

## COMPARISON OF PHYLOGENIES DERIVED FROM TWO MOLECULAR DATA SETS IN THE AVIAN GENERA *PIPILO* AND *SPIZELLA*

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**ABSTRACT.**—We sequenced 433 bp of the mitochondrial DNA (mtDNA) cytochrome *b* (cyt *b*) gene from four species in the Brown Towhee complex (*Pipilo* spp.) and six species in the genus *Spizella*. Phylogenies derived from sequence data were compared to those derived from mtDNA restriction fragment length polymorphism (RFLP) data collected from the same individuals (Zink and Dittmann 1991, 1993), allozyme and sequence data were also combined. In *Spizella*, the sequence and RFLP data placed the American Tree Sparrow (*S. arborea*) basal and the Black-chinned and Field sparrows (*S. atrogularis* and *S. pusilla*) as sister taxa, but conflicted on the placement of Brewer's, Chipping, and Clay-colored sparrows (*S. breweri*, *S. passerina*, and *S. pallida*). Phylogenetic analysis of the combined sequence and RFLP data set for *Spizella* supports the two previously published hypotheses for the genus based on RFLP's alone (Zink and Dittmann 1993). Monophyly of *Spizella* including the American Tree Sparrow is supported. The *Pipilo* sequence tree was congruent with Zink and Dittmann's (1991) RFLP Dollo parsimony tree, suggesting that the White-throated Towhee (*P. albicollis*) is the basal member of the complex and not the sister-taxon to the Canyon Towhee (*P. fuscus*) as suggested by the RFLP Wagner parsimony tree and allozyme and morphometric data (Zink 1988). The *Pipilo* sequence and RFLP data agree in placing Abert's Towhee (*P. aberti*) as the nearest relative of the California Towhee (*P. crissalis*). Phylogenetic analysis of the combined data for *Pipilo* supports the basal position of the White-throated Towhee, but we still consider the position of this taxon unresolved. Overall, sequence and RFLP data produced significantly congruent phylogenetic trees in both genera, suggesting each type of data provides useful phylogenetic information. Received 23 Nov. 1994, accepted 14 May 1995.

Analyses of molecular data such as allozyme frequencies, restriction fragment length polymorphisms (RFLP's), and direct sequences of mitochondrial DNA (mtDNA) yield inferences about character evolution and phylogenetic relationships (Hillis et al. 1990, Avise 1994). These techniques, however, differ in their ability to resolve phylogenetic relationships along the taxonomic hierarchy (Avise 1986). Relatively few direct comparisons of phylogenetic patterns in different molecular data sets are available.

In studies of birds, phylogenetic trees derived from allozymes and mtDNA RFLP data were generally congruent (Zink and Avise 1990, Zink and Dittmann 1991). MtDNA, however, provided more characters for systematic analysis (Avise and Zink 1988). Direct sequencing of mtDNA

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may provide an enhanced view of molecular evolution and the evolutionary history of avian taxa because it reveals fine-scale patterns of variation not apparent in RFLP's (Edwards and Wilson 1990, Di Rienzo and Wilson 1991, Birt-Friesen et al. 1992, Edwards 1993). Our purpose was to compare phylogenetic trees derived from sequence data with those derived from RFLP data.

RFLP-based (restriction site and fragment) cladograms exist for four members of the Brown Towhee complex (Abert's Towhee [*Pipilo aberti*], White-throated Towhee [*P. albicollis*], California Towhee [*P. crissalis*], and Canyon Towhee [*P. fuscus*]) (Zink 1988, Zink and Dittmann 1991), and RFLP (restriction fragments only) cladograms exist for six members of the genus *Spizella* (American Tree Sparrow [*Spizella arborea*], Black-chinned Sparrow [*S. atrogularis*], Brewer's Sparrow [*S. breweri*], Clay-colored Sparrow [*S. pallida*], Chipping Sparrow [*S. passerina*], and Field Sparrow [*S. pusilla*]) (Zink and Dittmann 1993). We compared phylogenetic trees derived from cytochrome *b* (cyt *b*) sequence data with previously published trees (Zink and Dittmann 1991, 1993). We also combined the data sets to produce "total evidence" trees (Eernisse and Kluge 1993), to see if phylogenetic topologies were stable.

