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Authors: Winker, Kevin, and Graves, Gary R.

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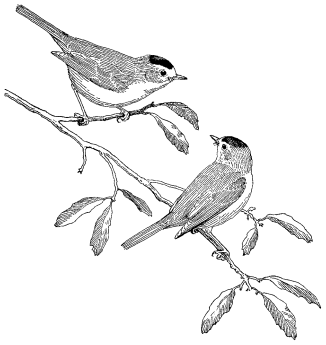
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GENETIC STRUCTURE OF BREEDING AND WINTERING POPULATIONS OF SWAINSON'S WARBLER

KEVIN WINKER[1,2,3] AND GARY R. GRAVES[1]

ABSTRACT.—Swainson's Warbler (*Limnothlypis swainsonii*) is a species of conservation concern because of its small wintering range in the Caribbean Basin, relatively low population densities, and habitat fragmentation in its core breeding range in the southeastern United States. We investigated microsatellite DNA variation among 11 breeding populations from eastern Texas to Virginia and two populations from wintering areas in Jamaica and Mexico. Analyses of six polymorphic loci indicated a moderate level of gene flow among breeding populations, relatively small effective population sizes (<200 individuals in each sampled population), and subtle population variation. We detected no evidence of population bottlenecks in breeding or wintering populations. Bayesian assignment tests suggested that substantial mixing of breeding populations may occur in wintering areas. Genetic differences between the Mexican and Jamaican populations indicate they may be drawn from different subsets of breeding populations. Patterns of genetic variation among breeding and wintering populations suggest a network of local and regional conservation programs may be necessary to maintain genetic diversity in Swainson's Warbler. *Received 4 May 2007. Accepted 17 December 2007.*

Genetic differentiation in migratory species is often associated with migratory divides where populations that winter in different regions meet during the breeding season in parapatric contact zones (Salomonsen 1955). Studies of *Sylvia* warblers (Sylviidae) in Europe have demonstrated that migratory behaviors can have a strong genetic basis and can evolve rapidly (Berthold and Querner 1981; Helbig 1991, 1996; Berthold 2003; Bearhop et al. 2005). Experimental crosses between populations that winter in different regions produced offspring that exhibited intermediate degrees of migratory orientation and restlessness. Helbig (1991) suggested that hybrids between populations of Eurasian Blackcap (*Sylvia atricapilla*) from opposite sides of the migratory divide would be selected against, because they would probably attempt to migrate across the Mediterranean and end in the uninhabitable expanses of the Sahara Desert. This example suggests a plausible mechanism for maintenance of genetic structure in breeding populations of migratory species that winter in different areas (allohiemy).

Swainson's Warbler (*Limnothlypis swainsonii*) is a sparsely-distributed wood warbler

[1] Department of Vertebrate Zoology, MRC-116, and Laboratory of Molecular Systematics, National Museum of Natural History, Smithsonian Institution, P. O. Box 37012, Washington, D.C. 20013, USA.

[2] Current address: University of Alaska Museum, 907 Yukon Drive, Fairbanks, AK 99775, USA.

[3] Corresponding author; e-mail: ffksw@uaf.edu

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(Parulidae) that breeds in the unglaciated southeastern United States and winters in the Caribbean Basin (Meanley 1971; Brown and Dickson 1994; Graves 2001, 2002). Geographic variation in plumage color is subtle and the species is currently regarded as monotypic (Brown and Dickson 1994). Although locally common, Swainson's Warbler has been ranked as one of the most vulnerable breeding songbirds in the southeastern United States because of habitat fragmentation, relatively low population densities, and a small disjunct wintering range (Morse 1989, Terborgh 1989, Hunter et al. 1993, Rappole 1995). Most contemporary breeding populations occur in second-growth forest on alluvial soils in the Mississippi Valley and on the coastal plain from eastern Texas to southeastern Virginia (Graves 1998, 2001, 2002). The nonbreeding distribution is poorly known (Brown and Dickson 1994, Graves 1996), but the primary wintering areas appear to be in Cuba (Kirkconnell et al. 1996), Jamaica (Graves 1996), and in humid forests of mainland Middle America from Veracruz to Tabasco in Mexico (Winker et al. 1992, Winker et al. 1999b) and in Belize (K. Winker, unpubl. data).

Winker et al. (2000) compared allozyme variation at 26 loci among five breeding populations of Swainson's Warbler. Allele frequencies at five loci indicated modest population structure, chiefly between samples in the Mississippi Valley from Arkansas and populations on the coastal plain from Louisiana to Virginia; patterns of genetic variation were inconsistent with an isolation-by-distance model. It was hypothesized the observed population structure was due to genetic drift due to the absence of barriers to gene flow in the contemporary landscape. Alternatively, genetic structuring could be influenced by the warbler's divided wintering range (Greater Antilles vs. mainland Middle America). If migratory behavior is under genetic control in this nocturnally migrating species, interbreeding between populations that winter on the mainland and those that winter in the Greater Antilles might produce offspring that end their migrations over open water in the Caribbean or in the Gulf of Mexico.

We investigated allelic variation at six polymorphic microsatellite loci in 11 breeding populations of Swainson's Warbler sampled from eastern Texas to Virginia and two populations from wintering areas in Jamaica and Mexico. We had three principal objectives: (1) characterize microsatellite diversity within breeding and wintering populations, (2) examine the evidence for mixing of breeding populations on wintering areas, and (3) contrast microsatellite and allozyme variation in the subset of breeding populations studied by Winker et al. (2000).

