounds. Recent analytical advances provide powerful new approaches for detecting and evaluating ecologically meaningful population structure in potentially high-gene-flow scenarios (Waples and Gaggiotti 2006, Faubet and Gaggiotti 2008, Hubisz et al. 2009). We characterized population genetic structure and dispersal patterns in breeding populations of the Saltmarsh Sparrow (*Ammodramus caudacutus*), a species of high conservation concern (U.S. Department of Interior 2008) that is globally vulnerable to extinction because of its limited range and obligate habitat requirement (IUCN Red List criteria; BirdLife International 2004). The Saltmarsh Sparrow is the only passerine species, globally, that is found exclusively in tidal marshes during all parts of its life cycle (Greenberg 2006). Its breeding range extends from Maine to Virginia (Greenlaw and Woolfenden 2007), with an estimated 90% of the global population breeding in a narrow strip of patchily distributed tidal-marsh habitat along the northeastern coast of the United States (Hodgman et al. 2002). It also winters in salt-marsh habitat along the Atlantic coast from Virginia to Florida and the Gulf coast of Florida (Greenlaw and Woolfenden 2007). The reliance of Saltmarsh Sparrows on the limited and patchily distributed salt-marsh habitat may influence their population dynamics and spatial structure. Obligate dependence on a patchily

distributed habitat, coupled with patch area sensitivity (Shriver et al. 2004), may restrict gene flow in Saltmarsh Sparrows in comparison to species that occupy more continuous habitats. Evidence of site fidelity and natal philopatry (DiQuinzio et al. 2001) further suggest the potential for population structure over a relatively fine scale in Saltmarsh Sparrows. Elucidating population structure and dispersal of Saltmarsh Sparrow breeding populations may aid in conservation management and also yield insight into the factors that influence gene flow in avian species.

We used microsatellite genotyping in conjunction with individual- and population-based analyses to assess genetic variation of Saltmarsh Sparrows from nine coastal marshes in the northeastern United States. Our objectives were to (1) characterize population genetic structure, (2) quantify dispersal rates among marshes, and (3) evaluate the ability of the genetic data to identify source–sink population dynamics in this system. We expected to detect spatial genetic structure in Saltmarsh Sparrows from geographically separated marshes and predicted strongest divergence for populations separated by the largest geographic distance.

METHODS

Study system and sample collection.—We sampled Saltmarsh Sparrows during June and July of 2006–2008 at multiple subsites within nine marshes in the northeastern United States within the northern half of the species' breeding range (Table 1). Study marshes were located in Wells, Maine (Furbish Marsh, Rachel Carson National Wildlife Refuge [NWR]); Scarborough, Maine (Scarborough Marsh, Rachel Carson NWR); Hampton, New Hampshire (Hampton Marsh); Rye, New Hampshire (Fairhill Marsh); Stratham, New Hampshire (Chapman's Landing); Newburyport, Massachusetts (Parker River NWR); Narragansett, Rhode Island (John H. Chafee NWR); Shirley, New York (Wertheim NWR); and Oceanside, New York (Marine Nature Center; Fig. 1). Most sites were sampled in 1 year, and three sites were sampled over 2 or 3 years. Multiyear sampling was conducted at these sites to ensure adequate sample sizes and avoid potential biases that would result from nonrandom sampling. Temporally replicated samples provide an effective means of distinguishing between stable genetic signals and patterns resulting from sampling artifacts, and pooling genetic data across years can therefore be useful to account for stability of social structure over time (Waples 1998, Frantz et al. 2008). We deployed two to six 12-m mist nets with 36-mm mesh to capture a target sample of 50 birds from each site. In conjunction with an ongoing toxicology study (Lane et al. 2011), blood samples (30–50 μ L) were drawn from the cutaneous ulnar vein using a nonheparinized capillary tube with methods approved by the Institutional Animal Care and Use Committee of the University of New Hampshire (protocol 070604); a few blood drops were transferred to Whatman filter cards and stored at room temperature for later genetic analysis.

DNA extraction and microsatellite analysis.—DNA was extracted from blood samples using a DNeasy Blood Kit (Qiagen, Valencia, California) according to manufacturer protocol. Some studied marshes were located in an overlap zone within which the Saltmarsh Sparrow is known to hybridize with a congener, Nelson's Sparrow (*A. nelsoni*) (Shriver et al. 2005, Walsh et al. 2011). For this reason, we performed a genetic barcoding RFLP assay (Walsh et al. 2011) to confirm the species identity

TABLE 1. Genetic diversity of Saltmarsh Sparrows from nine marshes in the northeastern United States (n = number of individuals sampled). Observed (H_O) and expected (H_E) heterozygosities, F_{IS} , number of alleles, allelic richness, and private alleles for each population are averaged across 10 microsatellite loci.

