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HISTORICAL BIOGEOGRAPHY OF THE NEW WORLD SOLITAIRES (*MYADESTES* SPP.)

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Abstract.—Solitaires (*Myadestes* spp.) are montane-forest birds that are widely distributed throughout the New World, ranging from Alaska to northern Bolivia and including both Hawaii and the West Indies. To understand the origins of this impressive distribution, we used five mitochondrial gene sequences to reconstruct the historical biogeography of the genus. The resulting phylogeny indicates a rapid initial spread of the genus to occupy most of its contemporary continental range at least as far south as lower Mesoamerica, plus Hawaii and the Greater Antilles. The North American *M. townsendi* appears to be the sister taxon of the rest of *Myadestes*. *Myadestes obscurus* of Hawaii is more closely allied to Mesoamerican lineages than to *M. townsendi*. The strongly supported sister relationship of the two West Indian taxa, *M. elisabeth and M. genibarbis*, indicates a single colonization of the West Indies. A more recent node links the Andean *M. ralloides* to the Mesoamerican *M. melanops* and *M. coloratus*. A standard molecular clock calibration of 2% sequence divergence per million years for avian mitochondrial DNA suggests that the initial diversification of *Myadestes* occurred near the end of the Miocene (between 5 and 7.5 mya). Cooler temperatures and lower sea levels at that time would have increased the extent of montane forests and reduced overwater dispersal distances, possibly favoring range expansion and colonization of the West Indies. The split between South American and southern Mesoamerican lineages dates to ~3 mya, which suggests that *Myadestes* expanded its range to South America soon after the Pliocene rise of the Isthmus of Panama. Despite the demonstrated capacity of *Myadestes* for long-distance dispersal, several species of *Myadestes* are highly differentiated geographically. Phylogeographic structure was greatest in the West Indian *M. genibarbis*, which occurs on several islands in the Greater Antilles and Lesser Antilles, and in the Andean *M. ralloides*. The phylogeographic differentiation within *M. ralloides* was not anticipated by previous taxonomic treatments and provides a further example of the importance of the Andes in the diversification of Neotropical birds. Overall, the historical biogeography of *Myadestes* suggests that range expansion and long-distance dispersal are transient population phases followed by persistent phases of population differentiation and limited dispersal. *Received 9 October 2005, accepted 17 July 2006.*

Key words: Andes Mountains, Hawaii, late Miocene, mitochondrial DNA, North Peruvian Low, over-ocean dispersal, Panama Land Bridge, phylogeography, range expansion, West Indies.

Biogeografía Histórica de los Zorzales del Género *Myadestes*

Resumen.—Los zorzales del género *Myadestes* son aves de bosques montanos que se encuentran ampliamente distribuidas en el Nuevo Mundo, desde Alaska

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hasta el norte de Bolivia, incluyendo a Hawai y a las Antillas. Con el objetivo de entender el origen de esta impresionante distribución, utilizamos secuencias de cinco genes mitocondriales para reconstruir la biogeografía histórica de *Myadestes*. La filogenia resultante indica una expansión inicial rápida del género para ocupar la mayor parte de su rango continental, al menos hasta la parte baja de Mesoamérica hacia el sur, además de Hawai y las Antillas Mayores. La especie norteamericana *M. townsendi* parece ser el taxón hermano del resto de los *Myadestes*. La especie *M. obscurus* de Hawai está más estrechamente emparentada con linajes mesoamericanos que con *M. townsendi*. La relación de taxones hermanos entre las dos especies de las Antillas (*M. elisabeth* y *M. genibarbis*) está fuertemente apoyada, lo que indica una colonización única de estas islas. Un nodo más reciente conecta a la especie andina *M. ralloides* con las especies mesoamericanas *M. melanops* y *M. coloratus*. Una calibración estándar del reloj molecular de 2% de divergencia en secuencias por millón de años para el ADN mitocondrial de las aves, sugiere que la diversificación inicial de *Myadestes* sucedió cerca del final del Mioceno (entre 5 y 7.5 millones de años antes del presente). Las temperaturas más frías y los niveles más bajos del océano existentes durante ese período podrían haber incrementado la extensión de los bosques montanos y reducido las distancias de dispersión sobre el agua, posiblemente favoreciendo la expansión del rango de *Myadestes* y su colonización de las Antillas. La separación entre los linajes de América del Sur y del sur de América Central sucedió hace cerca de tres millones de años, lo que sugiere que *Myadestes* expandió su rango hacia América del Sur poco después del levantamiento pliocénico del Istmo de Panamá. A pesar de la evidente habilidad de dispersión a grandes distancias que presenta *Myadestes*, varias especies del género se encuentran altamente diferenciadas geográficamente. La estructura filogeográfica fue más marcada en la especie *M. genibarbis*, la cual se encuentra en varias de las Antillas Mayores y Menores, y en la especie andina *M. ralloides*. La diferenciación filogeográfica existente en *M. ralloides* no había sido anticipada por tratamientos taxonómicos previos, y provee un nuevo ejemplo de la importancia de los Andes en la diversificación de las aves neotropicales. En general, la biogeografía histórica de *Myadestes* sugiere que la expansión de los rangos de distribución y los eventos de dispersión a grandes distancias son fases transitorias, que están seguidas por fases de diferenciación poblacional y dispersión limitada.

Species formation depends on a fine balance between dispersal, necessary for establishing allopatric populations, and reduced gene flow, which permits genetic divergence. How this balance is achieved and the relationship between dispersal capacities and the diversification of clades are poorly understood (Coyne and Orr 2004). This conflict could be resolved if phases of population expansion and contraction alternated, providing opportunities for the colonization of new regions and periods of reduced gene flow between populations necessary for the accumulation of species differences. Such historical patterns of population expansion and quiescence (Ricklefs and Bermingham 2002) could potentially be visualized by overlaying phylogenetic trees on the geographic distribution of contemporary taxa. Periods of expansion accompanied by long-distance dispersal would appear as nodes separating isolated populations or species in different areas; several such populations formed contemporaneously would suggest a transient phase of expansion occurring over a large area. Alternatively, dispersal might continue at a rate sufficient to establish new populations but not to prevent their genetic divergence (Johnson et al. 2000), in which case one would not expect to see contemporaneous formation of multiple independent lineages, but rather a more haphazard branching pattern within the phylogenetic tree. Testing these alternatives in a phylogenetic framework will ultimately require large samples of clades.

Here, we examine relationships among a single, moderately sized clade of passerine birds, the solitaires of the genus *Myadestes* (Turdidae), to explore a phylogenetic approach to understanding the balance between dispersal and restricted gene flow. *Myadestes* includes 13 species of generally sedentary forest songbirds that nonetheless are broadly distributed throughout the Western Hemisphere in montane forests of the Americas from Alaska to Bolivia, throughout much of the West Indies, and, most remarkably, as one of only six passerine lineages to have become established on the Hawaiian Islands, ~4,000 km from potential continental source populations (Ridgely and Tudor 1989, American Ornithologists' Union [AOU] 1998). Thus, although *Myadestes* has achieved remarkable feats of long-distance colonization, continued dispersal has not prevented the formation of highly differentiated populations. However, unlike other genera with multiple sympatric species (e.g., *Vireo, Dendroica, Vermivora*), species of *Myadestes* do not occur sympatrically (as "biological" species) except on the island of Kauai in the Hawaiian chain and locally in northern Mesoamerica.