METHODS

Data Collection.—Swainson's Warblers are territorial in breeding (Meanley 1971) and wintering areas (Graves 1996); they are also monogamous, although polygyny may occur (Graves 1992), and pairing occurs in breeding areas. We obtained tissue samples from 205 territorial males from breeding locations between 27 April and 31 May (1986–1996) in the southeastern United States (Fig. 1) under state and national permits: Sulphur River, Texas (TX1: $n = 17$); Sam Houston National Forest, Texas (TX2: $n = 20$); Atchafalaya River, Louisiana (LA1: $n = 22$); Tensas River, Louisiana (LA2: $n = 10$); Homochitto River, Mississippi (MS1: $n = 20$); Little Sunflower River, Mississippi (MS2: $n = 10$); White and Mississippi rivers, Arkansas (AR: $n = 20$); Apalachicola River, Florida (FL: $n = 24$); Ocmulgee River, Georgia (GA: $n = 20$); Cooper and Santee rivers, South Carolina (SC: $n = 21$); and the Great Dismal Swamp, Virginia, and Chowan River, North Carolina (VA: $n = 21$). These samples nearly span the latitudinal and longitudinal distribution of the core breeding range (Graves 2002). Individuals from five population samples (LA1, AR, FL, SC, and VA) were previously assayed in the allozyme study of Winker et al. (2000). Genetic samples from the wintering range were obtained in Veracruz ($n = 25$) and Tabasco ($n = 1$) in southern Mexico (MEX) and in the Blue Mountains of Jamaica (JAM: $n = 19$; Fig. 1). Voucher specimens (except for Jamaican samples, for which only blood was obtained) are housed in the National Museum of Natural History (Smithsonian Institution), Bell Museum of Natural History (University of Minnesota), and the Coleccion Nacional de Aves (Universidad Nacional Autonoma de Mexico).

Genomic DNA was extracted from body

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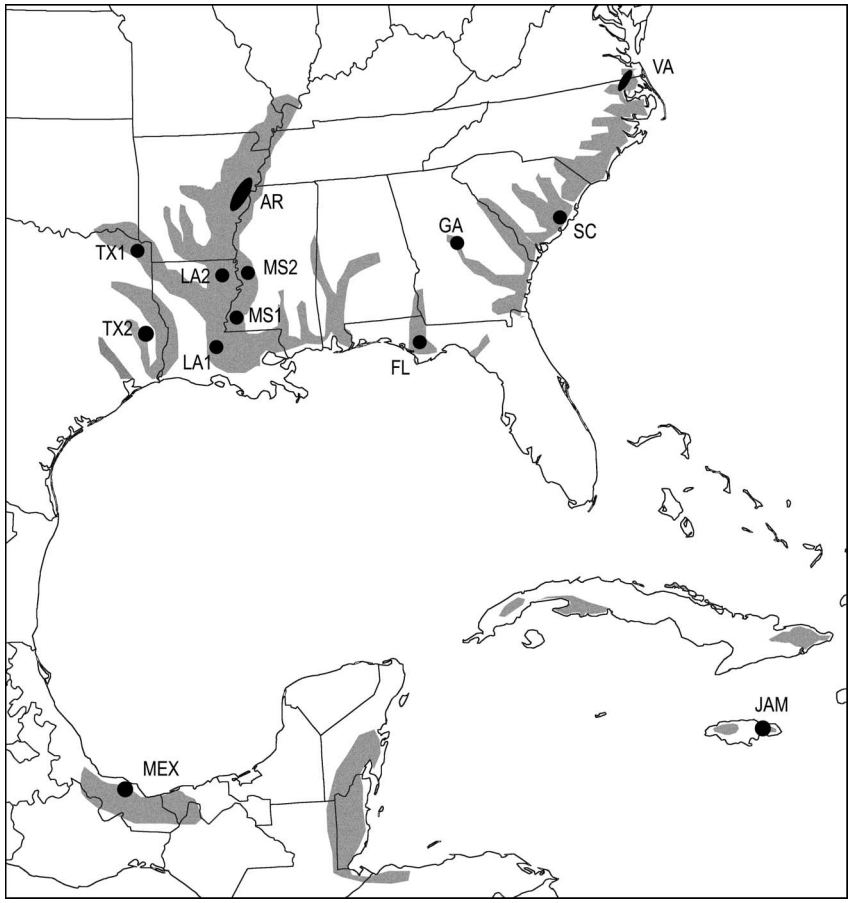


FIG. 1. Sampling localities within the principal breeding and wintering ranges of Swainson's Warbler (after Graves 2002).

tissues or from small pieces of museum skins using a diatomaceous earth/guanidine thiocyanate extraction protocol (Carter and Milton 1993) and diluted to 20 ng/μL for amplification of microsatellite loci developed for this species by Winker et al. (1999a). Extractions and amplifications were conducted in a PCR-free laboratory. All amplification batches included negative controls. Individuals were randomized across extractions, amplifications, and gel runs. Fragments were generated using dye-labeled primers and visualized on an ABI 373A automated sequencer. Fragment size was measured using an internal size standard (350 TAMRA) and GeneScan software (both from Applied Biosystems Inc., Foster City, CA, USA). All electropherograms were examined manually, allele scoring was done without reference to source population, and results were not sorted to population until completion of the study.

