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POSTGLACIAL POPULATION EXPANSION DRIVES THE EVOLUTION OF LONG-DISTANCE MIGRATION IN A SONGBIRD

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Abstract.—The evolution of long-distance migratory behavior from sedentary populations is a central problem in studies of animal migration. Three crucial issues that remain unresolved are: (1) the biotic and abiotic factors promoting evolution of migratory behavior, (2) the geographic origin of ancestral sedentary populations, and (3) the time scale over which migration evolves. We test the role of postglacial population expansions during the Quaternary in driving the evolution of songbird migration against prevailing views favoring the role of intraspecific competition. In contrast to previous attempts to investigate these questions using interspecific phylogenies, we adopt an intraspecific approach and examine the phylogeography of a North American songbird, the chipping sparrow (*Spizella passerina*), which exhibits both long-distance migratory behavior in temperate North America and sedentary behavior in Mexico and Central America. We show that migratory populations descend from sedentary populations in southern Mexico and that migration has evolved as a result of a northward population expansion into temperate North America since the last glacial maximum 18,000 years ago. Migration appears to have evolved rapidly in some species as populations colonized areas of high seasonality in the temperate zone. The phylogeography of the yellow-eyed junco (*Junco phaeonotus*), a strictly sedentary species, provides a null model supporting the view that northward range expansions were driven solely by environmental factors and not by a predisposition to evolve migratory behavior. These results provide the strongest evidence to date that historical climate patterns can drive the rapid evolution of avian migration in natural populations, and they suggest a general mechanism for the repeated evolution of migration within and across bird lineages.

Key words.—Evolution of migration, Holocene, *Junco*, phylogeography, postglacial expansion, *Spizella*.

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The breeding and wintering ranges of numerous migratory bird species are separated by thousands of kilometers (Marra and Greenberg 2005), and prevailing theories attempting to explain the evolution of such a pattern have focused on the role of intraspecific competition (Gauthreaux 1982; Cox 1985). According to the prevailing ''tropical-origin hypothesis,'' migration has evolved in sedentary populations at southern latitudes as individuals in the original sedentary breeding populations undertook exploratory dispersal flights and colonized northern habitats of increasing seasonality (Cox 1968, 1985). Individuals returning south from breeding localities to the north of the original range would leap-frog sedentary populations to avoid intraspecific competition, and migratory distance and periodicity would grow as populations spread into increasingly seasonal environments. This scenario does not take into account the role of Quaternary glacial cycles in driving the rapid postglacial range expansions documented in birds (Milá et al. 2000; Veit et al. 2005) and other vertebrate groups (Taberlet et al. 1998; Hewitt 2000), which has been proposed (Gauthreaux 1980; Bell 2000; Zink 2002; Pérez-Tris et al. 2004), but not adequately tested.

Rapid northward expansions from southern populations were driven by the amelioration of climatic conditions in northern latitudes following glacial maxima (Taberlet et al. 1998; Hewitt 2000; Milá et al. 2000) and exposed individuals to areas of high seasonality as they colonized temperate latitudes. According to the alternative ''temperate-origin hypothesis'' of the evolution of migration, migratory movements would have arisen at these latitudes as sedentary individuals were forced to seasonally vacate breeding areas to avoid increasingly harsh winters (Bell 2000).

Migratory behavior in birds is thought to be largely under genetic control (Berthold 1996; Møller 2001; Pulido et al. 2001) and thus amenable to study in a phylogenetic framework (Zink 2002). Studies on the evolution of migration have typically treated migratory behavior as a character in interspecific phylogenies to test hypotheses regarding the geographic and temporal origins of migration (Joseph et al. 1999; Cicero and Johnson 2002; Outlaw et al. 2003). However, this approach has revealed that migratory taxa are typically paraphyletic, with migratory behavior gained and lost repeatedly across well-differentiated sister lineages. Because species-level avian taxa typically have histories of isolation spanning several million years (Klicka and Zink 1997), interspecific genealogies have not always provided the necessary temporal resolution to investigate the evolution of labile traits such as migratory behavior.