Most species of *Myadestes* are tropical or Andean. Only one, *M. townsendi*, occurs north of the Mexico–United States border. It is the only member of the genus that exhibits substantial migratory movements, though some tropical species undertake localized altitudinal migrations (Howell and Webb 1995). Individuals of *M. townsendi* also are frequent autumn vagrants to eastern North America, as much as 2,000 km from the nearest breeding areas of the species (Bowen 1997). Within the New World tropics, other species of *Myadestes* are more-or-less continuously distributed, with allopatric replacement, wherever mountain ranges exceed 1,000 m in elevation. Several of these species, including the Andean *M. ralloides* and West Indian *M. genibarbis*, have large geographic ranges, allowing comparison of genetic differentiation within and between species and assessment of the genetic cohesion of species by means of gene flow. Assuming that molecular divergence is related to time, we ask whether the colonization of Hawaii and the West Indies, as well as the continental range expansion of *Myadestes* through Mesoamerica to the Andes, were contemporaneous and might have coincided with marked changes in climate during the late Tertiary.

Materials and Methods

Taxonomic background.—The genus *Myadestes* comprises 13 species (Sibley and Monroe 1990, AOU 1998; Table 1). These include five Hawaiian species (three probably extinct, one critically endangered) formerly placed in the genus *Phaeornis* that are now recognized as belonging to *Myadestes* (Pratt 1982, AOU 1998, Fleischer and McIntosh 2001; also see Lovette et al. 2002). Figure 1 shows the distribution of the species of *Myadestes*.

The phylogenetic position of *Myadestes*, including the identity of a suitable outgroup for the genus, has been the subject of some debate. Typically, *Myadestes* has been considered part of the "true thrush" group, either as a member of the family Turdidae (AOU 1998) or within the subfamily Turdinae in the family Muscicapidae (Sibley and Ahlquist 1990). However, citing similarities to a few aberrant Old World thrushes and the absence of several synapomorphies of true thrushes (Turdidae), Olson (1989) erected a separate subfamily, Myadestinae, within Muscicapoidea, sister to Turdinae. This classification was supported by Pasquet et al. (1999), who found a relationship between *Myadestes* and the African thrush genera *Stizorhina* and *Neocossyphus*. In the most thorough study to date, Klicka et al. (2005) demonstrated that *Myadestes* is part of a basal thrush clade that includes North American bluebirds in the genus *Sialia* and African ant-thrushes in the genus *Neocossyphus*. This clade is congruent with Olson's subfamily Myadestinae. Furthermore, Klicka et al. (2005) clearly demonstrated that *Entomodestes* and *Cichlopsis* are not closely related to *Myadestes*, as some earlier classifications had suggested (Meyer de Schauensee 1970).We follow Klicka et al. (2005) and use *Sialia* to root the *Myadestes* phylogeny, though these genera split early within the diversification of Myadestinae.

Molecular methods.—To gain an overview of genetic variation in *Myadestes*, we sampled 63 individuals throughout the range of the genus and sequenced the complete ATP synthase 6 (ATP6, 642 base pairs [bp]) and ATP synthase 8 (ATP8, 168 bp) genes (these genes partially overlap, and we collectively refer to them as ATP6&8). Because we lacked DNA samples from four of the five Hawaiian species, *M. obscurus* was the single representative of the Hawaiian

TABLE 1. Species, museum or tissue collection and catalogue number, GenBank accession number, and collecting location for the samples included in the present study. An asterisk indicates that the sample was included in the four-gene analysis (see text). *Myadestes myadestinus*, *M. woahensis* (extinct), *M. lanaiensis* (possibly extinct), and *M. palmeri* are Hawaiian species of *Myadestes* not included in the present study.

Species	Museum–collection and number[1]	GenBank accession number(s) ATP6&8	ND2	Cyt-b	COI	Location
Myadestes coloratus (7)	LSUMZ B1395*	DQ470707	DQ469615	DQ463689	DQ469629	Panama: Darien: Cerro Pirre
	LSUMZ B1370	DQ470726				Panama: Darien: Cerro Pirre
	LSUMZ B1372	DQ470706				Panama: Darien: Cerro Pirre
	LSUMZ B2174	DQ470728				Panama: Darien: Cerro Pirre
	LSUMZ B1396	DQ470727				Panama: Darien: Cerro Pirre
	MVUP 1982 (STRI PA-CO1)	DQ470724				Panama: Darien: Serrania de Maje
	MVUP 1979 (STRI PA-CO2)	DQ470725				Panama: Darien: Serrania de Maje
Myadestes elisabeth (1)	ANSP A5550*	DQ470682	DQ469610	AF295084	DQ469623	Cuba: Pinar del Rio: P.N. La Guira
Myadestes genibarbis (15)	FMNH 331091*	DQ470684	DQ469611	DQ469624	DQ463685	Jamaica: Surrey: Portland
	FMNH 331093	DQ470685				Jamaica: Surrey: Portland
	FMNH 331090	DQ470686				Jamaica: Surrey: Portland
	STRI RD-MGE1*	AF281021		AF295083		Dominican Republic: Valle Nuevo
	STRI RD-MG3	AY115157				Dominican Republic: Valle Nuevo
	STRI RD-MG7	AY115156				Dominican Republic: Parque Bahoruco
	STRI DO-MGE1	AY115154				Dominica: Belle Fille
	STRI DO-MGE2	AY115155				Dominica: Belle Fille
	STRI DO-MGE3	DQ470683				Dominica: Belle Fille
	STRI MA-MGE2	AY115151				Martinique: Fond Baron
	STRI MA-MGE14	AY115150				Martinique: Fond Baron
	STRI MA-MGE7	DQ470687				Martinique: Fond Baron
	STRI SL-MGE1	AY115152				St. Lucia: Edmund's Forest
	STRI SL-MGE2	AY115151				St. Lucia: Edmund's Forest
	STRI SL-MGE3	AY115153				St. Lucia: Edmund's Forest
Myadestes melanops (6)	LSUMZ B16017*	DQ470689	DQ469614	AF295087	DQ469628	Costa Rica: Heredia: Finca La Fontana
	LSUMZ B16046	DQ470690				Costa Rica: Heredia: Finca La Fontana
	STRI PA-MME1520	DQ470691				Panama: Chiriqui: Continental Divide

Table 1. Continued.