#### MATERIALS AND METHODS

The following specimens (general locality, voucher number [ARMZ = specimens with RMZ field catalogue numbers in the American Museum of Natural History, B = Louisiana State University], and Genbank accession number) were used: American Tree Sparrow (Alberta, B16372, U26190), Black-chinned Sparrow (California, B3859, U26191), Brewer's Sparrow (Arizona, B20007, U26192), Clay-colored Sparrow (Louisiana, B19765, U26198), Chipping Sparrow (California, B?; North Carolina, B?; Manitoba, B16505; Yukon, B18047, U26197), Field Sparrow (Texas, B15578, U26200), Abert's Towhee (Arizona, ARMZ2249, ARMZ2250; California, B14314, U26189), White-throated Towhee (Mexico, ARMZ2186, ARMZ2192, ARMZ2193, U26202), California Towhee (Baja California, ARMZ2159, ARMZ2160, U26193; California, B14334, B14336, B14351, ARMZ2396, U26194), Canyon Towhee (Arizona, ARMZ2373, ARMZ2375, U26195; Texas, B16731, B16733, U26196).

MtDNA was isolated from frozen tissues and purified in cesium chloride density equilibrium gradients following the protocols of Lansman et al. (1981), Avise and Zink (1988), and Dowling et al. (1990). MtDNA samples were the same as those used by Zink and Dittmann (1991, 1993). Purified mtDNA was amplified with the polymerase chain reaction (PCR) (Saiki et al. 1988). Symmetric amplifications were conducted in 30  $\mu$ l reactions containing 0.625 units of *Thermus aquaticus* polymerase (Perkin-Elmer Cetus, Boehringer Mannheim), 1.25 mM  $MgCl_2$ , and dNTP's at a final concentration of 0.05 mM each. Primers L14841 (made by Operon; number refers to primer discussed in Kocher et al. (1989) and H15299 (Hackett 1992) were used at a concentration of 0.5  $\mu$ M, and the concentrations of buffer components were 8.33 mM tris-HCL (pH 8.3) and 41.67 mM KCl. The thermal cycling regime consisted of an initial cycle of 3 min denaturation at 94°C, 1 min primer annealing at 50°C, and 1 min extension at 72°C. This was followed by 33 cycles of 1 minute each at 94°C, 55°C, and 72°C, and then a final extension of 10 min at 72°C. The presence and size of amplified product was verified by electrophoresis of 4  $\mu$ l of reaction product

through a 1% agarose gel (SeaKem LE, FMC) in 1× TBE buffer. A 433 base-pair section was amplified from all samples.

The same primers were used to sequence the light and heavy strands of the amplified product using either a Silver Sequence kit (Promega), or a Sequenase PCR Product Sequencing Kit (United States Biochemical). Excess dNTP's and primers were removed from PCR product either by filtration (Millipore cat. no. UFC3 TTK 00) for silver sequencing, or by enzymatic treatment with Exonuclease I and Shrimp Alkaline Phosphatase (United States Biochemical) for Sequenase sequencing. Sequenced product was run through 0.4 mm, 6% polyacrylamide gels with a top buffer of either 0.8× or 1× TBE and a bottom buffer of 1× TBE. Glycerol-tolerant gels (with taurine-based buffer TTE) were also used. Sequences were visualized by silver staining (Silver Sequence, Promega; Caetano-Anolles and Gresshoff, 1993) or autoradiography (<sup>35</sup>S), depending on the sequencing protocol used.