We contrast competing hypotheses on the evolution of bird migration (tropical origin vs. temperate origin) using an intraspecific phylogeographic approach and examine patterns of mitochondrial DNA (mtDNA) genetic diversity, haplotype genealogy, and genetic structure to infer the distributional, demographic, and evolutionary history of the chipping sparrow (*Spizella passerina*), a common songbird with long-distance migratory populations in the temperate zone of North America and sedentary populations in the highlands of Mexico and Central America (Middleton 1998). First, we determine whether sedentary populations found in Mexico and Guatemala are ancestral to migratory populations in the United States and Canada (gain of migration; Cox 1985; Rappole 1995), or vice versa (loss of migration; Klein and Brown

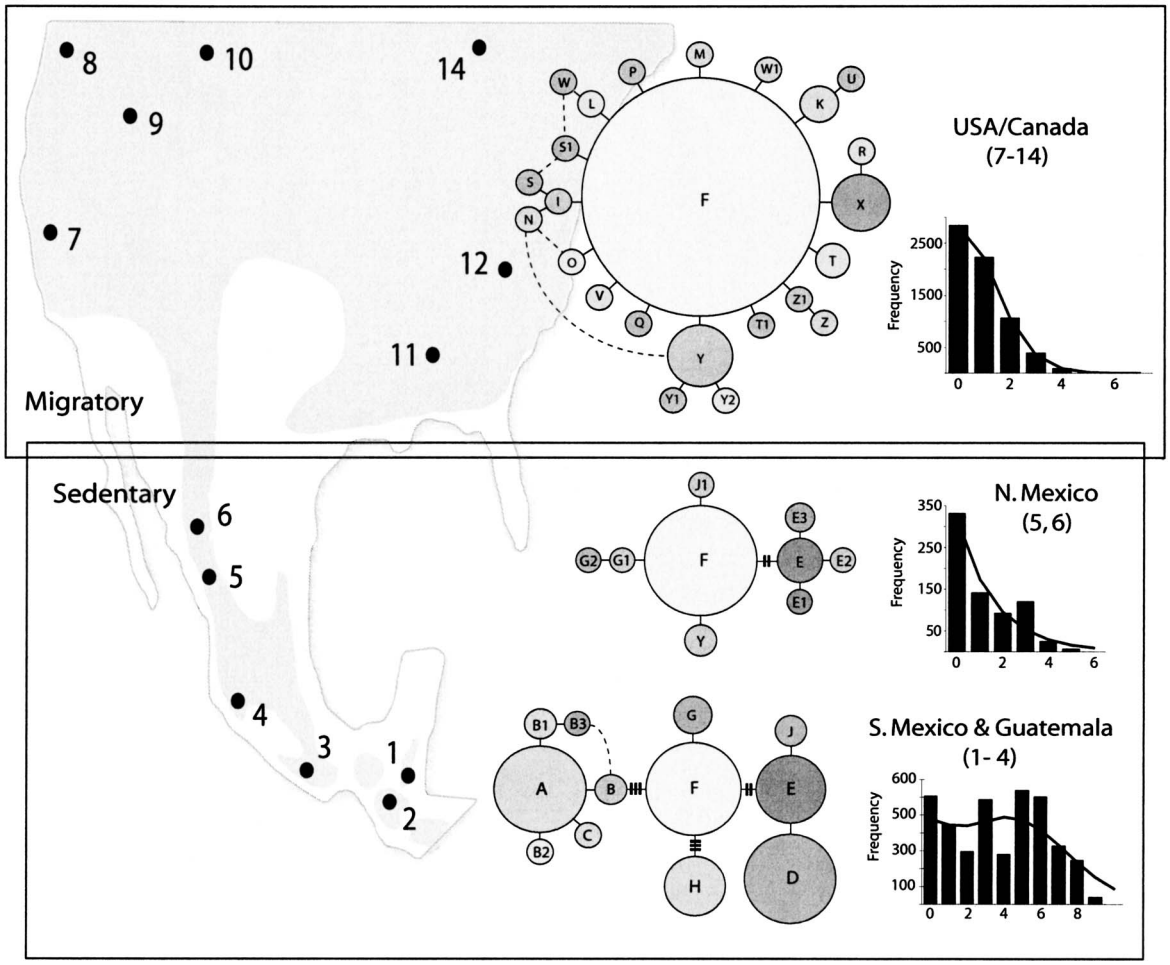

FIG. 1. Breeding range of the chipping sparrow (shaded area), sampling sites, haplotype networks of mtDNA control-region sequences, and mismatch distributions. Sampling localities (black dots) with sample sizes in parentheses are 1: Petén (26) and 2: Huehuetenango (6) in Guatemala; 3: Oaxaca (13), 4: Jalisco (46), 5: Durango (20), and 6: Chihuahua (21) in Mexico; 7: California (13), 8: Washington (39), 9: Idaho (8), 10: Montana (11), 11: Alabama (5), 12: North Carolina (9), and 13 (not shown): Massachusetts (16) in the USA; and 14: Ontario (14) in Canada. Haplotype frequencies per site and additional locality information provided in Appendix Table A1 (available online only at http://dx.doi.org/10.1554/06-153.1.s1). Each circle in minimum-spanning networks represents a haplotype, with size proportional to the haplotype's frequency in the population. Unhatched network branches represent a single nucleotide substitution, and hatch marks along branches represent additional substitutions. Broken lines represent alternative pathways of equal likelihood. Haplotypes A, B, B1, B2, B3, and C were restricted to Guatemala. Histograms correspond to observed frequencies of pairwise nucleotide differences, and lines represent the expected frequencies under a sudden expansion model.