Species	Museum–collection and number[1]	GenBank accession number(s) ATP6&8	ND2	Cyt-b	COI	Location
	STRI PA-MME5424	DQ470692				Panama: Chiriqui: Continental Divide
	STRI PA-MME5468	DQ470693				Panama: Chiriqui: Cerro Hornito
	STRI PA-MME5484	DQ470694				Panama: Chiriqui: Cerro Hornito
Myadestes obscurus (2)	STRI HW-MOS1*	DQ470695	DQ469608	AF295080	DQ469621	Hawaii
	LSUMZ B25041	DQ470696				Hawaii (USA: Texas: Houston Zoo)
Myadestes occidentalis (6)	FMNH BMM287*	DQ470698	DQ469612	DQ469626	AF295085	Mexico: Oaxaca: Sierra de Miahuatlan
	FMNH BMM087	DQ470699				Mexico: Hidalgo: 5 km east of Tlanchinol
	FMNH BMM205	DQ470697				Mexico: Michoacan; Cerro Tancitaro
	FMNH 343293	DQ470701				Mexico: Guerrero: Sierra de Atoyac
	FMNH 343291	DQ470700				Mexico: Jalisco: Sierra de Manantlan
	MBM 10995	DQ470733				Guatemala: Queztaltenango
Myadestes ralloides (17)	LSUMZ B11939*	DQ470703	DQ469617	DQ463687	DQ469631	Ecuador: Esmeraldas: El Placer
	LSUMZ B11983	DQ470721				Ecuador: Esmeraldas: El Placer
	LSUMZ B11920	DQ470720				Ecuador: Esmeraldas: El Placer
	LSUMZ B11770	DQ470719				Ecuador: Esmeraldas: El Placer
	LSUMZ B12197	DQ470704				Ecuador: Pichincha: Mindo
	LSUMZ B12107	DQ470722				Ecuador: Pichincha: Mindo
	LSUMZ B12121	DQ470723				Ecuador: Pichincha: Mindo
	STRI EC-MRA4380	DQ470705				Ecuador: Zanora-Chinchipe
	LSUMZ B5466*	DQ470709	DQ469616	DQ463686	DQ469630	Peru: San Martin: 20 km northeast of Tarapoto
	LSUMZ B206	DQ470708				Peru: Cajamarca: Machete
	LSUMZ B225*	DQ470730	DQ469618	DQ463690	DQ469632	Peru: Cajamarca: Machete
	LSUMZ B1653	DQ470729				Peru: Pasco: Santa Cruz:
	LSUMZ B7954	DQ470710				Peru: Pasco: Playa Pampa
	LSUMZ B7975	DQ470731				Peru: Pasco: Playa Pampa
	LSUMZ B22779	DQ470717				Bolivia: La Paz: Cerro Asunta Pata
	LSUMZ B22715*	DQ470702	DQ469619	DQ463688	DQ469633	Bolivia: La Paz: Cerro Asunta Pata
	LSUMZ B22782	DQ470718				Bolivia: La Paz: Cerro Asunta Pata

TABLE 1. Continued.

Species	Museum–collection and number[1]	GenBank accession number(s) ATP6&8	ND2	Cyt-b	COI	Location
Myadestes townsendi (4)	LSUMZ B20975*	DQ470711	DQ469609	AF295082	DQ469622	USA: California: San Bernardino County
	LSUMZ B21456	DQ470712				USA: California: San Bernardino County
	MBM 13256	DQ470735				USA: Idaho: Kootenai County
	MBM 9637	DQ470734				USA: Arizona: Coconino County
Myadestes unicolor (7)	FMNH 343288*	DQ470716	DQ469613	AF25086	DQ469627	Mexico: Veracruz: Sierra Santa Martha
	FMNH 343289	DQ470715				Mexico: Veracruz: Sierra Santa Martha
	LSUMZ B18083	DQ470713				Mexico
	LSUMZ B18084	DQ470714				Mexico
	FMNH 343288*	DQ470716	DQ469613	AF25086	DQ469627	Mexico: Veracruz: Sierra Santa Martha
	FMNH 343289	DQ470715				Mexico: Veracruz: Sierra Santa Martha
	MBM 4414	DQ470732				Nicaragua: Matagalpa
Sialia mexicana (1)	UWBM 50089*	DQ470681	DQ469607	DQ463684	DQ469620	USA: Washington: Chelan County

Abbreviations: ANSP = Academy of Natural Sciences, Philadelphia; FMNH = Field Museum of Natural History, Chicago; LSUMZ = Louisiana State University Museum of Natural Sciences, Baton Rouge; MVUP = University of Panama Museum of Vertebrates, Panama City; UWBM = University of Washington Burke Museum, Seattle; and STRI = Smithsonian Tropical Research Institute, Balboa, Panama.

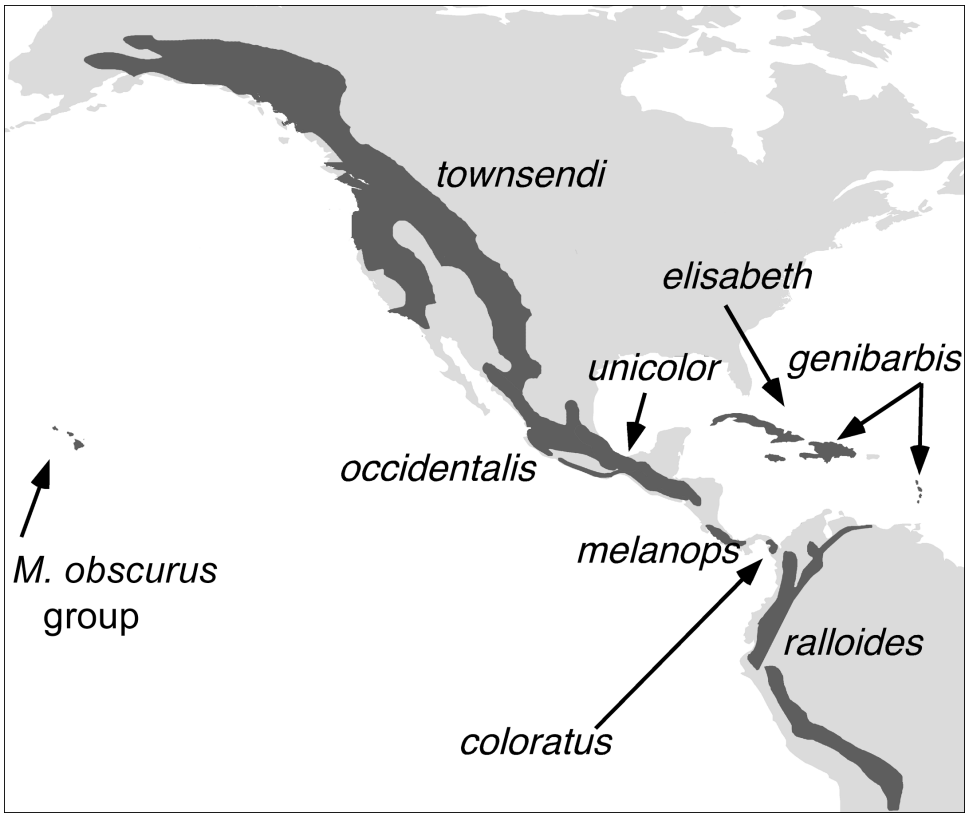

FIG. 1. Current distribution of the 13 species of solitaires in the genus *Myadestes*. Five species are historically known from the Hawaiian archipelago.

