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Genetic differentiation among populations of a migratory songbird: *Limnothlypis swainsonii*

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Population structure and gene flow were inferred from isozyme variation at 26 loci among five populations of *Limnothlypis swainsonii* (Swainson's Warbler; Parulidae), a Nearctic-Neotropic migrant songbird breeding in the unglaciated southeastern U.S.A. These populations exhibit relatively high levels of heterozygosity ($\bar{H}_o = 0.083$), and 16 of 26 loci were polymorphic in at least one population ($\bar{P} = 0.385$). Allelic frequencies were significantly heterogeneous at five loci, indicating a surprising degree of population structure for a migratory bird with no recognized subspecies ($F_{ST} = 0.043$). Moderate levels of gene flow are inferred ($Nm = 1.5$ to 11.7), yet population structure does not fit an isolation-by-distance model. Genetic heterogeneity is mostly due to differentiation between an Arkansas population and four populations from the coastal plain (from Louisiana to Virginia). Genetic drift may be responsible for much of the observed structure, but the lack of obvious barriers to dispersal between Arkansas and the coastal plain suggests that differentiation has been maintained by some other mechanism(s). Vicariance events on the breeding range, a split wintering range, or both could contribute to the pattern of differentiation observed.

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Genetic surveys of natural populations enhance our understanding of the ways in which ecological, historical, and demographic parameters influence the development and partitioning of genetic diversity. These surveys are useful in a wide range of evolutionary inquiries, including biogeography, conservation biology, and the study of microevolutionary processes. Early surveys of wild birds led to the general perception that genetic differentiation is lower in birds than in other vertebrates at both the population and species levels (e.g., Barrowclough and Corbin 1978, Avise and Aquadro 1982, Barrowclough 1983). This general trend is probably due largely to the greater mobility of birds, resulting in higher levels of gene flow and larger effective population sizes (Barrowclough 1983). Other relevant factors may include class-related differences in evolutionary rates or in the ages of the species studied (Avise 1983, Barrowclough 1983).

However, early surveys of genetic differentiation in birds focused on North Temperate species with continuous ranges, many of which were also migratory (e.g., Barrowclough 1980a, 1983, Evans 1987). These factors tended to accentuate differences in gene flow and population size and heighten the apparent disparity between birds and other vertebrates. As more studies have accumulated, many examples of birds with substantial differentiation at both the population and species levels have come to light. Factors that can be implicated in influencing differentiation include migratory behavior (Escalante-Pliego 1991), discontinuities in range (Baker et al. 1990, Peterson et al. 1992, Mundy et al. 1997), age of the species or populations involved (Mariaux and Braun 1996, Brumfield et al. 1997), and evolutionary rates of the genes under consideration (Wenink et al. 1993, Merilä et al. 1997). These factors all affect one or more basic evolutionary parameters, such as gene flow,

mutation, selection, or genetic drift. Thus, it seems clear that birds are subject to the same evolutionary forces as other organisms, and that the differences observed are quantitative rather than qualitative.

As genetic surveys of birds have accumulated, a second trend that has appeared is the tendency for tropical birds to have higher levels of differentiation than temperate ones at both the population and species levels (Braun and Parker 1985, Capparella 1988, Zink 1988, Hackett and Rosenberg 1990, Capparella 1991, Escalante-Pliego 1991, Peterson et al. 1992, Hackett 1993, Seutin et al. 1993, 1994, Bates and Zink 1994, Brumfield et al. 1997). For example, allozyme-based studies suggest that, on average, populations of Neotropical bird species exhibit levels of differentiation several-fold higher than those found in North Temperate birds (Table 1). Latitudinal differences in climate may be an important factor in producing this apparent difference between Neotropical and North Temperate birds. Seasonality correlates with latitude, and holarctic regions experience greater long-term climatic fluctuations than tropical regions (e.g., Cuffey et al. 1995, MacAyeal 1995, Thompson et al. 1995). Annual and long-term climatic fluctuations may have had profound homogenizing effects on the genetics of many North Temperate bird populations.

Table 1. Levels of population differentiation reported from studies of allozymes in Neotropical landbirds, with comparative summaries from other birds.