Analyses.—Basic statistics of allelic frequencies, genetic distance measures between populations, allelic diversity, and expected and observed heterozygosities were calculated using the computer programs BIOSYS-1 and GDA version 1.0 (Swofford and Selander 1981, Lewis and Zaykin 1999). Tests for Hardy-Weinberg (H-W) equilibrium, allelic heterogeneity, levels of population structure, and differences between population pairs were performed using GENEPOP version 3.1d (Raymond and Rousset 1995). Levels of population structure are given using the θ of Weir and Cockerham (1984), which is an unbiased estimator of traditional F_{ST}. We used CER-

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TABLE 1. Allele frequencies for six microsatellite loci among 11 breeding and two wintering populations of Swainson's Warbler (n = 250).

Locus (allele sizes)	Population (n)												
	TX1 (17)	TX2 (20)	LA1 (22)	MS1 (20)	LA2 (10)	MS2 (10)	AR (20)	FL (24)	GA (20)	SC (21)	VA (21)	MEX[a] (26)	JAM (19)
*Lsw*μ14 (184–200)													
1	0.029	0	0	0.025	0	0	0.05	0.021	0	0.071	0.048	0.02	0.132
2	0.118	0	0.091	0.05	0	0	0	0.021	0.025	0	0	0.02	0.026
3	0.294	0.3	0.182	0.3	0.4	0.55	0.25	0.354	0.375	0.286	0.262	0.38	0.211
4	0	0	0	0.025	0	0	0.025	0.063	0	0	0	0	0
5	0.235	0.35	0.432	0.425	0.3	0.4	0.425	0.354	0.325	0.357	0.5	0.4	0.342
6	0.324	0.35	0.273	0.175	0.25	0.05	0.225	0.188	0.25	0.286	0.167	0.18	0.289
7	0	0	0.023	0	0	0	0.025	0	0.025	0	0.024	0	0
8	0	0	0	0	0.05	0	0	0	0	0	0	0	0
*Lsw*μ18 (227–275)													
1	0	0.025	0	0	0	0	0	0	0	0	0	0	0
2	0.118	0.2	0.182	0.2	0.2	0.3	0.075	0.188	0.225	0.143	0.286	0.28	0.316
3	0.059	0.2	0.159	0.2	0.2	0.1	0.275	0.125	0.15	0.31	0.119	0.14	0.184
4	0.294	0.1	0.182	0.175	0.2	0.1	0.2	0.146	0.25	0.095	0.048	0.18	0.132
5	0.118	0.1	0.227	0.05	0.05	0.15	0.075	0.188	0.1	0.119	0.286	0.1	0.079
6	0.088	0.125	0.023	0.125	0.1	0.15	0.125	0.188	0.075	0.143	0.095	0.18	0.079
7	0.118	0.1	0.068	0.175	0	0.1	0.175	0.063	0.15	0.167	0.143	0.08	0.105
8	0.059	0.1	0.091	0.05	0.2	0.05	0.075	0.042	0.025	0	0	0.02	0
9	0.088	0	0.045	0.025	0	0	0	0.021	0	0	0.024	0	0.053
10	0.059	0.025	0.023	0	0	0	0	0	0.025	0.024	0	0	0
11	0	0	0	0	0.05	0.05	0	0	0	0	0	0	0
12	0	0.025	0	0	0	0	0	0	0	0	0	0.02	0
13	0	0	0	0	0	0	0	0	0	0	0	0	0.026
14	0	0	0	0	0	0	0	0.021	0	0	0	0	0
15	0	0	0	0	0	0	0	0.021	0	0	0	0	0.026
*Lsw*μ3 (256–290)													
1	0.029	0.025	0.045	0.075	0.2	0.05	0.05	0.042	0	0.024	0.095	0.08	0
2	0	0	0	0	0	0	0	0.021	0	0	0	0	0
3	0	0.025	0.023	0.025	0	0	0	0	0	0	0	0	0.026
4	0.029	0	0.023	0	0	0	0.025	0	0	0	0	0	0
5	0	0	0	0	0	0	0.025	0	0	0.024	0	0	0
6	0.5	0.45	0.5	0.475	0.35	0.55	0.5	0.438	0.475	0.429	0.5	0.58	0.605
7	0.118	0.125	0.068	0.125	0.2	0.05	0.1	0.146	0.175	0.143	0.095	0.02	0.053
8	0.118	0.075	0.136	0.075	0.05	0.15	0.075	0.125	0.175	0.167	0.19	0.12	0.053
9	0	0.125	0.023	0.05	0.15	0	0.125	0.083	0.05	0.024	0	0.1	0.105
10	0.029	0.05	0.068	0.05	0	0.15	0.025	0.083	0.075	0.071	0.048	0.06	0.105
11	0.088	0.025	0.023	0.025	0	0	0	0	0	0.024	0.024	0.02	0.026

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TABLE 1. Continued.