Sequences were read manually, and aligned to the sequence of the chicken (*Gallus gallus*) (Desjardins and Morais 1990). If conspecific sequences varied, each sequence was considered a separate haplotype. For *Pipilo*, a phylogenetic analysis that included all haplotypes was conducted to verify that all conspecifics grouped together. We computed statistics for nucleotide variation with the computer program MEGA (Kumar et al. 1993). Phylogenetic analyses of the sequence data were conducted using the computer programs PAUP 3.1.1 (Swofford 1993), Hennig86 (Farris 1988), and MEGA. All characters were analyzed as unordered. Dark-eyed Junco (*Junco hyemalis*) and Green-tailed Towhee (*Pipilo chlorurus*) (Genbank accession numbers U26199 and U26201, respectively) served as the outgroups for *Spizella* and the Brown Towhee complex. To test for the presence of phylogenetic signal in the sequence data sets, we used the computer program Random Cladistics (Siddall 1994) to conduct PTP tests (Faith and Cranston 1991) and used PAUP to obtain  $g_i$  statistics. We used the nearest neighbor interchange (NNI) application of the computer program Component (Page 1993) to test whether phylogenetic topologies from different data sets were congruent. Phylogenetic analyses of data sets combining the sequence data with Zink and Dittmann's (1991, 1993) RFLP data were conducted using PAUP. To determine the level of support for nodes in particular tree topologies, PAUP was used to bootstrap (Felsenstein 1985) the sequence and combined data sets (1000 replications were conducted for each analysis).

## RESULTS

*Spizella*.—Overall, the *Spizella* and *Junco* sequences varied at 85 of 433 sites, of which 33 were potentially phylogenetically informative (Appendix I). The four Chipping Sparrow specimens exhibited the same haplotype, despite the widespread sampling distribution. The variable nucleotide positions are distributed throughout the region sequenced and no insertions or deletions were noted. The distribution of variable sites by codon position is ten at the first position, six at the second position, and 69 at the third position. This variation resulted in 12 amino acid substitutions. The average transition:transversion ratio between the outgroup and ingroup in pair-wise comparisons was 3.96:1.00. A plot of total nucleotide substitutions vs substitutions at the third codon position in pair-wise comparisons between ingroup taxa and the outgroup (Fig. 1A) showed a clear linear relationship, suggesting no saturation of substitu-

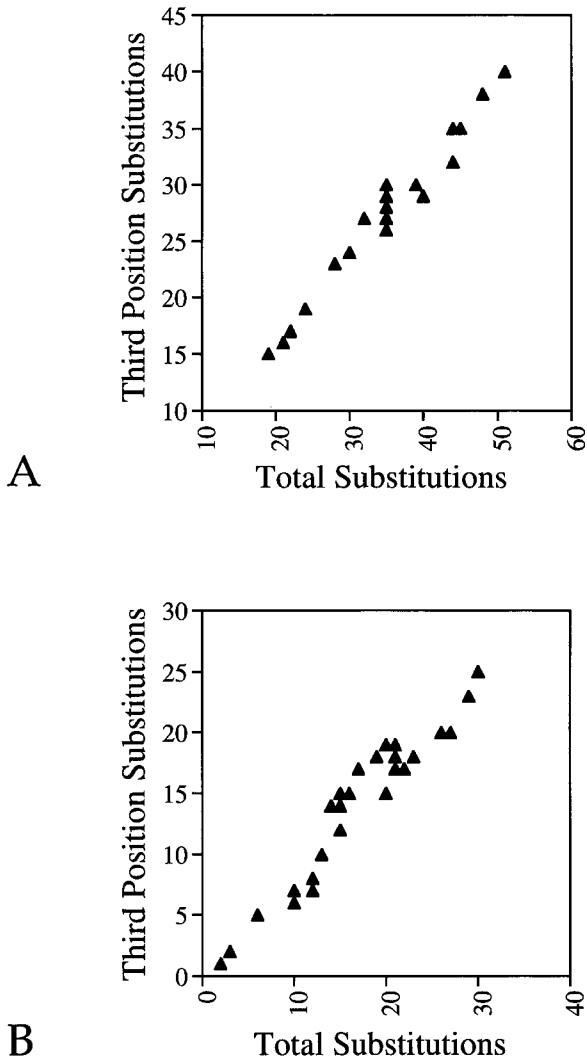
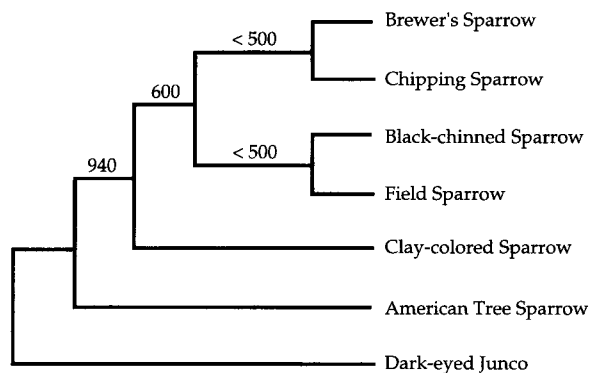