species (Pratt 1982). One individual of *Sialia mexicana* constituted the outgroup. Following our preliminary phylogenetic analysis, we selected one individual representing each of the major phylogroups recovered in the ATP6&8 phylogeny for additional analysis using a five-gene data set that produced 3.6 kbp of mitochondrial sequence: the entire ATP6 (642 bp), ATP8 (168 bp), NADH dehydrogenase subunit II (ND2, 1,041 bp), and cytochrome-*b* (1,143 bp) genes, as well as the first 612 bases of the cytochrome oxidase gene subunit I (COI). Some of these individuals had been sequenced in previous studies (Ricklefs and Bermingham 2001, Lovette et al. 2002). Individuals, GenBank accession numbers, sampling locations, and tissue-collection information are presented in Table 1.

Gene products were amplified from total genomic DNA as described in previous studies from our group (Hunt et al. 2001). We used the following primers: ATP6&8—COIIGQL, COIIIHMH (Joseph et al. 2004); ND2—MetB (CGAAAATGAT GGTTTAACCCCTTCC), TrC (CGGACTTTAGCA GAAACTAAGAG), and ND2MYAD (sequencing only) (ACAGCCATAAAATTCCCACC) (designed in the Bermingham lab); COI—COIf and COIa (Palumbi 1996); cytochrome *b*—CBVL14828 (CCA CCCTCCACTCAGGCCTAATCAA) and H16064 (GGAGTCTTCAATCTTTGGTTTACAAGACC) with CB8(1) (GGCCAAATATCATTTTGAGG) (designed in the Bermingham lab).

Mitochondrial DNA (mtDNA) is sometimes translocated to the nucleus, and nuclear copies of mtDNA genes (pseudogenes) have been amplified by mitochondrial gene primers (e.g., Sorenson and Quinn 1998). We took several precautions to ensure that our sequences were of mitochondrial origin. First, except for five Caribbean individuals, we extracted DNA from mitochondrion-rich muscle tissue rather than blood, thus decreasing the likelihood of amplifying nuclear copies of mtDNA genes. Second,

we observed no insertions, deletions, or nonsense codons in the aligned sequences, nor did the electropherograms contain double peaks, which would have indicated co-amplification of nuclear and mitochondrial copies. Third, we detected no significant differences in the rate of evolution between gene regions (see below), which might have resulted from the translocation of part of the sequenced mitochondrial genome to the nucleus. Fourth, we sequenced genes that are widely spaced along the mtDNA molecule, and thus a consistent phylogenetic signal recovered from nuclear DNA would require a translocation of most of the molecule. Sequences were aligned using SEQUENCHER, version 4.0 (Gene Codes, Ann Arbor, Michigan).

For the five-gene data set, a partition homogeneity test (Farris et al. 1995) implemented in PAUP* (Swofford 2002) failed to reject homogeneous phylogenetic signal between the five genes ($P = 0.31$), so we combined the genes into a single concatenated sequence for further analysis. The ATP6&8 genes overlap by 10 bp including the last three codons of the ATP8 gene and the first three codons of the ATP6 gene. Thus, in the combined data set, we duplicated the overlap (e.g., Hunt et al. 2001) to maintain the first-position reading frame throughout the sequence. For the ATP6&8 data set, a hierarchical likelihood ratio test in MODELTEST, version 3.07 (Posada and Crandall 1998), identified the general time reversal with gamma-distributed rate heterogeneity (GTR+G) model of nucleotide evolution as the best fit to out data. We reconstructed the phylogeny using a Bayesian phylogenetic inference with Markov chain Monte Carlo simulations implemented in MRBAYES, version 3.1 (Ronquist and Huelsenbeck 2003). We used the following parameter settings: a 4×4 nucleotide substitution model with six parameters (i.e., general time reversal) with four gamma rate categories using the vertebrate mitochondrial molecular code. We ran MRBAYES for 10^6 generations, sampling every 100 generations. We graphed the –ln likelihoods for the 10,001 sampled generations and found that the results reached stationarity after 3,000 sampled generations. Stationarity was confirmed using the "cumulative" function in the AWTY software package (Wilgenbusch et al. 2004). Therefore, we discarded the first 3,000 sampled generations as "burn-in" and created a consensus topology with the remainder.

For the five-gene data set, a hierarchical likelihood-ratio test implemented in MODELTEST, identified the GTR+G model but with different parameter estimates. Because MODELTEST does not consider site-specific among-site rate variation due to codon position (SS), we compared the GTR+G to a GTR+G+SS model using a hierarchical likelihood-ratio test, which found significant rate variation among codon positions ($\chi^2 = 979.1$, df = 10, $P < 0.0001$). This suggests that phylogenetic estimation can be improved by partitioning the data by codon-position, so we used similar parameters as in the ATP6&8 data set, except that we partitioned the concatenated data set by codon position. We ran MRBAYES for 8×10^6 generations, sampling every 1,000 generations. Stationarity and burn-in values were determined as above, and we discarded the first 1,500 generations and created a consensus topology with the remaining sampled generations. This MRBAYES analysis was replicated five additional times to ensure that the chains sampled the posterior distribution thoroughly. To explore the generality of these results with respect to method of phylogenetic inference, we also generated PAUP*-based maximum-likelihood (ML) topologies using a variety of subsets of the data (described below), including a partitioned ML topology. To perform the latter, we generated ML parameters for each gene individually in the concatenated data set using MODELTEST. Then we performed a heuristic ML search for the best 500 trees using the concatenated data set and the likelihood parameter estimates for this data set obtained earlier from MODELTEST. The consensus MRBAYES tree was added to this set of trees, and likelihood scores for each individual gene were calculated using the gene-specific likelihood parameters. The 501 trees were ranked using the sum of the likelihood scores for each gene. We repeated this analysis using codon position rather than gene to partition the concatenated data set.

We tested for a molecular clock in the five-gene data set as well as a reduced data set consisting only of the cytochrome-*b* data (MODELTEST identified the transversional model with rate variation among sites [TVM+G] as the most appropriate model for the cytochrome-*b*-only data set). Using PAUP*, we generated an ML tree (containing only *Myadestes*

spp.) via a heuristic search without a molecular clock enforced and compared the likelihood score of that topology with and without a molecular clock enforced. The cytochrome-*b* molecular-clock topology was translated to time using a 2% per million years rate of nucleotide divergence for model-corrected data (Fleischer et al. 1998, Lovette 2004).