Locus (allele sizes)	Population (*n*)												
	TX1 (17)	TX2 (20)	LA1 (22)	MS1 (20)	LA2 (10)	MS2 (10)	AR (20)	FL (24)	GA (20)	SC (21)	VA (21)	MEX[a] (26)	JAM (19)
12	0	0.05	0.023	0.025	0	0	0	0	0	0.048	0.024	0	0
13	0.059	0.05	0.023	0	0.05	0.05	0	0.021	0.025	0.024	0.024	0.02	0
14	0	0	0.023	0.025	0	0	0.025	0	0.025	0	0	0	0.026
15	0.029	0	0	0.025	0	0	0.025	0.042	0	0.024	0	0	0
16	0	0	0.023	0.025	0	0	0.025	0	0	0	0	0	0
*Lsw*μ5B (215–247)													
1	0	0	0	0	0.05	0.05	0	0	0	0	0	0.038	0
2	0.147	0.025	0.045	0.075	0.15	0.05	0	0	0.025	0	0.024	0.038	0
3	0.471	0.575	0.455	0.425	0.35	0.5	0.55	0.479	0.65	0.476	0.167	0.404	0.395
4	0	0	0.023	0	0	0	0	0	0	0	0	0.019	0
5	0.294	0.175	0.318	0.275	0.35	0.2	0.1	0.271	0.225	0.405	0.548	0.308	0.342
6	0.059	0.075	0.091	0.15	0.1	0.15	0.225	0.125	0.05	0.024	0.048	0.096	0.053
7	0.029	0.15	0.045	0.075	0	0.05	0.125	0.083	0.025	0.071	0.214	0.096	0.105
8	0	0	0	0	0	0	0	0.021	0.025	0	0	0	0.079
9	0	0	0	0	0	0	0	0	0	0	0	0	0.026
10	0	0	0	0	0	0	0	0.021	0	0	0	0	0
11	0	0	0.023	0	0	0	0	0	0	0.024	0	0	0
*Lsw*μ9 (109–121)													
1	0	0	0	0	0	0	0	0	0.025	0.024	0	0	0.026
2	0	0	0	0	0	0	0	0.042	0	0	0.024	0	0
3	0.618	0.825	0.727	0.625	0.6	0.65	0.825	0.708	0.675	0.833	0.786	0.577	0.842
4	0.382	0.175	0.25	0.35	0.4	0.35	0.175	0.25	0.3	0.143	0.19	0.423	0.132
5	0	0	0.023	0.025	0	0	0	0	0	0	0	0	0
*Lsw*μ19 (168–196)													
1	0	0	0	0	0	0	0	0	0	0	0	0.019	0
2	0	0	0	0	0	0	0	0	0	0	0	0.019	0
3	0.118	0.2	0.205	0.175	0.15	0.25	0.05	0.167	0.225	0.119	0.262	0.231	0.342
4	0.059	0.2	0.114	0.175	0.2	0.15	0.2	0.125	0.125	0.333	0.119	0.173	0.158
5	0.294	0.125	0.227	0.175	0.3	0.15	0.275	0.188	0.25	0.095	0.19	0.212	0.237
6	0.118	0.2	0.182	0.1	0.05	0.15	0.15	0.146	0.125	0.167	0.167	0.154	0.053
7	0.147	0.1	0.114	0.25	0.1	0.1	0.2	0.25	0.125	0.214	0.214	0.135	0.079
8	0.088	0.1	0.091	0.05	0.1	0.15	0.1	0.063	0.125	0.048	0.024	0.019	0.079
9	0.118	0.025	0.045	0.075	0.1	0	0.025	0.063	0	0	0	0.038	0.053
10	0.059	0.025	0.023	0	0	0	0	0	0.025	0	0.024	0	0
11	0	0	0	0	0	0.05	0	0	0	0.024	0	0	0
12	0	0.025	0	0	0	0	0	0	0	0	0	0	0

[a] Three individuals could not be scored at one locus each and $n = 25$ at loci 14, 18, and 3.

VUS version 1.0 (Marshall et al. 1998) to infer frequencies of null alleles. We used analysis of covariance (ANCOVA) to evaluate population variability in allelic diversity. The relationship between genetic and geographic distances among populations was assessed with Mantel and permutation tests using NTSYS-pc version 1.50 (Rohlf 1988). We examined geographic subsets of the population matrix with Spearman rank correlation coefficients (r_s). Pairwise comparisons of population parameters are not independent, because each population is subjected to multiple contrasts. Therefore, we emphasize the relative strength of the correlative relationship (r_s) between genetic and geographic distances for these populations rather than *P* values.

We used STRUCTURE, version 2 (Pritchard et al. 2000, Falush et al. 2003) to examine how well the predefined populations corresponded to genetic groups (*K*). Individual genotypes in this Bayesian clustering approach are assigned to clusters with Hardy-Weinberg equilibrium and linkage equilibrium achieved within each cluster. A Markov Chain Monte Carlo approach was used to identify the number of clusters (*K*) that are most likely given the observed genotypes. STRUCTURE was used twice for each defined *K* (1–11) after a burn-in of 10^5 iterations, followed by an additional 10^6 iterations on the full breeding area data set (11 populations). No prior information (e.g., on the population of origin of each individual) was used. Admixture and correlations models were used in which individuals can have mixed ancestry, and where the allele frequencies of closely related populations may be correlated. We further refined our analysis of genetic groups (*K*) using the approach of Evanno et al. (2005), which examines the second order rate of change of the log probability of data with respect to the number of clusters. These analyses were based on 20 independent STRUCTURE runs for each *K* under the same conditions of a 10^5 burn-in, plus another 10^6 iterations. A bootstrapped (100 replicate), neighbor-joining tree was developed using SEQBOOT, GENDIST, NEIGHBOR, and CONSENSE in the software package PHYLIP (Felsenstein 1993).

We tested for population bottlenecks using the computer program M (Garza and Williamson 2001). This test calculates the ratio (M) of total alleles to the range of allele sizes within populations. Reduced populations are expected to have a smaller M ratio than populations in mutation-drift equilibrium (Garza and Williamson 2001). Simulations estimating the probability of the observed M ratio used Garza and Williamson's (2001) suggested values for the proportion of one-step mutations (90%) and the average size of non-one-step mutations ($\Delta_g = 3.5$). We used 10,000 replicates for simulations and set θ ($4N_e\mu$) to 1, 10, and 25, values corresponding to equilibrium effective population sizes (N_e) before a bottleneck of 500, 5,000, and 12,500, respectively, at a mutation rate (μ) of 5×10^{-4} (Goldstein and Schlotterer 1999). Population sizes of Swainson's Warbler are unknown, but values of θ well above 1 seem reasonable given our field experience.