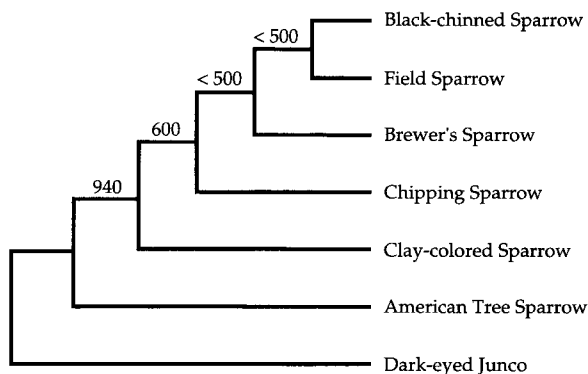
FIG. 1. A. Plot of total nucleotide substitutions vs third position substitutions in *Spizella*. B. Plot of total nucleotide substitutions vs third position substitutions in *Pipilo*.

tions (both transitions and transversions were considered together due to the low number of transversion events).

Tests for the presence of phylogenetic signal in the data set yielded conflicting results. The  $g_1$  statistic for the *Spizella* sequence data indicated a significantly left-skewed distribution of tree lengths ( $g_1 = -0.265623$ ),



A



B

FIG. 2. The two equally most parsimonious trees from the exhaustive search of the *Spizella* sequence data ( $I = 122$ ,  $ci = 0.762$ ,  $ri = 0.396$ ). Values at nodes refer to the number of times the node occurred in 1000 bootstrap replicates.

suggesting the presence of phylogenetic signal (Hillis 1991, Hillis and Huelsenbeck 1992). However, the PTP test of Faith and Cranston (1991) was not significant ( $P = 0.1788$ ), indicating a lack of phylogenetic signal. We recognize that these tests are controversial (Carpenter 1992, Kallersjö et al. 1992).

The exhaustive search of the sequence data yielded two equally most-parsimonious trees (Fig. 2), which both show the Black-chinned and Field sparrows as sister taxa, the American Tree Sparrow as the most basal member of the ingroup, and the Chipping Sparrow as the second most basal ingroup taxon. The two trees differ in the position of the Brewer's