RESULTS

We recovered 3,638 bases of mitochondrial DNA, including the complete coding region of cytochrome *b* (1,143 bp) and ND2 (1,041 bp), as well as the first 612 bases of COI and the entire coding region of ATP8 and ATP6 (842 bp), for individual birds representing each of the clades of *Myadestes* identified in the ATPase-based phylogeny. As expected for protein-coding mitochondrial genes, sequences aligned without gaps. Base frequencies were roughly similar among all five genes and typical of avian mitochondrial sequences. All were relatively deficient in guanine (average proportions of bases for the ATP6&8 and five-gene data sets were adenine: 30.2% and 28.7%, cytosine: 35.6% and 33.7%, guanine: 9.1% and 12.7%, and thymine: 25.0% and 24.8%). In the ATP6&8 phylogeography data set, 281 of 852 characters (33%) were variable; in the five-gene data set, 1,054 of 3,648 characters (29%) were variable. In both data sets, most variation was at the third codon position (ATP6&8 data set: 197 of 281 bp, 70%; five-gene data set: 815 of 1,054 bp, 77%).

Saturation plots of our data (Fig. 2) revealed saturation for transitions in third codon positions at model-corrected genetic distances exceeding 0.10. Other nucleotide changes and amino-acid substitutions did not appear to be saturated at genetic distances observed in the present study (Fig. 2B). The saturation point for transitions (Fig. 2A) corresponded to the depth of the basal divergences in our topology (Fig. 3).

Phylogeography of Myadestes.—The phylogenetic reconstruction based on ATP6&8 recovered monophyletic groupings that are consistent with the current taxonomy of *Myadestes* (Fig. 4). In addition, the reconstruction demonstrated extensive phylogeographic structure across the range of two species of *Myadestes*: *M. genibarbis* and *M. ralloides*. Within *M. genibarbis*,

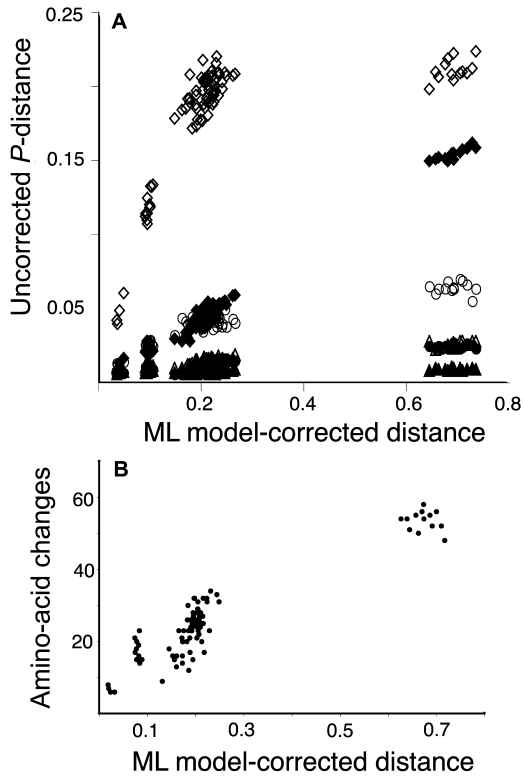

FIG. 2. (A) Saturation plot by codon position and substitution types for the five-gene data set. Open diamond = third-position transitions; closed diamond = third-position transversions; open triangle = second-position transitions; closed triangle = second-position transversions; open circle = first-position transitions; closed circle = first-position transversions. (B) Amino-acid saturation plot for the five-gene data set. Concavity is a signal of substitution saturation, whereas linearity suggests that substitutions are not saturated.

the deepest node separated the population on Jamaica from those on Hispaniola, Dominica, St. Lucia, and Martinique: the average ML model-corrected distance between Jamaican and other *M. genibarbis* populations averaged 4.1% (26–31 substitutions). The ML-corrected pairwise sequence differences among populations on Hispaniola, Dominica, Martinique, and St. Lucia varied between 0.4% and 0.9% (3–9 substitutions).

The ATP6&8 consensus tree revealed a deep split between populations of *M. ralloides* north

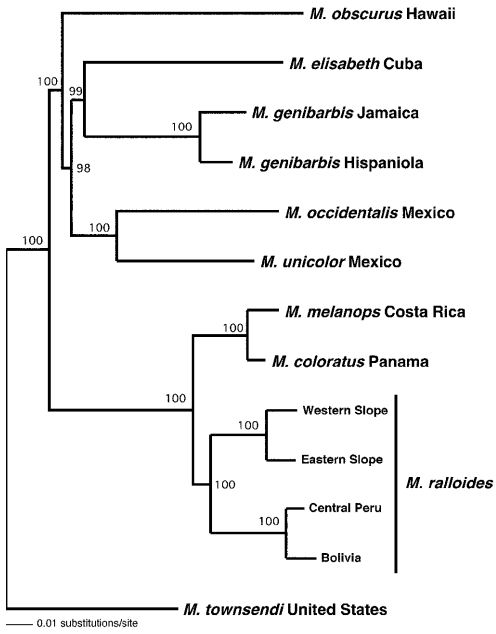

FIG. 3. Phylogram of *Myadestes* obtained by maximum-likelihood Bayesian analysis of 13 individuals representing major phylogroups of *Myadestes* rooted (not shown) on *Sialia mexicana*. Individuals were sequenced for the ATP6&8, ND2, cytochrome-*b*, and COI mitochondrial gene regions. The tree represents the majority-rule consensus of 7,001 sampled trees generated by MCMC (see text) with posterior probabilities indicated.

and south of the Marañon River; corrected differences varied from 5.3% to 7.3% (6.0% average). Furthermore, additional phylogeographic structure was observed within each of these areas. North of the Marañon River, western and eastern Andean phylogroups were recovered with a cross-Andean corrected average divergence of 2.9% (20–23 substitutions). South of the Marañon, two *M. ralloides*-mtDNA clades representing the eastern Andean cloud forests of Peru and Bolivia, respectively, differed by an average of 1.9% corrected pairwise sequence divergence (15 substitutions).

Within the eastern Panama endemic, *M. coloratus*, the ATP6&8 tree recovered two monophyletic phylogroups: one in the Darien highlands and one sampled from the Maje range west of the Darien highlands. These two populations differed, on average, by 1.7% corrected ATP6&8 sequence divergence (12–14 substitutions).

Species phylogeny of Myadestes.—The ATP6&8 phylogeny supported the phylogenetic distinctiveness of all named species of *Myadestes* and identified phylogeographic structure within *M. genibarbis* and *M. ralloides*. Accordingly, 14 mtDNA lineages representing one individual from each species of *Myadestes*, the major phylogroups of *M. genibarbis* (n = 2) and *M. ralloides* (n = 4), and the outgroup *S. mexicana* were sequenced for the complete ND2 and cytochrome-*b* genes and partial COI gene. Including the ATP6&8 genes, ~3.6 kb of the mitochondrial genome was used to infer phylogenetic relationships among the 14 lineages, and all subsequent analysis and discussion of species relationships in *Myadestes* are based on the five-gene data unless stated otherwise.