Estimates of $4N_e\mu$ were obtained using MIGRATE (Beerli and Felsenstein 2001), where N_e is effective population size and μ is the microsatellite mutation rate. Our estimates of long-term effective population sizes (N_e) were made using a mutation rate (μ) of 5×10^{-4} (Goldstein and Schlötterer 1999). Estimates of levels of gene flow among breeding populations were made using the rare alleles method (Slatkin 1985, Barton and Slatkin 1986, Slatkin and Barton 1989) as implemented in GENEPOP version 3.1d (Raymond and Rousset 1995) and assignment tests; the latter (Cornuet et al. 1999) enable a more direct estimate of gene flow by calculating the likelihood that an individual genotype originated from the population where it was obtained. These tests remove an individual from the sample and compare it with the remainder (Rannala and Mountain 1997, Cornuet et al. 1999) to identify the most likely breeding population of origin for wintering individuals. We used an α of 0.01, a stringency level shown to have high levels of accuracy in assigning populations of origin for dispersing individuals (Berry et al. 2004). We used the Dunn-Sidák correction (Sokal and Rohlf 1995) where appropriate to adjust probabilities for simultaneous statistical tests.

RESULTS

Variability of Microsatellite DNA.—The six microsatellite loci exhibited 5–16 alleles per locus (Table 1). Sixty-seven alleles were de-

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TABLE 2. Sample sizes (n), average allelic diversity (A), and expected and observed heterozygosities (H_e and H_o) for six microsatellite loci in breeding and wintering populations of Swainson's Warbler.

Population	n	A	H_e	H_o
Arkansas (AR)	20	6.17	0.676	0.667
Florida (FL)	24	6.83	0.724	0.660
Georgia (GA)	20	6.00	0.687	0.658
Louisiana 1 (LA1)	22	7.50	0.712	0.652
Louisiana 2 (LA2)	10	5.17	0.754	0.750
Mississippi 1 (MS1)	20	6.83	0.734	0.700
Mississippi 2 (MS2)	10	5.33	0.698	0.767
South Carolina (SC)	21	6.17	0.674	0.690
Texas 1 (TX1)	17	6.33	0.733	0.667
Texas 2 (TX2)	20	6.50	0.687	0.725
Virginia (VA)	21	5.83	0.667	0.690
Mexico (MEX)	26	6.50	0.705	0.620
Jamaica (JAM)	19	6.33	0.672	0.684

tected across all loci, ranging from a minimum of 32 detected in the MS2 population (n = 10 individuals) to a maximum of 45 in the LA1 population (n = 22 individuals). Ten alleles were unique to a single population (FL = 3; JAM = 2; LA2 = 1; MEX = 2; TX2 = 2). The number of alleles detected per population was correlated ($r^2 = 0.54$; $P < 0.005$) with sample size. Populations from localities that drain into the Atlantic Ocean (VA, SC, GA) had significantly lower allelic diversity (ANCOVA, $F_{1,8} = 9.57$; $P = 0.015$) than populations from drainages that empty into the Gulf of Mexico after factoring out the effects of sample size (FL, MS1, MS2, LA1, LA2, AR, TX1, TX2; Table 2). An overall heterozygote deficiency ($P = 0.011$) was caused by loci *Lsw*μ5B and *Lsw*μ19 (Table 3). Heterozygote deficiency can be caused by a number of factors, including inbreeding, the Wahlund effect, and null alleles. Inferred frequencies for the latter possibility suggested that null alleles were not responsible for the H-W disequilibrium (Table 3).

Population Structure.—Breeding populations had significant but weak structure (θ = 0.0068, $P < 0.00005$; Table 4) where θ is the unbiased estimator for F_{ST}; this was driven by heterogeneous distributions of alleles in loci *Lsw*μ5B ($P < 0.00005$) and *Lsw*μ18 (P = 0.039; Table 4). The Bayesian assessment of population clusters reflected this weak structure with the highest probabilities of K occurring for 1–7 populations (Fig. 2A). Further testing to identify the true number of genetic clusters (K), performed separately for both breeding and wintering populations, suggested that 2–4 populations are involved (2–4 among breeding populations and 2–3 in the wintering samples), although the peak height of delta K in both sets of analyses suggested a lack of strong signal in the data set (Fig. 2B, C). A bootstrapped distance tree (10,000 replicates) provided little support for any breeding population associations; just two populations formed one supported clade (FL and MS1 supported by 60% of bootstrap replicates; not shown).

Mantel and permutation tests (NTSYS-pc) of the pooled breeding population data set indicated that genetic distance was at best only weakly associated with geographic distance (Z = 0.27, P = 0.11; 10,000 random permutations). However, when population contrasts were partitioned by geographic region, a clearer view of population differentiation

TABLE 3. Exact tests for Hardy-Weinberg equilibrium (P-values; GENEPOP, Raymond and Rousset 1995) and inferred frequencies of null alleles (CERVUS, Marshall et al. 1998).

Locus	P	Null alleles
*Lsw*μ14	0.293	0.006
*Lsw*μ18	0.185	0.016
*Lsw*μ3	0.429	0.011
*Lsw*μ5B	0.029	0.045
*Lsw*μ9	0.616	0.004
*Lsw*μ19	0.035	0.019

TABLE 4. Allelic heterogeneity and levels of population structure (θ and associated P-values; Weir and Cockerham 1984) among 11 breeding and between two wintering populations of Swainson's Warbler (GENEPOP, Raymond and Rousset 1995).