Taxon	F_{ST}	Source
Formicariidae		
Gymnopithys leucaspis	0.365	Hackett 1993
Gymnopithys salvini	0.333	Hackett 1993
Pithys albifrons	0.037	Hackett 1993, Capparella 1987
Myrmoborus myotherinus	0.170	Hackett 1993, Capparella 1987
Dendrocolaptidae		
Glyphorynchus spirurus	0.232	Hackett 1993, Capparella 1987
Pipridae		
Pipra coronata	0.125	Hackett 1993, Capparella 1987
Chiroxiphia pareola	0.194	Hackett 1993, Capparella 1987
Tyrannidae		
Mionectes oleagineus	0.132	Capparella and Lanyon 1985
Parulidae		
Geothlypis trichas[1]	0.080	Escalante-Pliego 1991
Geothlypis beldingi	0.059	Escalante-Pliego 1991
Geothlypis poliocephala	0.199	Escalante-Pliego 1991
Geothlypis aequinoctialis	0.553	Escalante-Pliego 1991
Emberizidae		
Atlapetes brunneinucha	0.280	Peterson et al. 1992
Chlorospingus ophthalmicus	0.312	Peterson et al. 1992
Zonotrichia capensis	0.118	Lougheed and Handford 1992
Average	0.213	
Birds in general	0.049	Barrowclough 1983 (25 taxa)
Birds in general	0.048	Evans 1987 (23 taxa)
Nearctic birds	0.038	Barrowclough and Johnson 1988 (18 taxa)

[1] Estimate includes only resident neotropical populations.

Two influences seem particularly important in this regard because of their effects on population structure and gene flow. Long-term phenomena such as glaciations can cause dramatic fluctuations in the size and shape of a species' geographic range. This in turn affects the size of populations, their degree of isolation, and the residency times during which they may undergo differentiation. The relative historic stability of a species' range falls along a continuum of possible stability states. Long-term stability is likely to be an important factor favoring differentiation among populations simply by allowing time for its development through genetic drift or local adaptation. The modification of geographic ranges may create opportunities for gene flow or colonization that inhibit population differentiation. As an example, several North Temperate vertebrates show lower levels of genetic variation and/or population structure in formerly glaciated portions of their ranges, including salamanders (Highton and Webster 1976), fishes (Bernatchez and Wilson 1998), Dall sheep (Sage and Wolff 1986), and five bird species (Väisänen and Lehväslaiho 1984, Gill et al. 1993, Zink and Dittmann 1993, Merilä et al. 1996).

Also, the short-term phenomenon of climatic seasonality increases with latitude, promoting seasonal migration in a higher proportion of the breeding avifauna (Newton and Dale 1996a, b). Although a comprehensive comparison of dispersal distances between migratory and sedentary birds has not been made, vagility and vagrancy are notoriously high among migratory birds, and it seems safe to assume that effective dispersal distances are greater in this group, leading to higher levels of gene flow and concomitantly lower levels of differentiation in North Temperate bird populations.

Broad comparisons of genetic population structure between North Temperate and tropical birds are therefore likely to contrast migratory organisms with unstable range history against sedentary organisms with relative range stability. The relative importance of these factors in producing the average differences observed can be gauged by systematically studying species that vary in range characteristics and migratory behavior. Here we examine a seasonal migrant that has presumably had a relatively stable range history.

The focal species, *Limnothlypis swainsonii* (Parulidae: Swainson's Warbler, AOU 1998), is a rather uncommon Nearctic-Neotropic migrant that breeds mainly in second growth floodplain forest across a relatively continuous breeding range in regions of southeastern U.S.A. that were unglaciated during the Pleistocene

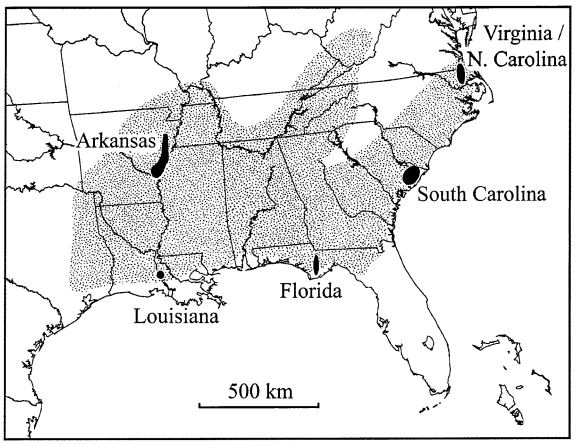

Fig. 1. Primary breeding range of *Limnothlypis swainsonii* and distribution of sampled populations in the southeastern United States of America. Clockwise from upper right, sampled populations were from Virginia/North Carolina (VA/NC), South Carolina (SC), Florida (FL), Louisiana (LA), and Arkansas (AR).

(Fig. 1; Meanley 1971, Pielou 1991). Its primary wintering range is split between the Caribbean (Cuba and Jamaica) and mainland Middle America (southeastern Mexico and Belize). The genus is monotypic, and no intraspecific geographic variation is recognized (Brown and Dickson 1994). Individuals weigh approximately 15 g, begin breeding near the end of their first year, live as long as 8 yr (Graves, unpubl. data), are territorial, and breed in pairs (although they are rarely polygynous; Graves 1992).