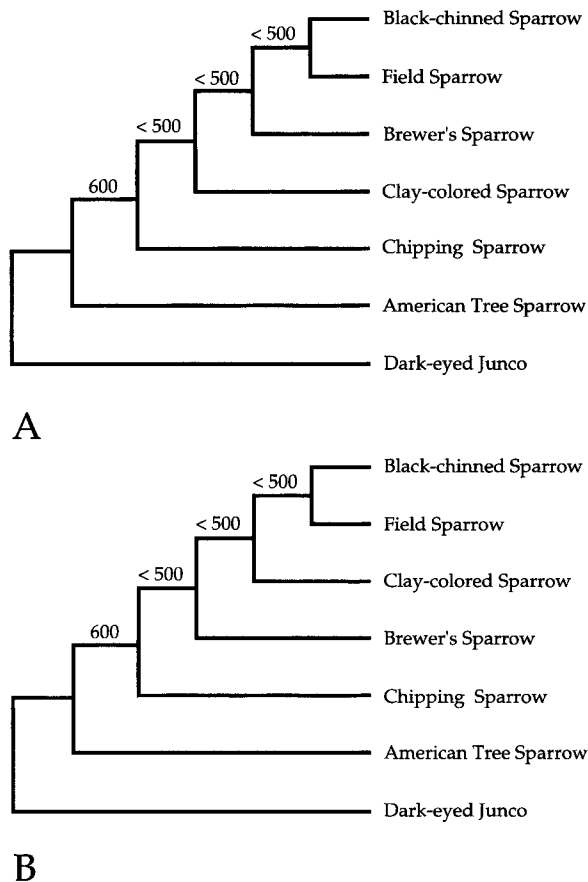


FIG. 3. The single best topology reported for RFLP data on *Spizella* (Zink and Dittmann 1993) derived from A = maximum parsimony, B = Fitch-Margoliash analyses. Analysis of combined RFLP and sequence data produced two equally most parsimonious trees (1 = 366, ci = 0.525, ri = 0.377) with topologies identical to those of A and B. Values at nodes refer to the number of times the node occurred in 1000 bootstrap replicates of the combined data set.

and Clay-colored sparrows. The only relationship proposed by the sequence data that was supported in greater than 50% of bootstrap replicates was the clade containing all ingroup taxa except American Tree Sparrow.

An exhaustive search of the combined sequence and RFLP data yielded no novel phylogenetic hypotheses, as the two equally most-parsimonious trees feature the topologies of Zink and Dittmann's (1993) maximum parsimony and Fitch-Margoliash trees (Fig. 3). The bootstrap analysis of

the combined data strongly supports the basal positions of the American Tree and Clay-colored sparrows suggested by the RFLP data, but shows less than 50% support for relationships among the other four ingroup taxa (Fig. 3).

*Pipilo*.—The numbers of haplotypes for the *Pipilo* species were Abert's Towhee, 2; California Towhee (California), 3; California Towhee (Baja California), 2; Canyon Towhee (Arizona), 1; Canyon Towhee (Texas), 1; and White-throated Towhee, 1. Average haplotype divergence among conspecifics was: Canyon Towhee = 1.4% (between Texas and Arizona), California Towhee = 0.52% (including Baja California and California samples; there was no geographic variation), and Abert's Towhee = 0.15%.

A branch and bound search of all *Pipilo* haplotypes yielded two equally most-parsimonious trees (not shown) which differed only in that one tree did not show the Canyon Towhees from Texas and Arizona as sister taxa. Because all other conspecific haplotypes grouped together, taxa corresponding to those used by Zink and Dittmann (1991) (one Canyon Towhee from Arizona, one California Towhee each from California and Baja California, one Abert's Towhee, and one White-throated Towhee) were selected for direct comparison of the phylogenetic pattern from RFLP data. When conspecific haplotypes varied, the most complete sequence was chosen. The *Pipilo* sequences (including Green-tailed Towhee) varied at 46 sites, of which 27 were potentially phylogenetically informative (Appendix II). Variable nucleotide positions were distributed throughout the region of *cyt b* sequenced. The distribution of variable sites by codon position was six at the first position, three at second position, and 37 at third position, resulting in eight amino acid substitutions. The average transition:transversion ratio in pairwise comparisons between the outgroup and ingroup was 10.8:1.0. A plot of total nucleotide substitutions vs third position substitutions (transitions and transversions combined) (Fig. 2B) showed a clear linear relationship, suggesting no saturation of changes for observed transitions or transversions.

Tests for the presence of phylogenetic signal in the *Pipilo* sequence data set conflicted. Randomization tests (Faith and Cranston 1991) indicated no significant phylogenetic signal ( $P = 0.1718$ ), whereas the  $g_1$  statistic indicated a significantly left-skewed distribution of tree lengths ( $g_1 = -0.349542$ ), suggesting the presence of phylogenetic signal (Hillis 1991, Hillis and Huelsenbeck 1992).