	Breeding		Wintering	
Locus	θ	P^a	θ	P^a
Lsw:14	0.003	0.122	0.014	0.098
Lsw:18	0.007	0.039	−0.012	0.585
Lsw:3	−0.009	0.924	−0.014	0.455
Lsw:5B	0.034	0.000	−0.012	0.338
Lsw:9	0.012	0.192	0.144	0.004
Lsw:19	−0.001	0.387	−0.005	0.577
Overall	0.007	<0.00005	0.011	0.044

[a] Adjusted α for series of tests on individual loci is 0.0083. An α of 0.05 for exact tests (bottom row) is not adjusted.

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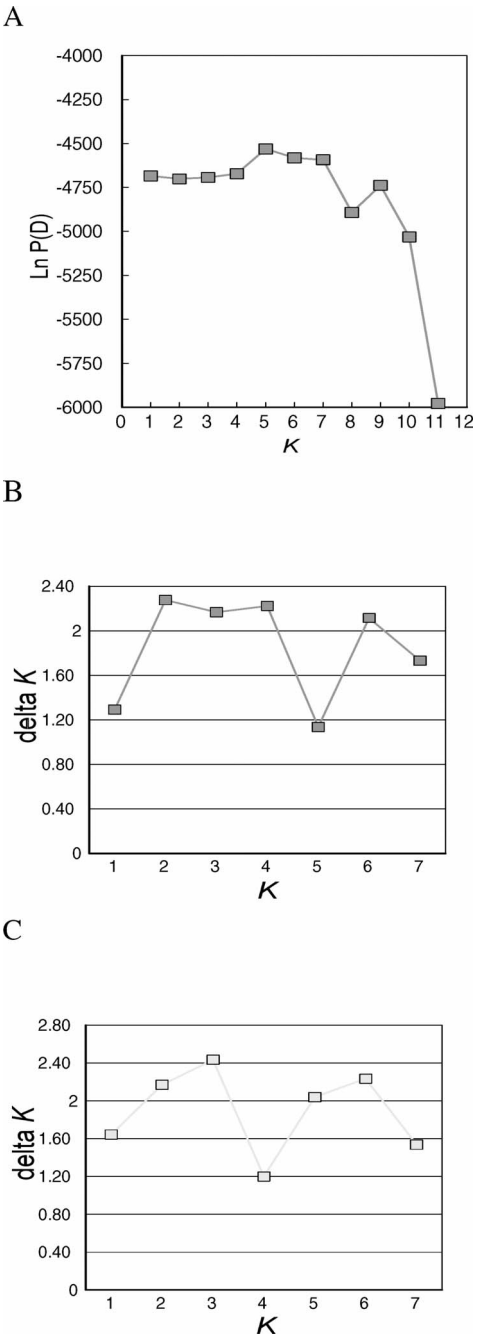


FIG. 2. A. Probabilities, ln P(D), of population samples coming from *K* genetic groups using Bayesian analyses of the full breeding area data set (STRUCTURE Version 2, Pritchard et al. 2000; Falush et al. 2003). The set of 11 breeding populations oversampled the number of actual genetic clusters present, a value that ranges from 1 to 7. The second and third figures show delta *K*, the second order rate of change of ln P(D) in relation to *K* (Evanno et al. 2005), of breeding (B) and wintering (C) populations suggesting that 2–4 genetic clusters are most probable among the 11 sampled breeding populations, and that just 2–3 are most likely represented in the wintering populations (although peak heights and signal in these data sets are low).

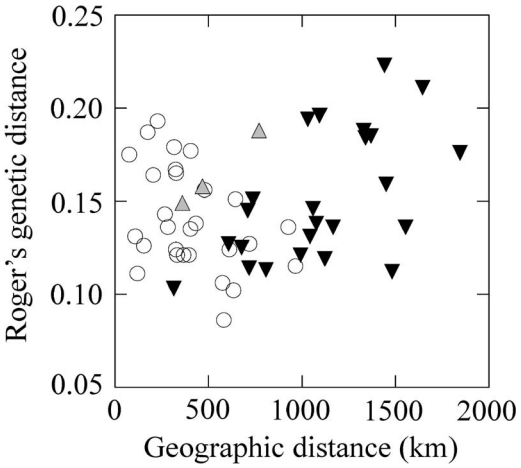


FIG. 3. Rogers' (1972) genetic distance and geographic distance between breeding populations of Swainson's Warbler: (circles) pairwise comparisons between localities that drain into the Gulf of Mexico (TX1, TX2, LA1, LA2, MS1, MS2, AR, FL); (gray triangles) pairwise comparisons between localities that drain into the Atlantic Ocean (GA, SC, VA); (black triangles) pairwise comparisons between Gulf and Atlantic drainage localities.

emerged (Figs. 1, 3). Pairwise comparisons between Gulf populations (n = 28 contrasts) indicated a slightly negative relationship between genetic and geographic distance (r_s = −0.39). The relationship between genetic and geographic distance was substantially weaker (r_s = −0.23) when pairwise comparison was limited to the seven populations from the Mississippi and Sabine river drainages (n = 21 contrasts) of the western Gulf. In contrast, pairwise contrasts (n = 24) between populations from Atlantic drainages with those from Gulf drainages exhibited a markedly positive correlation (r_s = 0.49), suggesting a weak longitudinal trend toward genetic isolation-by-distance. The most geographically isolated population in our survey (VA) also exhibited the greatest average pairwise genetic distance

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from other populations. The most centrally located population (FL) also showed the lowest average genetic distance between populations.