Sampling location	Latitude	Longitude	Years sampled	n	H_O	H_E	F_{IS}	Percent of alleles	Allelic richness	Percent of private alleles (private allelic richness)
Scarborough, Scarborough, Maine (Rachel Carson NWR)	43.56N	70.36W	2007–2008	40	0.786	0.826	0.048	10.6	8.7	2 (0.37)
Furbish, Wells, Maine (Rachel Carson NWR)	43.28N	70.58W	2006–2007	64	0.774	0.801	0.034	11.3	8.5	1 (0.31)
Chapman's Landing, Stratham, New Hampshire	43.04N	70.92W	2008	30	0.790	0.803	0.016	9.6	8.4	1 (0.36)
Fairhill, Rye, New Hampshire	43.03N	70.72W	2008	35	0.808	0.797	-0.014	9.8	8.4	0 (0.27)
Hampton Beach, Hampton, New Hampshire	42.92N	70.81W	2008	45	0.784	0.799	0.019	10.2	8.3	1 (0.28)
Parker River, Newburyport, Massachusetts (Parker River NWR)	42.77N	70.80W	2006–2008	72	0.794	0.816	0.026	12.7	8.8	6 (0.35)
John H Chafee NWR, Narragansett, Rhode Island	41.45N	71.44W	2007–2008	53	0.756	0.793	0.046	11.1	8.5	2 (0.35)
Wertheim NWR, Shirley, New York	40.76N	72.09W	2007	29	0.717	0.772	0.072	9	7.8	1 (0.27)
Marine Nature Center, Ocean-side, New York	40.62N	73.62W	2008	19	0.768	0.772	0.007	8.2	8.0	2 (0.28)

of sampled individuals. This test eliminated individuals that were morphologically similar to Saltmarsh Sparrows but had mtDNA of Nelson's Sparrows. Although our approach was not able to distinguish and eliminate from the data set potential hybrid individuals with Saltmarsh Sparrow mtDNA, this likely only affected a very small number of individuals. Previous findings indicated that female Nelson's Sparrows mate more randomly than female Saltmarsh Sparrows (Rising and Avise 1993,

Shriver et al. 2005) and that introgression is asymmetrical, with hybrids more morphologically and genetically similar to Saltmarsh Sparrows (Shriver et al. 2005). Therefore, using morphological features to distinguish the species in the field, followed by removal of individuals with Nelson's mtDNA, likely resulted in successful screening of the majority of hybrid individuals. DNA was amplified using 11 microsatellite loci: Aca01, Aca04, Aca05, Aca08, Aca11, Aca12, Aca17, Aca21 (Hill et al. 2008), Esc μ 1, Esc μ 6 (Hanotte et al. 1994), and As μ 15 (Bulgin et al. 2003). The 12.5- μ L polymerase chain reactions contained 2 μ L of eluted genomic DNA, 0.3–0.8 μ M of each primer (labeled with Hex, Ned, or Fam), 1.5–2.5 mM MgCl₂, 1X PCR buffer (Promega, Madison, Wisconsin), 0.2 mM of deoxyribonucleotides, and 1 unit of Taq DNA polymerase (Promega). Cycling conditions were as follows: 30–32 cycles of 94°C for 30 s, 51–56°C for 45 s, 72°C for 1 min, and a final extension step at 72°C for 5 min. Optimal annealing temperatures were 51°C for As μ 15, 55°C for Esc μ -1 and Esc μ -6, and 56°C for Aca01, Aca04, Aca05, Aca08, Aca11, Aca12, Aca17, and Aca21. Amplified products were electrophoresed on an automated DNA sequencer (ABI 3130 Genetic Analyzer; Applied Biosystems, Foster City, California), and individual genotypes were scored manually using PEAKSCANNER software (Applied Biosystems). Positive controls were used in conjunction with the program ALLELOGRAM (Morin et al. 2009) to standardize allele calls across electrophoretic runs. Alleles were binned manually according to the normalized raw scores generated by ALLELOGRAM.

We used the program MICRO-CHECKER (Van Oosterhout et al. 2004) to check the data set for scoring errors and null alleles. We identified null alleles in Aca21 and subsequently dropped this locus from the final data set. We tested for linkage disequilibrium using the randomization method implemented in the program FSTAT (Goudet 1995). To assess genetic diversity, unbiased

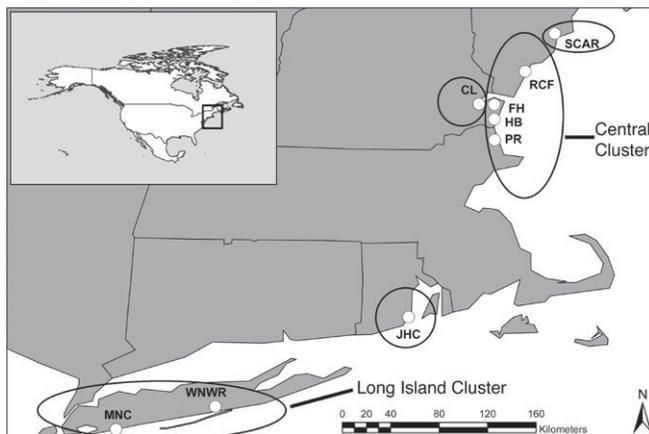


FIG. 1. Location of marshes along the northeastern coast of the United States, where Saltmarsh Sparrows were sampled for population genetic analyses. Abbreviations: SCAR = Scarborough Marsh, RCF = Furbish, CL = Chapman's Landing, FH = Fairhill Marsh, HB = Hampton Beach, PR = Parker River, JHC = John H. Chafee, WNWR = Wertheim National Wildlife Refuge, and MNC = Marine Nature Center. Circles define marshes that belong to five population groupings identified by spatial analysis of molecular variation, Bayesian clustering, and multivariate analysis (see text).