1994; Buerkle 1999; Marshall and Baker 1999). Second, we time the inception of migration by estimating the divergence time between migratory and sedentary lineages. Third, we compare the timing of the evolution of migration with that of major climatic events during the Quaternary. Finally, to assess the relative importance of historical factors and ancestral genetic factors in driving the evolution of migratory behavior, we compare the phylogeographic pattern of the chipping sparrow to that of the yellow-eyed junco (*Junco phaeonotus*), a strictly sedentary species with similar ecology and distribution to sedentary chipping sparrow populations in the Mesoamerican highlands.

METHODS

Sampling and Laboratory Analysis

Breeding individuals were captured in the field using mist nets, and blood and/or feather samples were collected for genetic analysis. Primers for polymerase chain reaction amplification of the hypervariable region I of the mitochondrial control region were H417 and LGL2 (Tarr 1995). We sequenced 328 base pairs from the mtDNA control region of 115 migratory chipping sparrows from eight localities in the United States and Canada and of 132 sedentary chipping sparrows sampled at six sites in Mexico and Guatemala (Fig. 1). We used the same primers to obtain 349 base pairs from 124 yellow-eyed juncos sampled throughout the species' range in Mexico and Guatemala (Fig. 2). Preliminary surveys of sequence variation in two coding regions (cytochrome *b* and cytochrome *c* oxidase I) yielded a single haplotype in samples from across the species range; thus, coding regions were not included in the study. DNA extraction, amplification, and sequencing protocols are as described previously (Milá et al. 2000). Some of the sequences obtained from blood samples produced a few double peaks in the sequence