Wintering populations exhibited significant but weak structure ($\theta = 0.0111$, $P = 0.044$; Table 4). This was driven largely by locus *Lsw*μ9 ($P = 0.004$; other loci $P > 0.098$; Table 4). The loci responsible for breeding and wintering population structure were different (Table 4).

Allozyme and Microsatellite Comparisons.—We compared genetic distance matrices derived from allozymes and the microsatellite loci examined in this study for five breeding populations (LA1, AR, FL, SC, VA). The null hypothesis that the two matrices were not associated could not be rejected with Mantel and permutations tests ($Z = 0.18$, $P = 0.30$; 10,000 random permutations) indicating the two nuclear genetic marker systems examined for this subset of breeding populations exhibited discordant patterns of differentiation.

Gene Flow.—The rare alleles method, an indirect technique to estimate the number of migrants per generation, inferred $Nm = 9.16$ among breeding populations after correction for sample size (where mean sample size was 18.6 and mean frequency of private alleles $P[1] = 0.026$). Assignment tests, which are more reflective of contemporary gene flow, indicated that three to seven individuals (15–70%) from each breeding population had genotypes that were significantly unlikely to have originated there (averaging 4.4 individuals or 25% per population; Table 5). These values ranged from two to five individuals per population (averaging 3.2 individuals or 18% per population; Table 5) when adjusted for type-I error (Dunn-Sidák test). These numbers were similar in the two wintering populations (averaging 4.5 individuals per population, or 3.5 with the Dunn-Sidák correction; Table 5). The genotypes of three individuals from Florida and single individuals from Mississippi (MS1), South Carolina, and Texas (TX2) could not be assigned to any breeding population (all with $P < 0.00005$). Similarly, two individuals from Jamaica and one from Mexico could not be assigned to any breeding or wintering population. Both the rare alleles method and assignment tests suggested a moderate amount of gene flow among breeding populations ($Nm = 3.2$–9.2).

TABLE 5. Assignment test results comparing genotypes of individuals with genotypic characteristics of the breeding populations from which they were sampled (GeneClass, Cornuet et al. 1999).

Population	*n*	Mean Bayesian probability (± SD)[a]	Genotypes not from sampled population[b]
Arkansas (AR)	20	0.37 ± 0.38	5
Florida (FL)	24	0.34 ± 0.30	5
Georgia (GA)	20	0.32 ± 0.31	3
Louisiana 1 (LA1)	22	0.28 ± 0.29	5
Louisiana 2 (LA2)	10	0.11 ± 0.20	7
Mississippi 1 (MS1)	20	0.29 ± 0.29	4
Mississippi 2 (MS2)	10	0.16 ± 0.27	3
South Carolina (SC)	21	0.31 ± 0.32	3
Texas 1 (TX1)	17	0.23 ± 0.25	4
Texas 2 (TX2)	20	0.32 ± 0.28	5
Virginia (VA)	21	0.38 ± 0.30	4
Mexico (MEX)	26	0.35 ± 0.34	4
Jamaica (JAM)	19	0.32 ± 0.29	5

[a] Averaged Bayesian posterior probabilities of membership among a population's individuals (Rannala and Mountain 1997, Cornuet et al. 1999).
[b] Number of individuals with probabilities of membership from population of origin with $P < 0.01$.

Long-term Population Size.—We obtained estimates of $4N_e\mu$, where N_e is effective population size and μ is the microsatellite mutation rate. These analyses suggested uniformly small long-term effective population sizes (N_e) ranging from a low of 44 (LA2) to a high of 174 (LA1; Table 6). There was no evidence for population genetic bottlenecks in breeding or wintering populations at any of the modeled values of θ (1, 10, and 25; $P > 0.1$), despite these rather low estimates of long-term effective population size.

Evidence of Winter Mixing.—We compared the allelic frequencies of wintering populations from Mexico and Jamaica with those of each of the 11 breeding populations to investigate the genetic relationships between breeding and wintering populations. No genetic differences were found between any pairwise combination of wintering and breeding population when α was adjusted for multiple tests (Table 7). Evidence of geographic segregation of breeding populations in wintering areas remained weak under a less conservative approach (no adjustment of α). Allelic frequencies of the Mexican wintering population were significantly different from those of breeding populations from Arkansas (AR) in the Mis-

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TABLE 6. Estimates of $4N_e\mu$ and the 95% confidence interval (following Beerli and Felsenstein 2001) where N_e is effective population size and μ is the mutation rate of microsatellite loci. Subsequent estimates of long-term effective population sizes (N_e est.) and the corresponding 95% confidence intervals are based on a mutation rate of 5×10^{-4} (Goldstein and Schlötterer 1999) and are well below contemporary census sizes of these populations.