estimates of expected and observed heterozygosities were calculated in FSTAT. The F_{IS} values estimated in FSTAT were used to test for deviations from Hardy-Weinberg equilibrium. Significance testing was performed using 10,000 randomization steps with a Bonferroni adjustment ($\alpha = 0.05$, $P = 0.00036$). The number of private alleles was calculated in GENALEX, version 6.1 (Peakall and Smouse 2006), and allelic and private allelic richness were estimated using the rarefaction method, which corrects for sample-size difference, implemented in the program HP-RARE (Kalinowski 2005).

Population structure.—To characterize genetic differentiation among marshes, we calculated pairwise F_{ST} values and performed significance testing using 1,000 permutations in FSTAT, with a Bonferroni adjustment for multiple tests ($\alpha = 0.05$, $P = 0.001$). For sites that were sampled in multiple years, we used pairwise F_{ST} values to test for annual variation in allele frequencies and F_{IS} values to test for nonrandom sampling between years. There were no significant differences in F_{ST} values and no significant F_{IS} values when the same site was compared over multiple years (data not shown), allowing us to combine multiyear data for these marshes. Small and nonsignificant F_{IS} values for all nine marshes in the final data set further indicated that our analyses were not biased by nonrandom sampling (see results and Table 1). To evaluate whether genetic variation was correlated with geography, we tested for isolation-by-distance effects by comparing matrices of geographic distance (Euclidean) and genetic distance (linearized F_{ST}) using a Mantel test with 10,000 permutations implemented with the “vegan” package (Oksanen et al. 2011) in R statistical software (R Development Core Team 2010).

We tested for the presence of hierarchical structure and identified genetically similar population clusters using multiple methods: (1) a spatial analysis of molecular variance using the program SAMOVA (Dupanloup et al. 2002); (2) the Bayesian clustering approach of STRUCTURE, version 2.3.2 (Pritchard et al. 2000); and (3) a multivariate analysis using discriminant analysis of principal components (DAPC; Jombart et al. 2010). Using multiple analytical methods is recommended because it can lead to less biased assessments of population structure (François and Durand 2010, Kanno et al. 2011), and multivariate analyses are useful complements to Bayesian clustering approaches (Patterson et al. 2006, Jombart et al. 2010). SAMOVA uses genotypic data in conjunction with geographic coordinates of the sample locations to designate genetically similar population groups. We ran SAMOVA for $K = 1-9$ potential populations and compared F_{CT} values across runs to identify the most appropriate number of groups for the data.

We used the LocPrior clustering algorithm implemented in STRUCTURE to sort individuals into appropriate population clusters (Pritchard et al. 2000, Hubisz et al. 2009). The LocPrior model accounts for sampling locations and assumes that the probability that an individual is assigned to a cluster varies among locations. This method is appropriate for detecting weak genetic structure and is desirable in that it does not find structure where it does not exist (Hubisz et al. 2009). We conducted five runs for each value of $K = 1-9$; each run consisted of a 300,000 burn-in followed by 200,000 iterations. We used the admixture model, which calculates admixture proportions assuming that all individuals originated from the admixture of K parental populations (Pritchard et al. 2010), and assumed correlated allele frequencies (Falush et

al. 2003). We determined the most likely number of population clusters (K) by using the ΔK method of Evanno et al. (2005) and examining the bar plots. We conducted 25 additional runs for the most likely K and averaged results across runs using the “greedy” algorithm implemented in the program CLUMPP (Jakobsson and Rosenberg 2007); results were plotted in DISTRUCT (Rosenberg 2004).

We ran successive K -means clustering in the “find.clusters” function of DAPC, as implemented in the R package “adeigenet” (Jombart 2008), and used the Bayesian information criterion (BIC) to determine the optimal number of clusters. Following Jombart et al. (2010), we tested $K = 1-9$ and chose the optimal number of clusters based on the lowest associated BIC. For the optimal K value, the “dapc” function was then executed using group composition inferred from SAMOVA and STRUCTURE results. We retained 50 axes from the principal component analysis, which explained ~95% of the total variation in the data set.

We also used assignment tests and contingency tests for departure from panmixia and to evaluate the population structure that we inferred from the above methods (Waples and Gaggiotti 2006). To determine the probability of an individual originating from the population from which it was sampled, we used assignment tests in the program GENECLASS2 (Piry et al. 2004). The Bayesian approach of Rannala and Mountain (1997) and a Monte Carlo resampling algorithm (Paetkau et al. 2004) with 1,000 simulated individuals were used to calculate the probability of each bird’s genotype originating from the five clusters identified by SAMOVA and STRUCTURE. We evaluated the significance of the correct assignments with a chi-square test to determine whether the observed number of correct assignments was higher than the number expected by chance. Expected numbers of correct assignments were calculated in proportion to cluster sample sizes, assuming an equal probability of membership to any cluster. To test for the significance of the assignments for each population separately, we used a binomial test to evaluate whether observed values fell within an expected range as explained by a normal distribution. We also tested for differentiation among the inferred clusters using contingency tests of allele frequency heterogeneity, following the method of Raymond and Rousset (1995). Exact probabilities of single-locus pairwise comparisons were obtained in GENEPOP. Multilocus P values were computed for each comparison using Fisher’s method for combining probabilities across loci. Following Lugon-Moulin et al. (1999), we constrained the single-locus P values to be no smaller than 0.001, to prevent any single-locus result from dominating the overall test. Lastly, we calculated pairwise F_{ST} values among the inferred clusters using FSTAT.