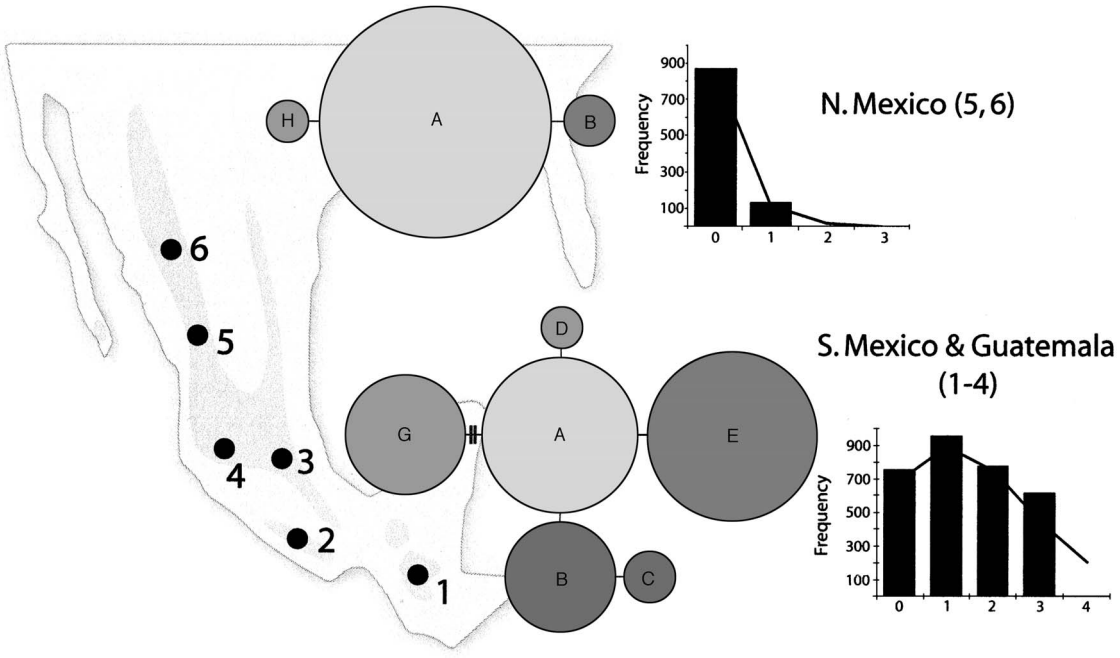

FIG. 2. Geographic range of the yellow-eyed junco (shaded area), sampling sites, haplotype networks of mtDNA control-region sequences, and mismatch distributions. Sampling localities (black dots) with sample sizes in parentheses are 1: Huehuetenango (12) in Guatemala; and 2: Oaxaca (15), 3: Distrito Federal (18), 4: Michoacán (11), 5: Durango (35), and 6: Chihuahua (26) in Mexico. Haplotype networks and mismatch distributions as in Figure 1. Haplotype frequencies per site and additional locality information in Appendix Table A2 (available online only).

chromatographs, suggesting the presence of double product and thus raising the possibility of nuclear copies of the targeted mtDNA control region fragment (Sorenson and Fleischer 1996). Re-extraction of genomic DNA from feather samples (in which the nuclear-to-mtDNA ratio is lower due to the predominance of epithelial cells) solved the problem in the majority of cases. A few samples for which double peaks persisted were excluded from the analysis. The sequences reported in this paper have been deposited in GenBank under accession numbers AY862812–AY862859.

Phylogenetic Analysis

Traditional bifurcating trees may not adequately represent intraspecific phylogenies, where ancestral and derived haplotypes can coexist in a given sample (Posada and Crandall 2001). To maximize inference power from haplotype relationships and frequencies, we constructed minimum-spanning networks of absolute distances between haplotypes using the molecular-variance parsimony algorithm (Excoffier and Smouse 1994) as implemented in Arlequin 2.0 (Schneider et al. 2000). In these networks, haplotypes are represented as circles at the nodes of a tree instead of at the tips, with the size of the circle being proportional to the frequency of the haplotype in the population.

Demographic History

We compared mismatch distributions of pairwise nucleotide differences among control region haplotypes with expectations of a sudden-expansion model (Rogers 1995) using Arlequin. To estimate the time since the beginning of an expansion, we used $\tau = 2ut$, where t is the time elapsed between initial and current population sizes, and $u = 2\mu k$, where μ is the mutation rate and k is the length of the sequence (Rogers and Harpending 1992). Because precise molecular clock calibrations are unavailable for most species, we used a conservative range of mutation rates (0.1, 0.15, and 0.2 substitutions/site/million years) based on previous studies of control-region variation in birds (Baker and Marshall 1997). To test the goodness of fit between the observed and expected mismatch distributions we used a parametric bootstrap approach that uses the sum of square deviations (SSD) between the observed and expected mismatch as a test statistic, as implemented in Arlequin. We also used Arlequin to generate Harpending's ''raggedness index,'' an estimate of the fluctuation in the frequency of pairwise differences (Harpending et al. 1993).