The mtDNA Bayesian analysis of *Myadestes* recovered strong support for North American *M. townsendi* as the sister to the rest of the lineages of *Myadestes* (Fig. 3). The remaining species of *Myadestes* fall into two reciprocally monophyletic clades: (1) all species representing northern Mesoamerica (*M. occidentalis* and *M. unicolor*), Hawaii (*M. obscurus*), and the West Indies (*M. elisabeth* and *M. genibarbis*); and (2) a southern and purely continental clade comprising the southern Mesoamerican species, *M. melanops* and *M. coloratus*, as well as the Andean *M. ralloides*. Nonetheless, the base of the five-gene mtDNA Bayesian phylogeny for *Myadestes* features multiple bifurcations with short internodes between the branching events. An ML analysis using a data set partitioned by gene recovered an alternative topology that differed with respect to three short internodes at the base of the phylogeny. In that topology, *M. townsendi* was sister to *M. obscurus* rather than being sister to the rest of *Myadestes*, and *M. elisabeth* was sister to a clade containing both *M. genibarbis* and the *unicolor–occidentalis* clade, rather than just being sister to *M. genibarbis*. However, this topology was not significantly better than the Bayesian consensus topology based on a one-tailed Shimodaira-Hasegawa (SH) test (Δ –ln L: 4.464 , P = 0.22). When the partition was by codon position, rather than by gene, a third topology was recovered that differed from the MRBAYES topology only in that the *ralloides–coloratus–melanops* clade was the first bifurcation of *Myadestes*, instead of *M. townsendi*. Likewise, this topology was not significantly better than the MRBAYES consensus using the SH test (Δ –ln L: 1.5235, P = 0.37). Given

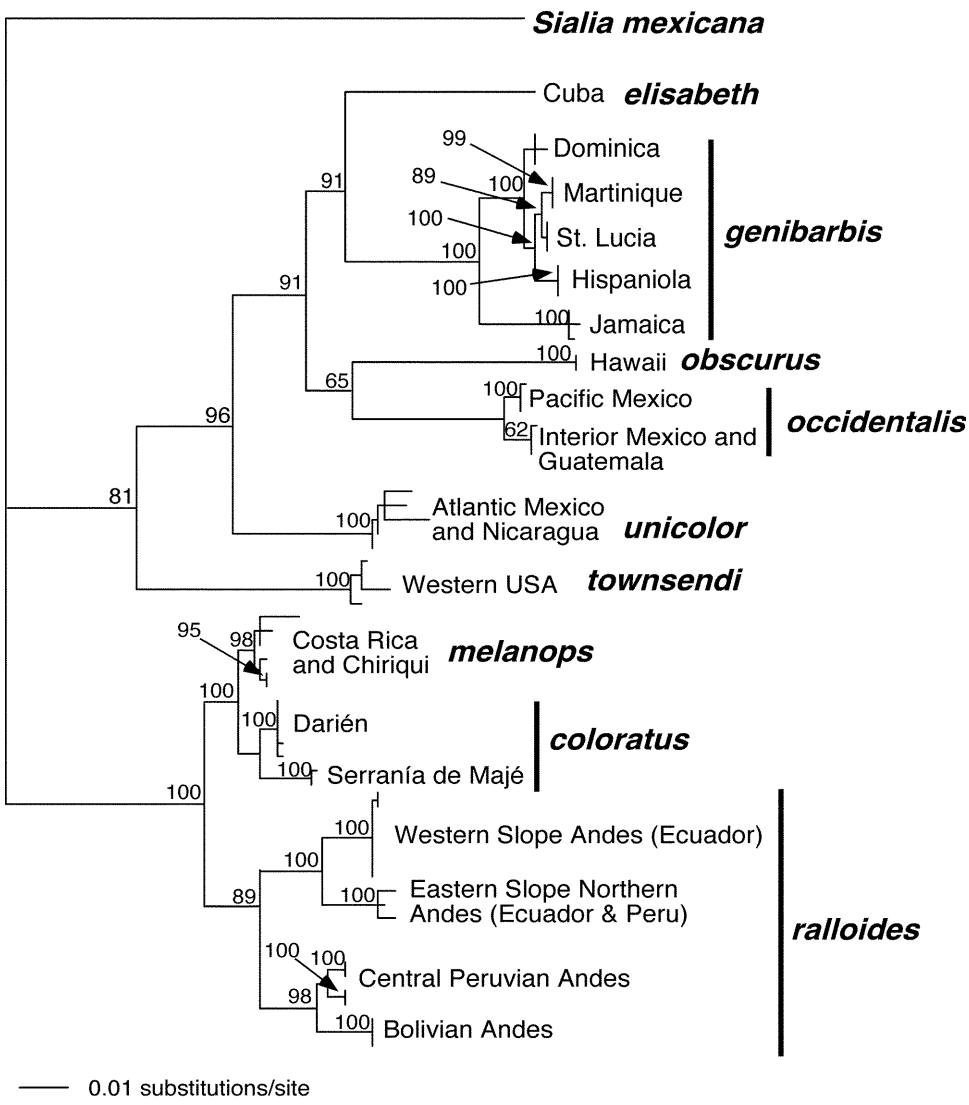

FIG. 4. Phylogeographic relationship of the solitaires (*Myadestes* spp.) obtained by maximum-likelihood Bayesian analysis of 63 individuals sequenced for the ATP6&8 mitochondrial gene region. The tree represents the 50% majority-rule consensus from 7,001 sampled trees generated by MCMC (see text) with posterior probabilities indicated.

these results, and given the fact that MRBAYES explicitly incorporates partitioned data sets in the phylogenetic inference of topology and branch lengths, we used the Bayesian consensus topology as our best estimate of relationships in *Myadestes*, given our data.

Toward the tip of the tree, all sister-pair species relationships were also well supported: the two northern Mesoamerican species (*M. unicolor* and *M. occidentalis*); the two West Indian species (*M. genibarbis* and *M. elisabeth*); and, in southern Mesoamerica, *M. melanops*, inhabiting the highlands of Costa Rica and western Panama, and the eastern Panama highland endemic, *M. coloratus*.

Additionally, the five-gene topology confirmed the phylogeographic structuring revealed by ATP6&8 sequences in Andean *M. ralloides*. Average pairwise distances between *M. ralloides* and *M. coloratus* (6.5%; range:

5.7–8.3%) and between *M. ralloides* and *M. melanops* (6.0%; range: 5.9–8.0%) only slightly exceeded the pairwise distance between *M. ralloides* populations across the Marañon valley (6.0%; range: 5.3–7.3%). Pairwise distances between *M. coloratus* and *M. melanops* averaged 2.0% (range: 1.4–3.6%), which is similar to the shallowest divergence between phylogroups within *M. ralloides*.