Dispersal and population connectivity.—We employed a Bayesian sampling approach implemented in the program BIMr, version 1.0, to estimate current migration rates among populations (Faubet and Gaggiotti 2008). BIMr differs from other Bayesian migration models (such as BAYESASS; Wilson and Rannala 2003) in that it employs a different sampling scheme and allows for higher migration rates (Faubet and Gaggiotti 2008). BIMr estimates the probability that an individual migrated during a previous generation instead of focusing on individual migration rates, with the effect that migration rates are allowed to vary between 0 and 1, rather than being constrained to low levels as in BAYESASS. This method is therefore more applicable to populations

with low F_{ST} values. We ran BIMr on the five clusters identified by SAMOVA and STRUCTURE using 20 pilot runs followed by a 100,000 burn-in and 200,000 iterations with five replicates to ensure chain convergence. The results from each run were compared for consistency. Here, we present results from the run with the highest acceptance rates.

RESULTS

Microsatellite analysis.—We genotyped 421 individuals. After removing 34 individuals that had Nelson's Sparrow-specific mitochondrial DNA, we were left with 387 individuals. Of this sample, 13 individuals (3.3%) had missing data for no more than two loci and the remainder yielded complete multilocus genotypes. Individual loci were variably polymorphic, with 4 to 29 alleles per locus. There were a total of 137 alleles; of those, 16 were found in only one population (Table 1). Private alleles were found in all populations, except Fairhill, with the highest number (6) in Parker River. Adjusted for sample size, however, private allelic richness was similar across sites and ranged from 0.27 to 0.37. Mean observed and expected heterozygosities ranged from 0.717 to 0.826 (Table 1). There were no significant deviations from Hardy-Weinberg and no departures from linkage equilibrium.

Population structure and connectivity.—Small but significant differences in genetic variation (F_{ST}) were detected among most sampled populations, with values ranging from 0.0001 to 0.0240. Chapman's Landing was the most differentiated population. The smallest F_{ST} values occurred in comparisons of Parker River and Hampton with all other populations. No isolation-by-distance effect was apparent across the nine marshes (Mantel test, $r = 0.327$, $P = 0.091$; Fig. 2A). However, when a single outlier, Chapman's Landing, was removed from the analysis, genetic differentiation

was positively correlated with geographic distance for the eight remaining marshes (Mantel test, $r = 0.568$, $P = 0.002$; Fig. 2B).

Results of the three independent methods indicated that individuals from the nine marshes did not form a single genetically homogeneous group. SAMOVA yielded small but significant F_{CT} values (0.0080 and 0.0079) for $K = 6$ and $K = 5$, respectively. For all values of K , the Chapman's Landing population was consistently selected first as the most differentiated population and the two Long Island populations were invariably grouped together. In STRUCTURE analyses, the delta K method indicated that $K = 3$ was optimal, and, like SAMOVA, STRUCTURE identified Chapman's Landing and the two Long Island populations as the most differentiated. DAPC identified $K = 5$ as the optimal number of clusters, with a sharp and clear decline in BIC values for $K = 5$. Based on the combination of these results, we chose $K = 5$ as the most likely number of populations; a principal component analysis also supported this result (Fig. 3). Furthermore, examination of the STRUCTURE bar plots showed consistent structuring of five clusters, with assignments skewed toward individual clusters (Pritchard et al. 2010). The value of r (the parameter that estimates the informativeness of the sampling location data in the LocPrior model) averaged over 25 runs (for $K = 5$) was 0.65. Values of r close to or less than 1 indicate that the inclusion of sampling locations is informative, whereas values of $r \gg 1$ imply that location data is uninformative when inferring ancestry (Hubisz et al. 2009). The five clusters identified by these analyses were, from north to south, as follows: (1) Scarborough; (2) Furbish, Fairhill, Hampton, and Parker River (Central cluster); (3) Chapman's Landing; (4) John H. Chafee; and (5) Wertheim and Marine Nature Center (Long Island cluster; Fig. 3). Hereafter, marsh names are used to report analyses of sampling sites, and cluster names are used for analyses of population groupings (genetic clusters). Chapman's Landing, Wertheim, and the Marine Nature Center showed the highest STRUCTURE assignment probabilities to their respective clusters (Q values ranging from 0.66–0.96), whereas Parker River and Hampton were fairly admixed.