We tested for sudden changes in effective population size with Fu's test of neutrality (Fu 1997), which detects departures from neutrality in scenarios characterized by an excess of rare alleles and young mutations. Significant, large negative values of F_s indicate an excess of recent mutations and reject population stasis. Significance of F_s was evaluated by using 1000 random permutations in Arlequin. As an independent assessment of population expansion we used a coalescence method that takes into account the haplotype genealogy to assess the goodness of fit of an exponential growth model and generates maximum likelihood estimates of the growth parameter g using Metropolis-Hastings Markov chain Monte Carlo simulations as implemented in the program Fluctuate (Kuhner et al. 1998). Each analysis run in Fluctuate consisted of 10 short chains (sampling increments of 10; 1000

steps per chain), 20 long chains (sampling increments of 10; 20,000 steps) and a random starting tree, with a starting g value of one. Values of g greater than 3SD(g) are considered evidence of a population expansion (Lessa et al. 2003).

Population Divergence

We estimated divergence times between populations using a model that generates nonequilibrium coalescent estimates of divergence time independent of gene migration rates between pairs of populations using the variance in pairwise differences between DNA sequences (Nielsen and Wakeley 2001). We generated estimates of effective population size (N), divergence time in generations (t), and migration rate (m) through Markov chain Monte Carlo simulations as implemented in the program MDIV (Nielsen and Wakeley 2001). We constrained parameters within the ranges θ (0, ∞), M (0, 30), and T (0, 20) and used a Markov chain of 2,000,000 cycles preceded by a burn-in period of 500,000 cycles for each pairwise population comparison. We used a generation time of one year (the approximate age of first breeding in small passerines) in all our calculations.

Results

Analysis of the 41 control-region haplotypes found in the chipping sparrow (which included 30 polymorphic sites, 22 transitions, and eight transversions), revealed marked differences in the demographic histories of migratory and sedentary populations. Migratory populations have undergone a recent expansion from a population of low genetic diversity as evidenced by a starlike phylogeny of haplotypes (Fig. 1) and reduced levels of haplotypic and nucleotide diversity (Table 1), a pattern that is consistent with a previous survey of mtDNA variation in U.S. populations of the species (Zink and Dittman 1993). A single ancestral haplotype, F, dominates all USA and Canadian samples, where it coexists with lower-frequency haplotypes that differ from F by one or two nucleotides (Fig. 1). Furthermore, the shape of the mismatch distribution of pairwise genetic differences for the migratory population fits a model of sudden expansion in effective population size (goodness-of-fit test, SSD = 0.000023, P = 0.9599). Haplotype F is also found in sedentary populations in Mexico, which, in contrast to migratory populations, show high levels of genetic diversity (Table 1) and a multimodal mismatch distribution with a higher raggedness index (r_{mig} = 0.0533, r_{mex} = 0.1161), as expected for a population that has maintained relatively long-term demographic stability. These results are corroborated by large negative values of Fu's F_s in migratory populations, indicative of a population expansion. Further, the estimate of the coalescent population growth parameter g is large and over 57 times its standard deviation, compared to a value for Mexican sedentary populations that is less than half and just over four times its standard deviation (Table 1). This evidence for an expansion in migratory populations (low genetic diversity, unimodal mismatch distribution, and large F_s and g values) contrasts with demographic stasis in sedentary populations. In addition, the dominance of haplotype F in migratory populations compared with more uniform frequencies in sedentary Mex-

Table 1. Genetic diversity and population expansion indices in chipping sparrow and yellow-eyed junco populations.