Molecular clock of Myadestes.—Although root-to-tip lengths were roughly similar in the five-gene data set, a strict molecular clock was marginally rejected by a likelihood-ratio test on the consensus topology, which showed significant rate variation among lineages (χ^2 = 19.79, df = 11, P = 0.05). However, a molecular clock was not rejected for the cytochrome-*b* data alone (χ^2 = 10.1, df = 11, P = 0.52). Thus, we estimated the age of species from cytochrome-*b* sequence divergence constrained by the five-gene phylogeny shown in Figure 3. We used the general avian mtDNA calibration for cytochrome *b* of 2% sequence divergence per million years, or 1% of branch length per million years (Lovette 2004). We performed an internal check on the general avian mtDNA clock by using the formation of the Panama land bridge between 3.4 and 3.1 mya (Coates and Obando 1996) to date the separation of the Andean *M. ralloides* from the ancestor of the southern Mesoamerican *M. melanops* and *M. coloratus*. The corrected sequence divergence between these two clades is 0.074, yielding 2.18–2.36% sequence divergence per million years. The internal check of the mtDNA clock for *Myadestes* is sufficiently consistent with the 2% mtDNA cytochrome-*b* clock that remaining molecular clock calculations use only the 2% tick rate. The deepest node in the cytochrome-*b* tree, which represents the divergence of *M. townsendi* and the rest of the southern clade (*M. melanops*, *M. coloratus*, *M. ralloides)* dates to 7.6 mya. In a span of ~2 million years, the lineages comprising the modern geographic distribution of *Myadestes* were formed. The most recent species-level split, between *M. melanops* and *M. coloratus*, dates to 1.0 mya. The deepest subspecific split in Andean *M. ralloides* dates to the Pliocene (3.4 mya), whereas more recent splits date to the Pleistocene (0.9–0.7 mya). In West Indian *M. genibarbis*, the divergence between Jamaican and Hispaniola populations dates to the early Pleistocene (1.6 mya).

Discussion

The phylogeny recovered using the extended data set of five mitochondrial genes provides a strong basis for inferring the diversification and history of geographic range expansion in the genus *Myadestes*. The short internodes of the mtDNA tree for *Myadestes* (Fig. 3) suggest that the ancestral species expanded its geographic range in the late Miocene to include most of the contemporary range of the genus, with the probable exception of South America and the Lesser Antilles. Although possible, it seems less likely that the late Miocene simply marked the onset of diversification of a widespread ancestor. The colonization of South America or, alternatively, the back-colonization of southern Mesoamerica from the south, was delayed for several million years until the Pliocene. This marked the beginning of the range expansion and diversification of *Myadestes* at the southern continental limit of its geographic range. In the early Pleistocene, *M. genibarbis* spread between Hispaniola and Jamaica, and subsequently through the Lesser Antilles.

Both the Hawaiian and the Caribbean clades apparently originated from what are now Mesoamerican populations rather than migratory populations farther to the north. Although a sister-group relationship between the North American *M. townsendi* and the Hawaiian members of the clade has long been posited based on morphological and behavioral characters (Mayr 1943, Pratt 1982), previous molecular phylogenies on the basis of small samples of the mitochondrial genome (Fleischer and McIntosh 2001, Lovette et al. 2002) did not unambiguously identify the sister to the Hawaiian solitaires (see also Fig. 4). However, the Bayesian results from our five-gene data set for a broad sampling of New World *Myadestes* shows the ancestor of the Mexican and West Indian taxa to be the sister to *M. obscurus* (100% posterior probability).

The colonization of Hawaii by *Myadestes* is difficult to time closely. Fleischer and McIntosh (2001) used 700 bp of cytochrome *b* to estimate model-corrected pairwise genetic distances between *M. obscurus*, *M. genibarbis*, and *M. townsendi*. On the basis of an average distance of 6.7%, they dated the colonization of Hawaii to <4 mya, which conflicts sharply with our estimate of ~7 mya, corresponding to the 15.2% average pairwise cytochrome-*b* sequence

divergence between *M. obscurus* and other members of the clade sister to it (Figs. 3 and 5). Fleischer and McIntosh's (2001) data were not available on GenBank, and so we cannot comment on the origin of this discrepancy.

The five-gene phylogeny provided strong support (100% posterior probability; Fig. 3) for a sister relationship between the northern Mesoamerican *M. occidentalis* and *M. unicolor*. The two species have mostly allopatric distributions but are narrowly sympatric in parts of their ranges, though *M. occidentalis* typically occurs at higher elevations (Howell and Webb 1995). The contemporary distributions suggest that the species diverged in allopatry, but 5.6% difference in mtDNA sequences between the two species is apparently associated with sufficient ecological or genetic divergence to permit coexistence locally at the edge of their ranges. The only other case of sympatry in *Myadestes* occurred on the Hawaiian island of Kauai between *M. myadestinus* (likely extinct) and *M. palmeri*, for which we have no information on genetic distance.

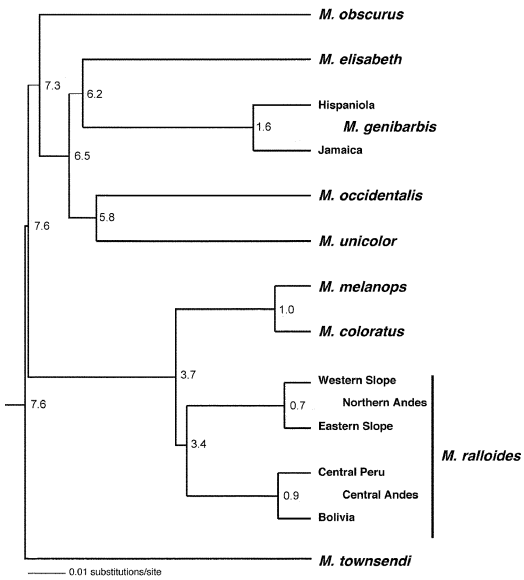

FIG. 5. Result of a maximum-likelihood heuristic search with an enforced molecular clock of the cytochrome-*b* mitochondrial gene region (see text) for the major phylogroups of *Myadestes*. Nodes are dated assuming a model-corrected molecular clock of 1.0% sequence divergence per lineage (Fleischer et al. 1998, Lovette 2004).

The species-level phylogeny shown in Figure 4 unites the three species of southern Mesoamerica and South America, with the *coloratus–melanops* clade in Panama and Costa Rica sister to the Andean *M. ralloides*. Earlier classifications (e.g., Hellmayr 1934, Meyer de Schauensee 1970) considered the three species one; more recent treatments (Sibley and Monroe 1990, AOU Union 1998) consider them a superspecies. Finally, the five-gene topology supports a sister relationship between the two West Indian species, *M. genibarbis* and the Cuban endemic *M. elisabeth* (Fig. 3).