Materials and methods

Population samples of 20 or more adults were collected from breeding territories between 27 April and 31 May 1986–1994 at five localities in the species' breeding range (Fig. 1), for a total of 109 individuals. Collecting localities were: White and Mississippi rivers in eastern Arkansas (AR); the lower Atchafalaya River, west of the Mississippi River in southern Louisiana (LA); the Apalachicola River in northwestern Florida (FL); the lower Cooper and lower Santee rivers in southeastern South Carolina (SC); and the Great Dismal Swamp and lower Chowan River in southeastern Virginia and northeastern North Carolina (VA/NC). Birds were frozen in liquid nitrogen within 30 minutes of death for transportation to the laboratory. Muscle, liver, heart, and kidney samples were taken from partially thawed specimens and stored at −80°C until preparation of homogenates for analysis. Specimens are deposited in the National Museum of Natural History, Smithsonian Institution.

Approximately 20 mg each of muscle, liver, heart, and kidney tissues were sliced from frozen samples and homogenized on ice in 200 µl of deionized water. This mixture was spun for 2 min at 14000 rpm and the supernatant was divided into 20 µl aliquots and frozen at −80°C until the ensuing electrophoretic experiments. Protein electrophoresis was performed on Titan III cellulose acetate plates (Helena Laboratories, Inc.) following the methods of Richardson et al. (1986). The 26 scored loci were from the following protein systems under the running conditions noted (abbreviations and Enzyme Commission numbers from Richardson et al. 1986 and Harris and Hopkinson 1976; buffers from the former): Buffer A: (1 h) PEP-LA 1 and 2 (3.4.11; the more cathodal locus was monomeric and probably PEP-VL, 3.4.11.11); (1.5 h) IDH 1 and 2 (2.7.1.1), LDH 1 and 2 (1.1.1.27), MPI (5.3.1.8), PK (2.7.1.40); (2 h) PEP-LGG 1 (3.4.11.4), PEP-PhePro (3.4.13.9); Buffer B: (1 h) αGPD (1.1.1.8), GPT (2.6.1.2), SORDH (1.1.1.14), MDH 1 and 2 (1.1.1.37), PGM 1 (2.7.5.1); (1.25 h) GOT (2.6.1.1); (1.5 h) ADA (3.5.4.4); (2 h) 6PGD (1.1.1.44), GPI (5.3.1.9), and GP 1 and 2 (general proteins); Buffer C: (45 min) GDA (3.5.4.3); (1.5 h) CK 1 and 2 (2.7.3.2); Buffer J: (1.5 h) AK (2.7.4.3). All individuals were examined at these loci. Electromorphs were labeled alphabetically in order of relative mobility from the origin, with the most anodally migrating allele coded as "a". Scoring of all loci was performed initially by KW then double-checked by MJB. Identity of alleles on different gels was confirmed by running selected individuals on cross-correlating gels.

Population statistics were calculated using the programs BIOSYS-1 (Swofford and Selander 1981), GENESTAT (Lewis 1989), and GENEPOP (Raymond and Rousset 1995). For comparison with historic literature we use traditional F_{ST} values (Nei 1973, Wright 1978; sometimes given as G_{ST}) except where stated otherwise (i.e., θ). Geographic and genetic distance matrices were compared using the Mantel test (Schnell et al. 1985, Rohlf 1988).

Gene flow among populations was indirectly estimated using two methods: the rare alleles method of Slatkin (1981, 1985) as elucidated by Barton and Slatkin (1986) and Slatkin and Barton (1989); and the F_{ST} method of Slatkin and Barton (1989). Although Cockerham and Weir (1993) showed that the simulations of Slatkin and Barton (1989) gave erroneous results when gene flow was high, their own simulations corrected this problem and emphasized the usefulness of the method for inferring gene flow. As Cockerham and Weir (1993: 863) stated, "there are conditions under which functions of *F*-statistics can provide gene-flow estimates of low bias." These conditions are those assumed by the standard island model under which gene flow is being inferred, including allelic neutrality and equilibrium, with gene flow and mutation (Cockerham and Weir 1993: 855, 863). Three things should be considered when using these methods. First, the two methods rely on different aspects of the data (see

Discussion). Secondly, "If F_{ST} values are little affected by selection, then they are quite useful in estimating migration rates but reveal nothing about selection, but if F_{ST} values reflect the action of selection, especially spatially variable selection, they reveal little or nothing about gene flow." (Cabe and Alstad 1994: 491). Finally, there is an historical component: F_{ST} values provide only an imperfect average if population sizes and rates of effective dispersal have varied through time (see also Bossart and Pashley Prowell 1998).