An exhaustive search of the selected haplotypes yielded a single most-parsimonious tree (Fig. 4) in which the California Towhees from California and Baja California were sister taxa, with Abert's Towhee, Canyon Towhee, and White-throated Towhee successively more basal. The boot-

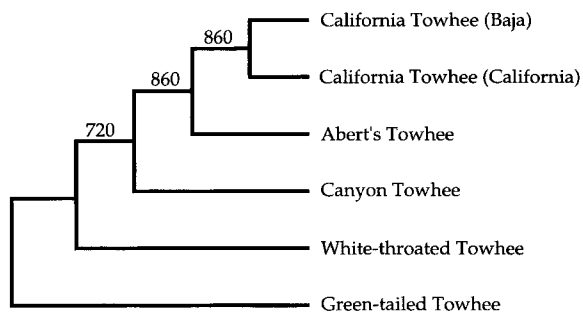


FIG. 4. Single most parsimonious tree ( $1 = 51$ ,  $ci = 0.824$ ,  $ri = 0.625$ ) from the exhaustive search of the *Pipilo* sequence data (also the topology of the RFLP Dollo parsimony tree [Zink and Dittmann 1991]). Values at nodes refer to the number of times the node occurred in 1000 bootstrap replicates.

strap of these haplotypes showed strong support for all nodes. Conducting the phylogenetic analysis with the Texas, instead of the Arizona, Canyon Towhee haplotype yielded a single tree of the same topology which is five steps longer ( $1 = 56$ ,  $ci = 0.839$ ,  $ri = 0.640$ ).

An exhaustive search of the combined sequence and RFLP data set yielded a single most-parsimonious tree ( $1 = 241$ ,  $ci = 0.900$ ,  $ri = 0.750$ ) which is congruent with the sequence data tree and Zink and Dittmann's (1991) Dollo parsimony tree (Fig. 4). All nodes were supported by at least 710 of 1000 bootstrap replicates.

#### DISCUSSION

*RFLP's vs sequence data.*—In phylogeny reconstruction, the phasing-out of restriction sites in favor of sequence data has been advocated (Wilson et al. 1989). However, because one is substituting single gene phylogeny estimates (sequence data) for an mtDNA genome-wide estimate (RFLP's), this may result in fewer informative characters in the sequence data set and a potentially less accurate phylogenetic estimate for the mtDNA genome (itself a single linkage unit). In both genera surveyed, the RFLP data sets contain more variable and phylogenetically informative characters (*Spizella*: 179 of 198 fragments variable, 67 informative; *Pipilo*: 98 of 119 sites variable, 77 informative) than the sequence data sets (*Spizella*: 85 of 433 nucleotides variable, 33 informative; *Pipilo*: 46 of 433 nucleotides variable, 27 informative). However, the *cyt b* sequence data provided information we could not have obtained from RFLP's (e.g. nucleotide substitutions by codon position), and one could sequence more DNA. The *ci*-values and tree lengths for RFLP and sequence data sets are not comparable owing to differing numbers of characters (Archie



1989). However, the *ri*-values, a measure of homoplasy that is not as influenced by the size of the data set, are similar for the two types of data (or higher for RFLP data), suggesting relatively equal amounts of "noise." Therefore, there are no obvious reasons to favor one data set over another based on these measures.

Several studies have found agreement between restriction site data and other evidence (Zink and Avise 1990, Dittmann and Zink 1991, Zink et al. 1991). In this study, the NNI tests (Page 1993) revealed that for both *Spizella* and *Pipilo*, sequence trees were significantly congruent ( $P = 0.0395$ ) with the RFLP parsimony trees. The most likely reason for significant ( $P < 0.05$ ) congruence is that each data set is "tracking" phylogeny. However, because the trees from each data set do not match exactly, further exploration of them is warranted.

In *Spizella*, one of the sequence trees (Fig. 2A) differs from the RFLP Fitch-Margoliash tree (Fig. 3B) only in the placement of the Clay-colored Sparrow and Chipping Sparrow. The other possible pairwise tree comparisons (Figs. 2, 3) differ by the placement of up to three taxa. For example, Fig. 2B and Fig. 3A agree only in the basal placement of the American Tree Sparrow and the sister-taxon relationship of Black-chinned Sparrow and Field Sparrow. Except for the basal position of the American Tree Sparrow, most suggested relationships do not exhibit high bootstrap values. Thus, if one were to compare only strongly supported nodes, there would be relatively few comparisons possible. However, the NNI tests suggested significant overall congruence, despite weak bootstrap support and topological differences, owing to the consistent basal placement of the American Tree Sparrow and the sister-group relationship between Black-chinned Sparrow and Field Sparrow. The relatively low *ri* values of the two data sets are similar (sequence *ri* = 0.40, RFLP *ri* = 0.42 [Zink and Dittmann 1993]), suggesting that character state changes are concentrated on terminal branches rather than on internal nodes (Farris 1989). This low "stemminess" is thought to decrease the probability that the correct topology has been found (Lanyon 1988, Rohlf et al. 1990). Phylogenetic resolution of the complete genus is not possible with either data set alone. It is likely that more data are required.