Assignment tests correctly assigned 72% of the individuals to the cluster from which they were sampled; the number of correct assignments was significantly greater than that expected by chance ($\chi^2 = 578.7$, $df = 4$, $P < 0.001$). Assignment probabilities varied by cluster (Table 2) and ranged from 58% to 95%. Scarborough and Chapman's Landing showed the highest assignment probabilities, with 95% and 83% correctly assigned, respectively. The lowest assignment probabilities were observed in the Long Island cluster, with only 58% of individuals correctly assigned. Binomial test results showed that observed assignments to each cluster were significant and fell outside that expected on the basis of a normal distribution ($Z > 1.98$ for all five clusters, $P < 0.01$). Contingency tests of allele-frequency heterogeneity detected significant differentiation at the $P < 0.001$ level for all pairwise multilocus comparisons of population clusters. Pairwise F_{ST} values among clusters ranged from 0.005 to 0.024 and averaged 0.009 overall. All pairwise F_{ST} values were significant after Bonferroni correction ($P < 0.005$).

Dispersal patterns.—Results from BIMr suggested that dispersal among marshes was asymmetrical (Table 3). Migration rates varied among the five clusters and ranged from 0.02 to 0.27. Chapman's Landing had the highest residency (1.00) and no immigrants;

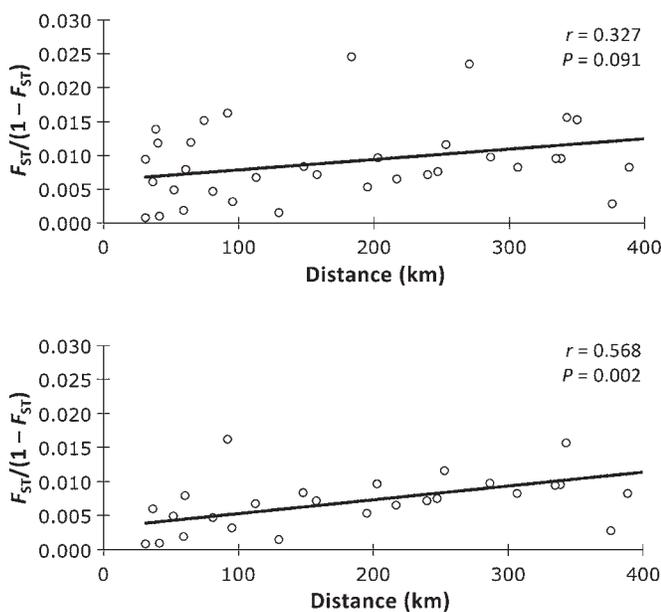


FIG. 2. Relationship of geographic and genetic (linearized F_{ST}) distance in Saltmarsh Sparrows (A) from all nine sampled marshes and (B) without Chapman's Landing (see text).