Results

Variation within populations

Variation was detected in 16 of the 26 presumed loci scored (Table 2). Within populations the percentage of polymorphic loci (P) ranged from 31%–42%, and among all individuals from all populations ($\bar{P}$) it was 38.5% (Table 3).

Levels of observed heterozygosity (H_o) over all loci varied from 0.062 to 0.113 among populations, and averaged 0.083 (± 0.007) (Table 3). Expected heterozygosity values (H_e, Table 3) varied from 0.067 to 0.118 and averaged 0.100 (± 0.031) (Table 3). Calculations of expected heterozygosities (H_e, Nei 1978) assume that genotypes occur at Hardy-Weinberg equilibrium within populations. This assumption was supported at all variable loci in all populations except for the locus GPI in the Arkansas population, which showed a heterozygote deficiency (Hardy-Weinberg exact test, Raymond and Rousset 1995, $0.07 < P \leq 1.0$; except GPI in Arkansas, where $P = 0.003$). Reexamination of the GPI data confirmed this result.

Differentiation among populations

Allelic frequencies among the five populations were significantly heterogeneous at five loci (Table 4; ADA, CK 2, GOT 1, PEP-LGG 1, and PEP-PhePro; Fisher exact test, Raymond and Rousset 1995). The traditional estimator of F_{ST} (Nei 1973, Wright 1978) for all populations equalled 0.043, while the unbiased estimator θ (Weir and Cockerham 1984) equalled 0.028. Overall heterogeneity was highly significant (Table 4; $P < 0.00005$), indicating significant population structure.

Examination of between-population genetic distance values (Rogers 1972, Nei 1978, Table 5) and a UPGMA dendrogram (Fig. 2) showed that most of the population-level differentiation among our samples occurred between Arkansas and the other four populations. When Arkansas was excluded, only one locus (GOT 1) showed significant heterogeneity in allele frequency among the four remaining populations (test as in Table 4; $P = 0.031$). Arkansas also had six of the 15 private alleles (and 22 of the 35 occurrences) among the five populations. Florida was also somewhat differentiated, showing seven private alleles and a clear contribution to heterogeneity at GOT 1 (Table 2).

The lack of concordance between geographic and genetic distances among populations suggested in Table 5 and Fig. 2 was confirmed by Mantel and permutation tests comparing the geographic distance matrix with Rogers' (1972) and Nei's (1978) genetic distance matrices ($Z = -0.051$, $P = 0.49$, and $Z = 0.23$ and $P = 0.22$, respectively; 10000 random permutations). Among the five populations there was no apparent association between geographic and genetic distances. Thus, genetic differentiation does not fit an isolation-by-distance model.

Indirect estimates using two methods suggest that moderate levels of gene flow are occurring among these five populations (approximately 1.5–11.7 individuals per generation; Table 6). Estimates obtained using the F_{ST}-based method were roughly twice the level obtained using rare alleles (see Materials and methods for possible reasons). Jackknife analyses (sequentially excluding single populations) suggest that gene flow occurs among the four non-Arkansas populations at approximately twice the rate as those levels occurring between Arkansas and any of the other populations (Table 6).

Discussion

Genetic variation at population and species levels

Levels of heterozygosity in *Limnothlypis* (Table 3) are higher than the average reported by Barrowclough (1983: 229) for single breeding populations of 30 species of birds ($\bar{H}_e = 0.053$), and higher than the average of 0.065 reported in a species-level comparison made by Evans (1987; 79 species). In fact, expected heterozygosity in the Arkansas population ($H_e = 0.118$) is exceeded by only one of the 30 species summarized by Barrowclough (1983: 229). Eleven of the 79 species summarized by Evans (1987) had higher heterozygosities, but that summary was not restricted to breeding populations. Our estimate of allozyme polymorphism at the species level ($\bar{P} = 0.385$) is also among the highest observed in Passeriformes (Corbin 1987, Evans 1987), and is also higher than the averages observed in insects (0.30) and vertebrates (0.15) (Selander and Johnson 1973, Nevo 1978, Richardson et al. 1986).

Such estimates of genetic variability must be interpreted cautiously, because they can be biased by sample size, loci examined, techniques employed, and other factors (Barrowclough 1983). Nevertheless, ours was a reasonably standard allozyme survey and it appears that *Limnothlypis* shows a high level of variation compared with birds studied in these early surveys, which have, on average, more northerly breeding ranges. This

fits a pattern exhibited in several taxa (Sage and Wolff 1986: 1093, Gill et al. 1993, Lewis and Crawford 1995).