	Population	h[1]	π[2]	τ[3]	r[4]	F_s[5]	g[6]
Chipping sparrow	Migrants	0.5681 ± 0.0552	0.00270 ± 0.00211	1.010	0.0533 (0.891)	−29.42 (<0.001)	2657.80 (46.54)
	Mexico	0.7234 ± 0.0406	0.00596 ± 0.00378	3.215	0.1161 (0.157)	−3.11 (0.125)	911.18 (205.77)
	N. Mexico	0.5866 ± 0.0859	0.00374 ± 0.00269	2.864	0.0728 (0.800)	−3.57 (0.028)	1809.13 (488.37)
	S. Mexico	0.7709 ± 0.0283	0.00694 ± 0.00429	3.398	0.1276 (0.110)	1.88 (0.818)	798.97 (172.21)
	Guatemala	0.5605 ± 0.0984	0.00211 ± 0.00183	0.814	0.1134 (0.330)	−2.71 (0.017)	2544.10 (800.67)
Yellow-eyed junco	N. Mexico	0.1293 ± 0.0667	0.00038 ± 0.00064	3.000	0.5684 (0.709)	−2.18 (0.010)	3353.85 (552.51)
	S. Mexico/Guatemala	0.7572 ± 0.0199	0.00403 ± 0.00277	1.873	0.0497 (0.710)	0.49 (0.645)	1327.16 (74.28)

[1] Haplotype diversity value ± standard error.
[2] Nucleotide diversity value ± standard error.
[3] τ statistic from mismatch distribution.
[4] Mismatch distribution raggedness index, with associated P-value in parentheses.
[5] F_s value from Fu's neutrality test, with associated P-value in parentheses.
[6] Growth parameter value from coalescence model generated with Fluctuate, with standard deviation in parentheses.

TABLE 2. Timing the evolution of migration. Maximum likelihood values of θ, M ($2Nm$), and T ($t/2N$) were estimated from a nonequilibrium coalescence model (Nielsen and Wakeley 2001), and divergence time estimates in years were based on three mutation rates from control region studies in avian taxa (0.10, 0.15, and 0.20 substitutions/site/million years). Values in parentheses correspond to the standard deviation from the mean after three runs of the MCMC chains for each population comparison.

Population pair	Θ (SD)	M (SD)	T (SD)	0.10 s/s/MY	0.15 s/s/MY	0.20 s/s/MY
Migrants/N. Mexico	5.15 (0.02)	2.17 (0.11)	0.22 (0.04)	8585	5723	4292
Migrants/S. Mexico	4.02 (0.02)	0.81 (0.01)	0.32 (0.03)	9804	6536	4902
N. Mexico/S. Mexico	1.67 (0.03)	0.90 (0.04)	0.33 (0.02)	4200	2800	2100

ican populations, suggests that migratory populations descend from an ancestral sedentary Mexican subpopulation.

A separate analysis of sedentary populations also revealed the signature of a population expansion in the northern Mexican sites Chihuahua (6) and Durango (5), where levels of genetic diversity and values for F_s and g are similar to those observed in the expanded migratory populations to the north (Table 1), and the frequency of haplotype F is markedly higher than in southern Mexican sites Jalisco (4) and Oaxaca (3) (Fig. 1). These results suggest that a bottlenecked sedentary population dominated by haplotype F expanded first through northern Mexico before reaching temperate North America, where populations subsequently acquired migratory behavior, and further suggest that migratory behavior was not a prerequisite for the expansion.

Two methods were used to estimate the maximum time to inception of migration in chipping sparrows. First, we estimated the divergence time between migratory populations and sedentary populations in northern Mexico. Second, we estimated the origin of migration as approximately the time to the onset of the northward expansion from the mismatch distribution of the migratory sample. Divergence time estimates between migrants and northern Mexico residents from the nonequilibrium coalescence model and from the mismatch distribution were 8585 to 4292 years bp (Table 2), and 7698 to 3849 years bp, respectively. Using a generation time of two years instead of one (not unreasonable given the typically high mortality in first-year birds), would double those estimates. Although approximate, these estimates coincide broadly with a time of rapid climatic amelioration to the north following the last glacial maximum 18,000 years bp (Wright et al. 1993), and suggest that chipping sparrow populations expanded north following the recession of the ice sheets, a pattern that is well documented for numerous vertebrate and invertebrate animal species (Hewitt 1996; Milá et al. 2000; Ruegg and Smith 2002; Lessa et al. 2003).