In *Pipilo*, the single most-parsimonious tree generated from the sequence data (Fig. 4) was topologically identical to Zink and Dittmann's (1991) Dollo parsimony tree. However, the sequence tree did not support the sister-taxon relationship between Canyon and White-throated towhees proposed by analysis of allozymes, morphometric data, and Wagner parsimony analysis of RFLP (sites or fragments) data (Zink 1988, Zink and Dittmann 1991). However, the two RFLP trees differ in length by only one step, and the sequence tree was significantly congruent (NNI,  $P =$

0.0395) with the Wagner parsimony tree. The bootstrap analysis of the restriction site data supported the Canyon and White-throated towhees as sisters in 780 of 1000 replicates (Zink and Dittmann 1991), whereas the bootstrap of the sequence data supported the basal position of the White-throated Towhee in 710 of 1000 replicates. We conclude that the position of the White-throated Towhee is unresolved by both data sets.

We conclude that neither statistics associated with RFLP or sequence trees, nor the phylogenetic patterns themselves, favor one data set over the other for phylogenetic analysis.

*Combined data and phylogenetic conclusions.*—When two data sets conflict, some suggest that the best estimate of phylogeny is acquired by combining the data (Eernisse and Kluge 1993). We assumed the sequence and RFLP data sets were essentially independent because few restriction sites are likely to occur within a small region such as was sequenced. Maximum parsimony analysis of the *Spizella* combined data set showed the phylogenetic hypotheses proposed by the RFLP maximum parsimony and Fitch-Margoliash (Fig. 3) trees as equally most-parsimonious, although one of the trees from sequence data (Fig. 2B) was not favored by the combined data. The basal position of the American Tree Sparrow and the sister taxon relationship between the Black-chinned and Field sparrows were supported by all three data sets (sequence, RFLP, and combined). The combined data do not support the “*passerina*” complex, consisting of the Brewer’s, Chipping, and Clay-colored sparrows, proposed by Mayr and Short (1970), which was also refuted by the RFLP data (Zink and Dittmann 1993).

The phylogenetic analysis of *Spizella* did not include the Worthen’s or Timberline sparrows (*S. wortheni*, *S. taverni*), for which we lacked specimens. Worthen’s Sparrow is assumed to be the sister taxon to the Field Sparrow (Mayr and Short 1970), and the Timberline Sparrow is assumed to be the sister taxon to the Brewer’s Sparrow (Sibley and Monroe 1990). Inclusion of these putative terminal taxa in a phylogenetic analysis might help to clarify phylogenetic relationships by stabilizing internal nodes (Weller et al. 1992). Thus, we consider both tree topologies in Fig. 3 as working hypotheses.

We questioned the monophyly of *Spizella* because the sequence data showed that the average divergence from the American Tree Sparrow to other congeners is greater than that from the other congeners to the Dark-eyed Junco (0.0896); this result agrees with the RFLP data (Zink and Dittmann 1993). To test whether the American Tree Sparrow belongs in *Spizella* or to a separate clade, we added sequence data of additional taxa to the analysis (Green-tailed Towhee, White-throated Towhee, Black-throated Sparrow [*Amphispiza bilineata*], Fox Sparrow [*Passerella ilia-*