Sage and Wolff (1986) suggested that glacially-induced range shifts alone could cause reduced variability. Given the relative instability of holarctic climate, population bottlenecks may occur more frequently among more northerly breeding landbirds (Gill et al. 1993, Merilä et al. 1996), and lowered long-term popu-

Table 2. Allele frequencies at variable loci in five populations of *Limnothlypis*. Ten monomorphic loci (αGPD, LDH 2, MDH 1, MDH 2, GPT, IDH 2, PK, AK, GP 1 and GP 2) were also scored and are included in analyses.

Locus	Allele	Population				
		AR N = 20	FL N = 24	LA N = 23	SC N = 21[1]	VA/NC N = 21[2]
SORDH	a	1.000	0.979	1.000	1.000	1.000
	b	0.000	0.021	0.000	0.000	0.000
6PGD	a	0.075	0.125	0.087	0.167	0.071
	b	0.925	0.875	0.891	0.833	0.929
	c	0.000	0.000	0.022	0.000	0.000
ADA	a	0.025	0.063	0.043	0.024	0.000
	b	0.625	0.833	0.913	0.929	0.905
	c	0.350	0.083	0.043	0.048	0.095
	d	0.000	0.021	0.000	0.000	0.000
CK 1	a	0.050	0.042	0.000	0.000	0.000
	b	0.500	0.500	0.478	0.595	0.357
	c	0.450	0.458	0.522	0.405	0.643
CK 2	a	0.025	0.000	0.000	0.000	0.000
	b	0.950	1.000	1.000	1.000	1.000
	c	0.025	0.000	0.000	0.000	0.000
GDA	a	1.000	1.000	1.000	0.952	0.976
	b	0.000	0.000	0.000	0.048	0.024
GOT 1	a	0.750	0.771	0.826	0.952	0.810
	b	0.000	0.083	0.000	0.000	0.000
	c	0.250	0.146	0.174	0.048	0.190
GPI	a	0.000	0.021	0.022	0.000	0.000
	b	0.025	0.042	0.087	0.024	0.000
	c	0.000	0.021	0.000	0.000	0.000
	d	0.000	0.000	0.000	0.024	0.048
	e	0.625	0.688	0.587	0.714	0.690
	f	0.225	0.125	0.196	0.190	0.143
	g	0.125	0.104	0.109	0.048	0.119
IDH 1	a	0.025	0.021	0.000	0.000	0.000
	b	0.000	0.063	0.022	0.048	0.000
	c	0.975	0.917	0.978	0.952	1.000
LDH 1	a	0.000	0.021	0.000	0.000	0.000
	b	1.000	0.979	1.000	1.000	1.000
MPI	a	0.000	0.021	0.000	0.000	0.000
	b	0.975	0.979	1.000	1.000	1.000
	c	0.025	0.000	0.000	0.000	0.000
PGM 1	a	0.000	0.000	0.043	0.024	0.024
	b	1.000	1.000	0.957	0.976	0.976
PEP-LA 1	a	1.000	1.000	0.978	1.000	1.000
	b	0.000	0.000	0.022	0.000	0.000
PEP-LA 2	a	0.025	0.000	0.000	0.000	0.000
	b	0.975	1.000	1.000	1.000	1.000
PEP-LGG 1	a	0.000	0.042	0.000	0.000	0.000
	b	0.850	0.958	1.000	1.000	1.000
	c	0.150	0.000	0.000	0.000	0.000
PEP-PhePro	a	0.300	0.000	0.000	0.000	0.000
	b	0.025	0.000	0.022	0.000	0.000
	c	0.675	0.979	0.891	0.975	0.976
	d	0.000	0.021	0.065	0.000	0.000
	e	0.000	0.000	0.022	0.025	0.024

[1] One individual was not scoreable at PEP-LA, PEP-LGG, or PEP-PhePro.
[2] Two individuals were not scoreable at IDH 2.

Table 3. Average observed heterozygosities (H_o), average expected heterozygosities (H_c), and proportion of polymorphic loci (P) among sampled populations over 26 isozyme loci.

Population	H_o	H_c	P[1]
Arkansas (AR)	0.113 ± 0.013	0.118 ± 0.039	0.42
Florida (FL)	0.090 ± 0.008	0.093 ± 0.032	0.42
Louisiana (LA)	0.084 ± 0.007	0.083 ± 0.032	0.35
South Carolina (SC)	0.062 ± 0.004	0.067 ± 0.027	0.35
Virginia/North Carolina (VA/NC)	0.064 ± 0.004	0.067 ± 0.028	0.31
Overall ($\bar{H}_o$, $\bar{H}_c$, $\bar{P}$)	0.083 ± 0.007	0.100 ± 0.031	0.385

[1] Polymorphic loci are those where the frequency of the most common allele is <0.99.

lation sizes, associated for example with glacial refugia, could similarly decrease genetic variation (Avise et al. 1984).