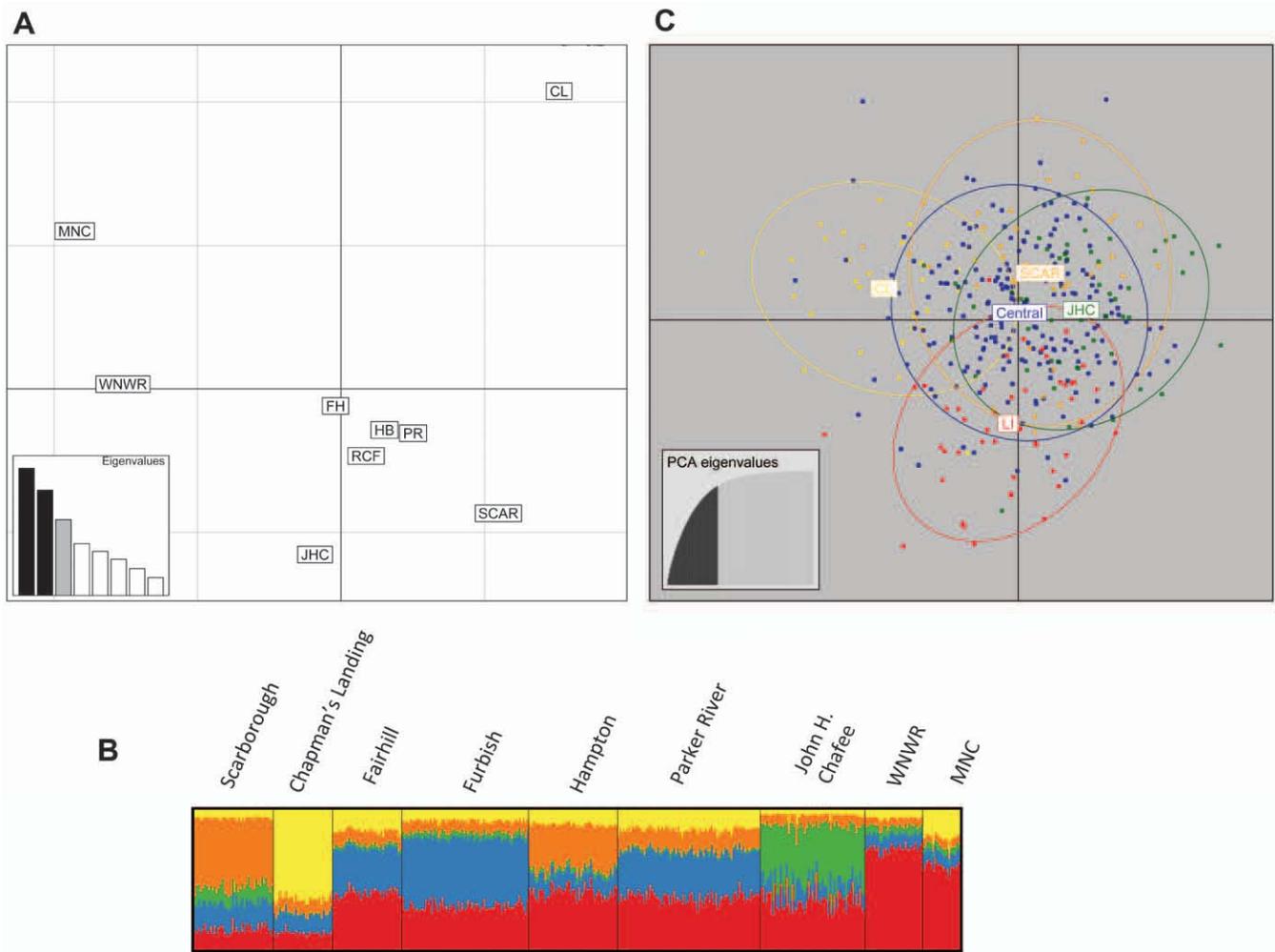


FIG. 3. Synthesis of Saltmarsh Sparrow population groupings identified by STRUCTURE, DAPC, and SAMOVA. (A) Principal component analysis of nine sampled marshes. (B) STRUCTURE bar plot showing individual membership to five genetic clusters, represented by different colors; vertical lines represent individuals. (C) Ordination plot of DAPC for the five genetic clusters. Genetic clusters are shown by ellipses of different colors, corresponding to the colors in the STRUCTURE plot (B), and dots represent individuals.

emigration rates ranged from 0.06 to 0.23 between Chapman’s Landing and other marshes (Fig. 4). High residency was also identified in the Long Island cluster (0.88), with very low immigration rates (2–4%). A relatively high proportion of individuals immigrated into and emigrated from the Central cluster, which had the

lowest residency rate, 27%, indicating that it was highly admixed. John H. Chafee and Scarborough had intermediate residency rates of 50% and 43%, respectively. Emigration out of John H. Chafee was notably low (2–3%), except to Scarborough (18%). Immigration and emigration rates for Scarborough ranged from 8% to 20% with all

TABLE 2. Results of GENECLASS assignment tests for five Saltmarsh Sparrow population clusters. *P* values for individual observations were calculated using a normal distribution; all observations are significant ($P < 0.01$).

Population cluster	Sample size	Percent correctly assigned	Observed number correctly assigned	Expected number correctly assigned	χ^2
Scarborough	40	95%	38	8	112.5
Chapman’s Landing	30	83%	25	6	60.16
Central	216	73%	158	43.2	305.07
John H. Chafee	53	70%	37	10.6	65.75
Long Island	48	58%	28	9.6	35.26

TABLE 3. Migration rates among Saltmarsh Sparrow population clusters inferred by the program BIMr. Rows represent the populations from which each individual was sampled, and columns represent the population from which they migrated. Values along the diagonal are the proportion of individuals identified as residents in the source population.

Into-From	Scarborough	Chapman's Landing	Central	John H. Chafee	Long Island
Scarborough	0.43	0.12	0.19	0.18	0.08
Chapman's Landing	0	1	0	0	0
Central	0.20	0.24	0.27	0.03	0.26
John H. Chafee	0.11	0.07	0.12	0.50	0.21
Long Island	0.02	0.05	0.03	0.02	0.88

populations, except Long Island. Migration rates between the geographically most separated populations, Long Island and Scarborough, were among the lowest (0.02 and 0.08 for immigration into Long Island and Scarborough, respectively). Population-specific F_{ST} values calculated in BIMr averaged 0.03 and ranged from 0.021 for Scarborough to 0.046 for John H. Chafee.

DISCUSSION

Genetic studies provide important information about dispersal and population connectivity, and have management implications when they uncover ecological differences among populations. Theory suggests that one migrant per generation ($Nm = 1$) is sufficient to homogenize genetic structure (Mills and Allendorf 1996). In an ecological context, however, much higher rates of gene flow are relevant, as substantial departure from random mating can occur at $Nm > 1$ (Waples and Gaggiotti 2006). Elucidating population structure under such high-gene-flow scenarios is challenging, but increasingly possible with powerful analytical approaches (Faubet and Gaggiotti 2008, Hubisz et al. 2009). Using these approaches, we documented patterns of fine-scale population structure, asymmetrical dispersal, and isolation-by-distance in a migratory passerine. These findings add to a growing body of work that contradicts expectations of genetic homogeneity for some highly mobile and migratory species.

Although genetic differentiation in Saltmarsh Sparrows was weak overall (mean $F_{ST} = 0.009$), the patterns of population structure that we observed were statistically significant and consistent across multiple, complementary, analytical approaches. Statistically significant departures from panmixia can be achieved with high power when using polymorphic genetic markers and must therefore be evaluated in light of their ecological context as well as the appropriateness of the sampling and analytical methods used (Waples and Gaggiotti 2006, Knutsen et al. 2011). By sampling a large number of unrelated individuals from each site and testing temporal replicates from a few sites, we eliminated the possibility of “noise” in the genetic signal that could have resulted from nonrandom sampling or temporal fluctuations in allele frequencies (Waples 1998). We therefore interpret the genetic structure that we observed in the present study as representative of stable population-level processes (Knutsen et al. 2011) that result from behavioral and ecological factors influencing Saltmarsh Sparrows.