Population	$4N_e\mu$	95% CI[a]	N_e est.	95% CI
Arkansas (AR)	0.18	(0.16–0.21)	92	(81–105)
Florida (FL)	0.24	(0.21–0.26)	118	(105–132)
Georgia (GA)	0.17	(0.15–0.20)	86	(75–98)
Louisiana 1 (LA1)	0.35	(0.30–0.41)	174	(150–204)
Louisiana 2 (LA2)	0.09	(0.08–0.10)	44	(38–51)
Mississippi 1 (MS1)	0.16	(0.14–0.18)	80	(71–91)
Mississippi 2 (MS2)	0.09	(0.08–0.11)	45	(39–53)
South Carolina (SC)	0.22	(0.19–0.25)	108	(96–123)
Texas 1 (TX1)	0.14	(0.13–0.16)	71	(63–81)
Texas 2 (TX2)	0.20	(0.18–0.23)	102	(89–117)
Virginia (VA)	0.16	(0.14–0.18)	78	(69–88)
Mexico (MEX)	0.34	(0.30–0.38)	170	(152–192)
Jamaica (JAM)	0.17	(0.15–0.19)	84	(74–96)

[a] Based on multiple runs after initial, random parameter estimates were used to seed additional runs and convergence on similar values was verified.

sissippi Valley and Virginia (VA) and South Carolina (SC) on the Atlantic coastal plain (Table 7). Similarly, allelic frequencies of the Jamaican wintering population were significantly different from those of breeding populations from Louisiana (LA2), Arkansas (AR), Texas 1 (TX1), and Virginia (VA; all $P < 0.02$; Table 7).

We assigned wintering individuals to their most likely breeding population by choosing the highest probability *P*-value from the array of breeding populations. All but two individuals from Mexico and two from Jamaica could be assigned to one of the 11 breeding populations ($P < 0.01$). Of the 24 assignable individuals from Mexico, only Arkansas (AR) and Georgia (GA) were eliminated as likely breeding populations; and among the 16 assignable individuals from Jamaica, only Louisiana (LA2), Mississippi (MS2), and Virginia (VA) were unlikely breeding sources. This suggests that individuals from a substantial number of geographically distinct breeding populations mix in wintering areas in Mexico and Jamaica.

DISCUSSION

The breeding distribution of Swainson's Warbler has decreased significantly during the past century because of deforestation of bot-

TABLE 7. Pairwise comparisons showing genetic similarities and differences between two wintering and 11 breeding populations of Swainson's Warbler (θ and associated *P*-values; GENEPOP).

	Mexico (MEX)		Jamaica (JAM)	
	θ	*P*[a]	θ	*P*[a]
Arkansas (AR)	0.0211	0.0126	0.0200	0.0107
Florida (FL)	−0.0046	0.5485	0.0081	0.1444
Georgia (GA)	0.0004	0.3073	0.0112	0.1641
Louisiana (LA1)	0.0006	0.1796	−0.0007	0.2652
Louisiana (LA2)	−0.0082	0.3890	0.0221	0.0070
Mississippi (MS1)	−0.0122	0.9319	0.0087	0.1468
Mississippi (MS2)	−0.0195	0.9580	0.0163	0.0831
South Carolina (SC)	0.0217	0.0115	0.0117	0.1059
Texas (TX1)	0.0015	0.0645	0.0201	0.0062
Texas (TX2)	0.0125	0.1380	0.0042	0.3184
Virginia (VA)	0.0207	0.0169	0.0173	0.0178

[a] Experiment error held at $\alpha = 0.05$, and adjusted alpha for each series of tests = 0.0045.

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tomlands, flood mitigation projects, and forestry practices that minimize early successional habitats (Twedt and Loesch 1999; Graves 2001, 2002). Several populations near the northern periphery of the warbler's breeding range have disappeared in recent decades and many of the remaining populations are isolated. We detected no evidence of genetic bottlenecks in breeding or wintering populations despite relatively small effective population sizes and fragmentation of the warbler's geographic range. However, the lower allelic diversity exhibited among Atlantic-drainage populations and the significant correlation between genetic and geographic distances observed in pairwise comparisons of Gulf-drainage populations with those sampled in Atlantic drainages suggests that subtle population structure exists among breeding populations. Clustering tests further suggested that breeding populations sampled in this study are composed of two to four genetic populations. Whether differentiation is caused by genetic drift, stochastic sampling effects, selection associated with the warbler's disjunct wintering range, or other factors is unknown.

The moderate levels of gene flow among breeding populations revealed by microsatellite data (Nm = 3.2–9.2) were consistent with the results of an earlier survey of allozymes (Winker et al. 2000) in a subset of five populations (Nm = 1.5–11.7). However, spatial patterns of genetic variation revealed by microsatellites and allozymes were discordant, a not uncommon event between molecular marker systems (Allendorf and Seeb 2000). Significant population structure was caused by two microsatellite loci in the present study and three of 16 loci examined in our earlier allozyme study.

Mixing of breeding populations in wintering areas is believed to be a common phenomenon because breeding ranges of most Nearctic-Neotropic migratory songbirds are considerably larger than their wintering ranges (Terborgh 1989). The signal of geographic structure in our microsatellite data is weak, but Bayesian assignment tests imply that at least six breeding populations (TX1, TX2, LA1, MS1, FL, and SC) could have contributed wintering individuals to both the Mexican and Jamaican wintering populations. However, genetic differences between the Mexican and Jamaican populations suggest they are comprised of different subsets of breeding populations.

CONSERVATION IMPLICATIONS

Should breeding populations of Swainson's Warbler be managed as a single conservation unit? Patterns of microsatellite variation among breeding and wintering populations suggest that multi-regional and international efforts will likely be required to maintain the current level of genetic diversity in the species. Implementation of a viable management plan for the species throughout its global range, however, is contingent upon the development of additional genetic markers that can more fully resolve the genetic structure of breeding populations and their distributions during the nonbreeding season. Future field efforts should focus first on obtaining genetic samples from breeding populations in the Appalachian and Ozark mountains and from wintering populations in Cuba and Belize.

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