The vast majority of *Limnothlypis* populations currently breed in deciduous bottomland forest on the Gulf and Atlantic coastal plains (Graves, unpubl. data). Given the ecological requirements of *Limnothlypis*, it is probable that breeding populations persisted in the major river corridors of the southeastern United States during the Wisconsinan glaciation. Evidence from recent field studies indicates that soils, hydrology, and habitat physiognomy are the major determinants of habitat selection by *Limnothlypis* (Graves, unpubl. data). While there is little evidence that floristics directly influence habitat selection, the recovery of mesic tree pollen from stratigraphic sediments dated from the Wisconsinan glaciation ($\sim$ 17500–29000 BP; Delcourt et al. 1980, Watts et al. 1992, Jackson and Givens 1994) demonstrates that plant taxa commonly found today in *Limnothlypis* habitat occurred locally in nearby locations during the Pleistocene. Although the breeding range of *Limnothlypis* may have fluctuated during the Pleistocene and Holocene, it remained unglaciated, and the species' range history has probably been relatively stable compared to those of more northerly-breeding migrant birds (Brown and Gibson 1983, Jacobson et al. 1987, Pielou 1991). We emphasize the importance here of considering relative range stabilities along a continuum of stability states, as even lowland tropical regions experienced ecosystem instabilities associated with the last glaciation (Colinvaux et al. 1996a, b).

Another possibility is that the high genetic variation in this species is due to a larger effective population size (N_e) caused by the increased vagility associated with seasonal migration. However, this seems unlikely considering the differentiated Arkansas population (and the inferred restriction of gene flow here) together with the relatively small census sizes of *Limnothlypis* populations. Many more northerly breeding species are also migratory and have larger census population sizes.

Table 4. Tests of allelic heterogeneity and F-statistics for the 16 variable loci among five populations.

Locus	P[1]	F_{ST}[2]	θ
6PGD	0.639	0.013	−0.007
ADA	0.000**	0.096	0.088
CK 1	0.193	0.025	0.006
CK 2	0.034*	0.030	0.016
GDA	0.180	0.026	0.010
GOT 1	0.023*	0.035	0.023
GPI	0.779	0.011	−0.013
IDH 1	0.363	0.023	0.006
LDH 1	1.000	0.017	−0.003
MPI	0.482	0.016	−0.003
PGM 1	0.560	0.015	−0.003
PEP-LA 1	0.776	0.017	−0.002
PEP-LA 2	1.000	0.020	−0.003
PEP-LGG 1	0.000***	0.098	0.099
PEP-PhePro	0.000***	0.155	0.165
SORDH	1.000	0.017	−0.003
Overall	0.000***		0.028
Mean		0.043	

* = P<0.05; ** = P<0.01; *** = P<0.001.
[1] GENEPOP Version 2.0; exact test on genic contingency table, chain of 100 000.
[2] BIOSYS-1 Version 1.7.

Table 5. Matrix of genetic distances among five *Limnothlypis* populations. Nei's (1978) unbiased genetic distance is above the diagonal, Rogers' (1972) genetic distance is below.

Population	1	2	3	4	5
1. AR	–	0.0055	0.0058	0.0088	0.0069
2. FL	0.043	–	0.0000	0.0002	0.0003
3. LA	0.043	0.024	–	0.0005	0.0000
4. SC	0.055	0.025	0.024	–	0.0022
5. VA/NC	0.046	0.026	0.019	0.025	–

Another possibility is that the high genetic variation in this species is due to a larger effective population size (N_e) caused by the increased vagility associated with seasonal migration. However, this seems unlikely considering the differentiated Arkansas population (and the inferred restriction of gene flow here) together with the relatively small census sizes of *Limnothlypis* populations. Many more northerly breeding species are also migratory and have larger census population sizes.

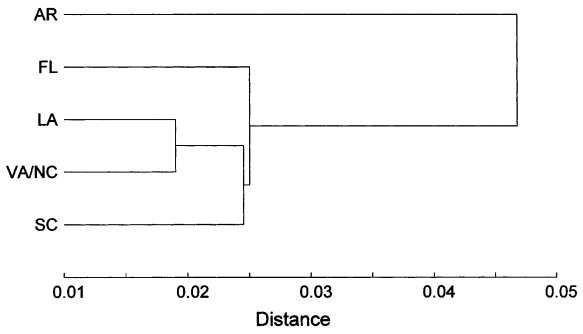

Fig. 2. UPGMA dendrogram of the genetic relationships among the five populations sampled (based on Rogers' [1972] genetic distance). Populations are from Arkansas (AR), Florida (FL), Louisiana (LA), Virginia/North Carolina (VA/NC), and South Carolina (SC).