If the northward expansion in chipping sparrows was induced mainly by climatic change and was not dependent on a genetic ancestral predisposition to readily evolve migratory behavior, then strictly sedentary species of similar range and ecology should show a pattern of population expansion concordant with that of sedentary chipping sparrows. To test this prediction, we examined the phylogeography of the yellow-eyed junco, a strictly sedentary emberizine species of similar habitat and distribution as sedentary chipping sparrows (Sullivan 1999). Northern populations in Durango and Chihuahua show strong predominance of a single haplotype, A (Fig. 2), and very low levels of genetic diversity (Table 1), whereas populations to the south show higher diversity and a lower relative frequency of haplotype A, suggesting that northern populations recently expanded from a small population in central Mexico.

DISCUSSION

Our results suggest that the main factor involved in the separation of migratory and ancestral sedentary ranges of the chipping sparrow was a sudden population expansion into temperate latitudes following the last glacial maximum. Results from our comparative approach support a northward postglacial expansion of sedentary populations of both the chipping sparrow and the yellow-eyed junco and suggest that migratory behavior was not a prerequisite for the northward expansion in chipping sparrows.

We hypothesize that chipping sparrow populations continued expanding north into the temperate zone, becoming migratory when they reached a latitudinal threshold at which migration was selectively favored to avoid harsh seasonal winters (Bell 2000). Thus, as predicted by the tropical-origin hypothesis of the evolution of migration, sedentary populations expanded north from southern Mexico into the temperate zone. This northward displacement of the breeding range, as opposed to a southward shift of the wintering range, is consistent with results from a broader study on the evolution of migration in shorebirds (Joseph et al. 1999). However, migratory behavior itself appears to have evolved in breeding populations at higher latitudes only, likely driven by the high annual seasonality found there, a conclusion which is in agreement with the temperate-origin hypothesis. Conceivably, migratory movements evolved as individuals vacated breeding sites during inclement winter months and returned to suitable breeding areas the following season, with the development of partially migratory populations as a likely intermediate step (Bell 2000; Berthold 2001). Indeed, the development of partial migratory behavior has been observed in house finch (*Carpodacus mexicanus*) populations recently introduced by humans into New York from sedentary populations in California (Able and Belthoff 1998), and the serin (*Serinus serinus*) has developed partial migration in recently colonized parts of northern Europe (Olsson 1969).

Whether the ability to evolve migratory behavior is an ancestral trait found in most birds, or whether selection acts on individuals to elicit migratory behavior de novo following each successive postglacial expansion, remains unclear, though the two hypotheses need not be mutually exclusive (Berthold 2001; Zink 2002). Alleles responsible for the expression of migration and related behaviors (fat deposition, zugunruhe, use of orientation compasses, etc.) could be found at low frequencies in sedentary populations, with selection driving their increase in frequency under the appropriate en-

vironmental conditions (Pulido et al. 1996; Berthold 2001). Our results suggest that population-level responses to large-scale, cyclical climatic change provided the environmental conditions that triggered this remarkable evolutionary response.

Previous work on the evolution of migration has relied on current patterns of geographic distribution and interspecific phylogenies, and the inference of evolutionary process has remained speculative (Gauthreaux 1982; Cox 1985). The phylogeographic approach used here sheds light on this elusive evolutionary process by recovering distributional, demographic, and evolutionary history from intraspecific genetic data. Our results are consistent with those of previous intraspecific studies in suggesting a very recent evolution of long-distance bird migration (Joseph et al. 2003; Pérez-Tris et al. 2004). However, our comparative approach reveals the predominant role of postglacial expansions in driving the process from southern sedentary populations. We propose that cyclical postglacial expansions might provide a general ecological mechanism for the evolution of long-distance migration that can account for the observed pattern of repeated evolution of migration within and across avian lineages.

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