ca], Golden-crowned Sparrow [*Zonotrichia atricapilla*], and Song Sparrow [*Melospiza melodia*]). We varied the number of taxa, and used different combinations of taxa to root trees (results not shown). The American Tree Sparrow consistently appeared basal in *Spizella* when all additional taxa were included, regardless of which taxa were used to root trees. However, depending on which additional taxa we chose to include, the American Tree Sparrow would sometimes appear as the sister to the Chipping Sparrow, or as a member of a clade composed of one or more of the additional taxa. Mayr and Short (1970) suggested that the American Tree Sparrow has no close relatives, and molecular evidence indicates that this taxon may represent a long branch at the base of the *Spizella* clade, isolated by extinctions or differing rates of evolution. The occasional placement of the American Tree Sparrow outside *Spizella* may be due to one long branch attracting another (Felsenstein 1978). However, because of uncertainty over the correct outgroup(s) to use in addressing this question (Smith 1994), our test is not definitive. We conclude that present evidence favors monophyly of *Spizella* including the American Tree Sparrow.

Although the *Pipilo* sequence and RFLP data sets conflicted minimally the data sets were combined in hopes of gaining support for one hypothesis over the other. Phylogenetic analysis of the combined data also placed the White-throated Towhee as the most basal ingroup taxon and this node had strong bootstrap support (71%). However, placing the White-throated and Canyon towhees as sister taxa required only an additional three (1.2%) steps with the combined data. Green-tailed Towhee may not be an appropriate outgroup to resolve the placement of the White-throated towhee and conflict over the placement of this taxon may represent a rooting problem (Smith 1994). To test this, we added Collared Towhee (*Pipilo ocai*) sequence to our analysis. Rooting the sequence data tree with either Collared Towhee or both Green-tailed and Collared towhees, however, did not change the topology of the tree. More data are required to resolve the placement of the White-throated Towhee.

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## APPENDIX I

MATRIX OF PHYLOGENETICALLY INFORMATIVE CHARACTERS IN *SPIZELLA*

Taxon	11111111222222233333344444
	355677001346780356689233477901122
	118136032655505532405847309184614
Dark-eyed Junco	GAGAGTATGAGCGTTGGGAAGGGGCTGGCCTG
Chipping Sparrow	.GTGA.TGTGATACC..T.G.A...TC...T..
Black-chinned Sparrow	..T.AGTAAG.TA....C.G...AATCA.T.CA
Brewer's Sparrow	..TG.GTATGA.....TT...A.A..CA.TT..
Field Sparrow	..TGAGTGT.....TTG..A.A.TCA...CA
American Tree Sparrow	AG.....C.GAT.CCA...GA.A....AA.TC.
Clay-colored Sparrow	AGTG.GTGTG.....ATTG.AAA.A.CAATT.A

A "dot" indicates that the base is the same as that found in the Dark-eyed Junco. Numbers refer to the positions 1–433 in the region 15374 to 14941 corresponding to the chicken sequence (Desjardins and Morais 1990).

## APPENDIX II

MATRIX OF PHYLOGENETICALLY INFORMATIVE CHARACTERS IN *PIPILO*

Taxon	111111222333333
	1122015668228447899
	16928321060030390514
Green-tailed Towhee	?GAGCTGAATTGAAAGCAGA
Canyon Towhee	G..ATC....CA..G.TG.G
California Towhee (Baja)	A.G.TCAGGCC.GGGAT.AG
California Towhee (California)	A.GGTCAGGCCAGGGAT.AG
Abert's Towhee	A?GATCAGG..AG.GA...G
White-throated Towhee	GAG....GG.C..G..TG..

A "dot" indicates that the base is the same as that found in the Green-tailed Towhee. Numbers refer to the positions 1–433 in the region 15374 to 14941 corresponding to the chicken sequence (Desjardins and Morais 1990).

## ERRATUM

In "The parasitic blow fly, *Protocalliphora spatulata*, in two new host species" by J.M. Fair and C.K. Miller (Wilson Bull. 107:179–181), all references to the scientific name *Protocalliphora hirundo* should be *P. hirudo*. Special thanks to Mia Revels for calling attention to this confusion between the similarity of the specific epithet *P. hirudo* and the specific epithet of a congener, *P. hirundo*.