Table 6. Two indirect estimates of gene flow (*Nm*; number of immigrants per generation), using average frequency of private alleles ($\bar{p}(1)$) and *F*-statistics for inference (see Materials and methods). Rows 2–6 give values obtained when one locality is removed from the analysis.

	Occurrences of private alleles	$\bar{p}(1)$	Nm_p	F_{ST}	Nm_F
Overall	35	0.0549	1.89	0.043	5.56
non-AR	17	0.0299	5.38	0.021	11.65
non-FL	28	0.0628	1.50	0.050	4.75
non-LA[1]	36	0.0529	2.01	0.049	4.85
non-SC	38	0.0527	2.03	0.040	6.00
non-VA/NC	35	0.0549	1.89	0.043	5.56

[1] More private alleles can occur in a subsample than in the total sample because alleles occurring at two locations will be private alleles in some subsamples.

Population differentiation: comparisons among species

As with measures of genetic variability, measures of differentiation can be biased by sample size, loci examined, techniques employed, and other factors. Because all of these factors cannot be controlled among studies, comparisons must be made in a general fashion and with caution. With this in mind, however, the following observations seem pertinent.

Excluding single-locus studies, allozyme data provide an average F_{ST} for landbirds of 0.050 (Barrowclough 1983, Evans 1987, Gill 1987, Johnson and Marten 1988, Baker et al. 1990, Zink and Klicka 1990). However, this average includes a study of Chaffinch *Fringilla coelebs* populations on oceanic islands (Baker et al. 1990). This species is a distant outlier ($F_{ST} = 0.386$), and if it is excluded the average F_{ST} for North Temperate Zone landbirds (0.045) falls to 0.022 (range 0.000–0.062). Genetic differentiation among *Limnothlypis* populations ($F_{ST} = 0.043$) is among the highest observed in Nearctic and Palearctic landbirds with continental distributions.

F_{ST}-values for this relatively continuously distributed species are most similar to tropical and southern Nearctic species with island or island-like distributions: migrant *Empidonax* flycatchers (Johnson and Marten 1988), migrant and nonmigrant *Zonotrichia leucophrys* (Baker 1975), *Aplonis* starlings (Corbin et al. 1974), and some species of Darwin's finches (Yang and Patton 1980).

The level of population differentiation displayed by *Limnothlypis* is remarkable when compared with other migrant wood warblers (Parulidae). Its mean F_{ST} of 0.043 is the highest value yet observed among migratory members of the family (among four species, see Barrowclough 1980b, Corbin 1987, Gill 1987, Zink and Klicka 1990). Moreover, genetic differentiation in *Limnothlypis* occurs among populations showing no obvious morphological differentiation, unlike some of the other species studied. Four nonmigratory tropical wood warblers all show higher values of F_{ST} (Table 1, genus *Geothlypis*).

In contrast, F_{ST} values for *Limnothlypis* would rank among the lowest observed in tropical landbirds (including island taxa, average $F_{ST} = 0.168$, range 0.020–0.553; Table 1 and references in Evans 1987). The apparent difference in population genetic structure between temperate and tropical birds has been noted using both nuclear and mitochondrial genetic markers of various kinds (Capparella 1988, 1991, Zink 1988, Hackett and Rosenberg 1990, Peterson et al. 1992, Hackett 1993, Seutin et al. 1993, 1994, Bates and Zink 1994). This pattern of increasing population subdivision from north to south is particularly compelling when several species from a single genus are examined (e.g., *Geothlypis*, Table 1; Escalante-Pliego 1991). The growing body of research on avian population genetics gives the overall impression that sedentariness, small population size, island-like distribution, and stable range history (e.g., lack of glaciation) are important factors promoting differentiation. These factors are more likely to be present in tropical species than in temperate ones. Resolution of the relative influences of these factors awaits further study (e.g., of low-latitude migrants) and the use of different methods (e.g., Bossart and Pashley Prowell 1998).

Differentiation: patterns, origins, and maintenance

Allozyme differentiation among *Limnothlypis* populations consists of mild but significant allele frequency differences at five loci and accumulated rare allele differences among populations. These differences are consistent with genetic drift as the proximate mechanism governing divergence. However, the data do not fit an isolation-by-distance model. The major axis of population differentiation occurs between the Arkansas population and the four coastal plain populations (Louisiana, Florida, South Carolina, Virginia/North Carolina; Fig. 2). The sampling localities from Arkansas and Louisiana both lie in the drainage of the Mississippi River and west of the river itself. They are about 435 km apart, well below the average distance between sample points of 830 km (range 435–1420 km).