Taken together, the results of hierarchical spatial analyses, Bayesian clustering, and multivariate analyses indicate that population substructure is most consistent with the existence of five population groupings that largely follow a pattern of geographic location for the nine sampled marshes (as depicted in Fig. 1). Despite considerable admixture, differentiation of these five population groupings was supported by contingency and assignment tests. The greatest differentiation occurred for the Chapman's Landing and Long Island populations. As predicted, the populations at the northern and southern extremes of the study area, Scarborough and Long Island, were among the most strongly differentiated. The Central cluster (Furbish, Fairhill, Hampton, and Parker River) was the least differentiated from all other populations. John H. Chafee showed intermediate levels of differentiation and admixture with both the Central cluster and Scarborough. Estimates of contemporary migration rates suggested demographic independence of Chapman's Landing and Long Island from all other populations, because of their high residency and low immigration rates (below the proposed 10% criterion for demographic independence; Waples and Gaggiotti 2006). Migration rates among the Central cluster, Scarborough, and John H. Chafee were higher (10–20%), indicating greater demographic connectivity among these marshes.

Our results indicate that Saltmarsh Sparrows exhibit population structure on a finer scale than is typically observed in migratory passerines. Previous studies have found low levels of genetic

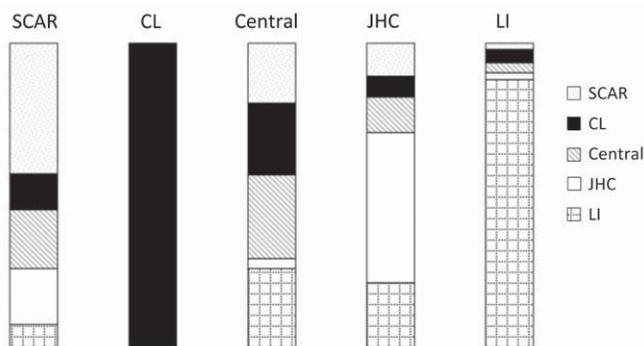


FIG. 4. Histogram summarizing the origin of individuals in each sampled population cluster. Shading shows the proportion of individuals that were resident or immigrated from each of the other clusters; immigration rates were inferred by BIMr. Abbreviations: Scar = Scarborough Marsh, CL = Chapman's Landing, JHC = John H. Chafee, and LI = Long Island.

variation in other Emberizidae. For example, genetic differentiation was both small and nonsignificant among fragmented populations of Brewer's Sparrow (*Spizella breweri breweri*; $F_{ST} = 0-0.02$; Croteau et al. 2007) across a distance of 190 km, and for populations of Reed Buntings (*Emberiza schoeniculus*) restricted to wetlands within an area of 200 km² ($F_{ST} = 0.005$; Mayer et al. 2009). Similarly, little genetic variation has been found within single subspecies of mainland Song Sparrows (*Melospiza melodia*) separated by distances ≤ 200 km, although marked fine-scale structure exists for sedentary island populations (Wilson et al. 2011). In this study, pairwise F_{ST} values were significant for 26 of the 36 comparisons among nine Saltmarsh Sparrow populations separated by distances of 31–420 km and significant for all pairwise comparisons of the five population clusters identified. We also found fine-scale structure, with significant differentiation ($F_{ST} = 0.014-0.024$) of Chapman's Landing from several nearby marshes from which it is separated by 38–270 km. Isolation-by-distance, which we observed across many of our study populations, is also atypical of the Emberizidae (Lee et al. 2001, Croteau et al. 2007, Mayer et al. 2009), with the exception of insular populations of nonmigratory Song Sparrows (Wilson et al. 2011).

An isolation-by-distance pattern of population structure indicates that genetic variation increases consistently with geographic distance, such that gene flow is sufficient to connect adjacent populations and prevent the formation of isolated demes, but long-distance dispersal is rare enough to prevent complete genetic homogenization (Slatkin 1993). This pattern of population structure, in which gene flow occurs most prevalently among neighboring marshes, is consistent with our limited current knowledge of Saltmarsh Sparrow dispersal ecology. Limited mark-recapture data suggest strong site fidelity for adults of both sexes (53–60% in New York, Greenlaw and Rising 1994; 34–37% in Rhode Island, DiQuinzio et al. 2001) and relatively high return rates for juveniles in comparison to other passerines (7%, Greenlaw and Rising 1994; 11.6–29.7%, DiQuinzio et al. 2001). DiQuinzio et al. (2001) found a 10% movement rate of color-banded individuals among marshes over a 4-year period, with most movements among adjacent marshes separated by short distances (0.4–5.8 km) and rare movements up to 26.4 km (the extent of their study area). Natal philopatry and breeding-site fidelity are important in structuring populations of other highly mobile species, for example some migratory seabirds (Rabouam et al. 2000, Friesen et al. 2007, Barlow et al. 2011).

In our study, one marsh, Chapman's Landing, did not follow the isolation-by-distance pattern and was strongly differentiated from all other marshes, irrespective of proximity. Notably, Chapman's Landing received no immigrants despite its close proximity to several marshes in the Central cluster, which had relatively high emigration rates to other sampled marshes. These findings suggest that additional factors besides geographic distance influence fine-scale structure in Saltmarsh Sparrows. Chapman's Landing, located ~15 km from the coast, is the most inland of the nine sampled marshes. Conversely, the Central cluster, which consists of large and continuous stretches of core marsh habitat, was highly admixed in comparison to other marshes. The inland location of Chapman's Landing, combined with its relatively small size, may influence the ability of dispersing individuals to detect it, because spatial scale and interpatch distances affect the movement and the

perceptual range of a species (Moilanen and Hanski 2006). Saltmarsh Sparrows likely follow a typical coastal migration pattern characteristic of birds breeding in tidal marshes, and they may therefore be less likely to encounter inland marshes. Furthermore, unsuitable habitat and the developed landscape inland of the coastal marshes may restrict dispersal into inland marshes. Divergence due to landscape variation has been found in other avian species; for example, reduced gene flow is associated with water barriers to dispersal in pantropical seabirds and Song Sparrows (Steeves et al. 2005, Wilson et al. 2011). DiQuinzio et al. (2001) found no movements between color-banded Saltmarsh Sparrows among mainland and island marshes, which suggests that the landscape may be influential in their movement patterns. Accordingly, to reach the marsh at Chapman's Landing, Saltmarsh Sparrows must fly across not only unsuitable terrestrial habitat, but also the potential dispersal barrier posed by the >6,000 acres of open water of the Great Bay Estuary.

Habitat availability and quality also heavily influence avian population structure (Fazio et al. 2004, Lindsay et al. 2008, Bruggeman et al. 2010). Saltmarsh Sparrows rely exclusively on patchily distributed marsh habitat, and their population structure and dispersal may be influenced by habitat or other environmental differences. Accordingly, the differentiation of Chapman's Landing may reflect habitat differences associated with inland marshes. Genetic differentiation has been associated with habitat gradients in other passerines over small spatial scales (Garant et al. 2005, Blondel et al. 2006). Similar to Chapman's Landing, Scarborough marsh is also located inland (although only 3.5 km inland), was differentiated from all other marshes, and had a high assignment probability. Nonetheless, it was more admixed than Chapman's Landing, with relatively high connectivity to most other marshes as inferred by estimated migration rates. The greater genetic connectivity of Scarborough may be a result of its geographic connection to the coastal marshes by continuous marsh habitat along the Scarborough River or may be attributable to its large size. Future studies with additional sampling of marshes along a habitat gradient are needed to confirm potential habitat-associated population differentiation.

Regardless of dispersal ability, species that are area-sensitive (With and King 2001) or habitat specialists (Harris and Reed 2002) tend to be most affected by landscape structure. The density of breeding adult Saltmarsh Sparrows is positively correlated with the area of available breeding habitat (Benoit and Askins 2002). Populations in high-quality habitats tend to produce more offspring (i.e., potential dispersers) and may serve as source populations for the colonization of lower-quality habitats (Kawecki 2008). This variable distribution and availability of high-quality habitat, along with the resulting differences in population productivity, are the defining components of source-sink theory (Pulliam 1988) and may explain the asymmetrical dispersal rates observed among Saltmarsh Sparrow populations. For example, emigration rates from John H. Chafee were low (0–3%, except into Scarborough), yet its residency was only 50% and it had immigration rates of 7–21%, which suggests that it might be a sink population. John H. Chafee is a small marsh, in the highly developed landscape of coastal Rhode Island, in which marsh habitat occurs in small, fragmented patches. By contrast, the large marshes of the Central cluster and Scarborough had much higher emigration

rates (typically 10–20%), which suggests a higher rate of dispersal from these potentially higher-quality marshes.

Asymmetrical dispersal can have evolutionary consequences for a species because gene flow affects the potential for local adaptation of populations. Source habitats tend to contribute proportionally more to the species' gene pool, and as a consequence they may "swamp" local selection processes (Dias 1996, Kawecki and Holt 2002, Kawecki 2008). From a conservation standpoint, the loss of local adaptive potential through metapopulation processes can be particularly detrimental to narrow endemics, including tidally restricted species, because local diversity is essential for adaptation to environmental changes (Pearman 2001). Conversely, the lack of immigration into edge habitats, such as Chapman's Landing, may enable local selection processes and lead to increased rates of local adaptation or the establishment of locally co-adapted gene complexes (Templeton 1986, Wilson et al. 2011). These issues are germane to the Saltmarsh Sparrow, given the impending threats of climate change, including increasing variation in tidal fluctuations and shifts in vegetation gradients, and the resulting changes these factors will have on habitat quality and availability (Hughes 2004, Bayard and Elphick 2011). In light of these threats, future studies should sample additional marshes to identify populations with high residency, genetic divergence, and high emigration rates that may have high conservation value because they may have unique local adaptations or function as important source populations.

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