There are no steep environmental gradients or obvious barriers to gene flow between southern Louisiana and eastern Arkansas that would promote differentiation. *Limnothlypis* was probably more or less continuously distributed in the lower Mississippi River valley prior to anthropogenic habitat changes. Yet differentiation is greater between these populations than between Louisiana and the other coastal plain populations, which inhabit widely separated drainages. This is a surprising pattern for an organism of riverine floodplains.

Provided that *Limnothlypis* populations meet the assumptions of the models under which gene flow is inferred (allelic neutrality and equilibrium in allele frequencies, with gene flow and mutation; Cockerham and Weir 1993), our results suggest that moderate levels of gene flow are occurring among the sampled populations (range 1.50–11.65; Table 6). Gene flow estimates among the four coastal plain populations were approximately twice as high as between Arkansas and these four other populations (Table 6). This pattern, which mirrors that of population differentiation (Fig. 2), was shown by both methods used to infer gene flow. These methods rely on different aspects of the data, and thus provide alternate perspectives on gene flow: the rare alleles method relies on a small portion of the data set (i.e., the private alleles), while the F_{ST} method is more dependent on loci showing significant differentiation (see Slatkin and Barton 1989). As noted, these estimates represent an historical average (see also Bossart and Pashley Prowell 1998), and there are many caveats to inferring ultimate causes from observed patterns of genetic differentiation (Barrowclough 1983, Cabe and Alstad 1994, Bossart and Pashley Prowell 1998). Yet there is nothing obvious in the present day breeding distribution of this species that suggests an explanation for this peculiar pattern of geographic structure.

The greater divergence of the Arkansas sample might simply be due to greater genetic drift if effective population size (N_e) in that population is sufficiently lower than in the others sampled. However, we have no evidence to suggest that N_e might be reduced in Arkansas. Census size of this population is in the thousands (Graves, unpubl. data). Past fluctuations in population size can dramatically reduce N_e, but there is no reason to believe that Arkansas has been more subject to fluctuation than other populations. Further, the high genetic variability observed in the Arkansas sample is inconsistent with reduced N_e.

Historical fragmentation of the breeding range also might have contributed to the observed pattern of population subdivision. The southeastern U.S.A. has witnessed vicariance events resulting in differentiation among many aquatic and terrestrial taxa (e.g., Highton and Webster 1976, Wiley and Mayden 1985, Avise 1992, Gill et al. 1993, 1999, Moncrief 1993, Bernatchez and Wilson 1998). The Arkansas gene pool may have originated from one of these events, but the Arkansas versus coastal plain axis of differentiation is not duplicated in other taxa of which we are aware.

If historic isolation and concurrent genetic drift are responsible for the differentiation of the Arkansas gene pool, as seems likely, then either recency of contact or low gene flow must be invoked for its continued existence. However, the relatively stable range history of this region makes very recent contact seem improbable. Similarly, given the levels of inferred gene flow among the non-Arkansas populations ($Nm = 5.4$ to 11.7), and relatively high dispersal distances in migrant landbirds (Barrowclough 1980a, Moore and Dolbeer 1989), a low species-wide level of gene flow also seems an unlikely explanation. Therefore, it seems that some other mechanism might be acting to maintain lowered gene flow between the Arkansas and coastal plain populations.

In this regard, the potential effects on differentiation of a split wintering range must be considered. The species' wintering range is split between the Caribbean (primarily Cuba and Jamaica) and mainland Middle America (primarily Mexico and Belize). Experimental studies of long-distance migrant *Sylvia* warblers (Muscicapidae: Sylviinae) have demonstrated that migratory behaviors such as seasonal fat deposition, timing of migration, and route selection (migratory direction) have a strong genetic basis (Berthold 1988). Experimental crosses between two populations of Blackcaps *Sylvia atricapilla* differing in migratory behavior showed intermediate migratory restlessness and migratory direction (Berthold 1988, Helbig 1991). Helbig (1991) suggested that these crosses would be selected against because their migrations would end in the Sahara, an unsuitable wintering region. We do not know where our sampled breeding populations winter, but if migration in *Limnothlypis* is under genetic control, offspring from crosses between parents of different wintering populations might end their autumn migrations somewhere over open water in the Gulf of Mexico or Caribbean. This would result in selection against crosses between these populations, and might contribute to genetic structure on the breeding grounds.

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