The range expansion and long-distance dispersal, followed by phases of population differentiation evident in the species-level phylogeny, are also readily apparent in the phylogeographic structuring of several species of *Myadestes*. In the case of *M. genibarbis*, the largest phylogeographic break occurs between the population on Jamaica and populations on Hispaniola, Dominica, Martinique, and St. Lucia (4.1%); the maximum divergence between Hispaniolan and Lesser Antillean populations was 0.9%. A plausible scenario for the colonization and spread of *Myadestes* in the West Indies posits the roughly contemporaneous arrival of the lineage in Cuba (*M. elisabeth*) and either Hispaniola or Jamaica (*M. genibarbis*). Following a moderately long period of evolutionary independence, *M. genibarbis* expanded its range to include the second island. Then, well after the initial differentiation of Jamaican and Hispaniolan populations, *Myadestes* spread from Hispaniola to colonize the Lesser Antilles. The absence of *M. genibarbis* from Puerto Rico and the northern Lesser Antilles indicates either that former populations on these islands have become extinct, probably within the past 0.5 million years given the relatively low level of differentiation between Hispaniolan and Lesser Antillean populations (<1.0%), or that *Myadestes* colonized the Lesser Antilles by long-distance dispersal, bypassing these islands. Under either hypothesis, what is clear is that geographic range expansion and long-distance dispersal of *Myadestes* in the West Indies are transient population phases interspersed by relatively long phases of population differentiation.

In the case of *M. ralloides* and its close relatives, *M. coloratus* and *M. melanops*, pulses of geographic expansion, followed by population differentiation under reduced gene flow, have

also punctuated the diversification history of the genus in the southern extreme of its range. The ancestor of *M. ralloides* colonized southern Mesoamerica, or possibly even South America, early in the geographic expansion of the genus, followed by a long period without contemporary evidence of geographic differentiation. Then, the lineage expanded again, coincident with the completion of the Panama land bridge in the late Pliocene, leaving the ancestor of *M. coloratus* and *M. melanops* in Mesoamerica, and the ancestor of *M. ralloides* in the Andes of South America. The subsequent history of *Myadestes* in both southern Mesoamerica (*M. coloratus* and *M. melanops*) and South America (*M. ralloides*) is one of independent and continued geographic expansion or differentiation, resulting in a contemporary pattern of strong mtDNA phylogeographic and biogeographic structure.

Within *M. ralloides*, the first split, which occurred shortly after the separation of Mesoamerican and South American lineages, divided populations north and south of the Marañon River. Model-corrected pairwise ATP6&8 distances across this break, a region of habitat unsuitable for *Myadestes*, averaged 6.0%. In the region of the Marañon River, the high Andean cordilleras are interrupted by the North Peruvian Low (NPL), also known to geologists as the Huancabamba Deflection (James and Sacks 1999). This ancient feature in the Andean orogeny created the lowest pass and most significant Andean biogeographic feature between Venzeuela and Bolivia. Ornithologists have long recognized the importance of this region to Andean bird communities (Vuilleumier 1969, Parker et al. 1985, Whitney 1994), as have biogeographers working with other taxa (Simpson 1975, Young 1992, Duellman and Wild 1993, Weigend 2002).

Our molecular-clock data suggest that the north–south diversification in *M. ralloides* occurred during the Pliocene (~3 mya; Fig. 5) and, therefore, that *M. ralloides* dispersed across the much older NPL rather than having been split vicariously by its formation. The Marañon break also coincides with subspecific distinctions within *M. ralloides* (see below). In a series of *M. ralloides* specimens at the American Museum of Natural History, M.J.M. observed that specimens north of the Marañon River had predominantly gray crowns, whereas chestnut crowns characterized southern populations. This difference, though subtle, was diagnostic for the two groups.

North of the Marañon River, suitable cloud-forest habitat supports *Myadestes* populations on both the eastern and western slopes of the Andes. The separation of these populations dates approximately to the mid-Pleistocene (0.7 mya). This phylogeographic break corresponds with subspecific classification of eastern-slope populations as *M. r. venezuelensis* and western-slope populations as *M. r. plumbiceps* (Ripley 1964). *Myadestes r. venezuelensis* differs from *M. r. plumbiceps* in that the former has a rufous mantle, whereas the mantle of the latter is dark chestnut (M. J. Miller pers. obs.). A third subspecies north of the Marañon River, *M. r. candelae*, is known only from the Magdalena valley in Colombia and was not included in the present study.

All populations south of the Marañon River are classified as the nominate subspecies *M. r. ralloides*. However, our phylogeographic analyses uncovered mtDNA differentiation between the central Peruvian and Bolivian *ralloides* (1.8%) similar to that between *M. r. venezuelensis* and *M. r. plumbiceps*. In this context, we note the unanticipated but similar depth of phylogeographic structure observed between Mesoamerican *M. coloratus* collected in the Darien highlands of eastern Panama and birds from the isolated Majé uplands 200 km to the west, where the species was only recently discovered (Angehr and Christian 2000). The Andes and Mesoamerican highlands are known for high levels of species replacement over distance in birds (Chapman 1926, Terborgh and Winter 1982, Remsen 1984, Parker et al. 1985, Fjeldså 1995). Our results for *Myadestes*, along with results of other studies that have addressed geographic variation below the species level (Brumfield and Remsen 1996; García-Moreno et al. 1999a, b; Eberhard and Bermingham 2004; Cheviron et al. 2005), suggest that comparative phylogeographic studies in the Andes provide more refined biogeographic information than is currently recoverable from prevailing subspecies and species designations and distributions. Such refinements to our understanding of evolutionary history should provide significant insights into climatic and earth-history variables that underlie phases of population expansion and differentiation.

Myadestes diversified within a complex and dynamic region during a period of rapid

environmental change. Climatic and topographical conditions of the late Miocene may have promoted rapid expansion in *Myadestes*. Sea levels were lower than at present (Haq et al. 1987), reducing the overwater distance between continental populations of *Myadestes* and the islands of the Greater Antilles. Furthermore, rapid and significant cooling at the end of the Miocene led to an expansion of montane forests (Graham 1987, 1999), which would have led to increased ranges and population sizes of *Myadestes*, thus increasing the probability of chance dispersal. The increase in montane forest would have played a role in the dispersal of *Myadestes* into what is now Costa Rica and Panama, and later across the land bridge into South America.

The most prominent feature of the phylogeny for *Myadestes* is the initial rapid spread of the ancestral lineage followed by millions of years without further apparent and evolutionarily significant geographic expansion. The persistence of evolutionarily isolated lineages, including those in Hawaii and the West Indies, over several million years suggests that many populations of *Myadestes* are able to resist extinction, in spite of the relatively small areas occupied by some species and their typically sedentary nature. Thus, *Myadestes* presents two faces to us in the form of phases of expansion and relative stasis. Range expansion could be promoted by favorable changes in the environment of a species or by favorable changes in the species itself, including the acquisition of resistance to pathogens or predators. The first possibility would be supported by simultaneous phases of expansion among species with similar ecological requirements. Unfortunately, comparable data on other tropical montane clades of birds are lacking at this point and await future studies. The only evidence in our data consistent with environmentally mediated geographic expansion is the low level of mtDNA haplotype divergence among individuals of *M. townsendi* individuals collected up to 1,500 km apart (Fig. 4). Whether *M. townsendi* represents an example of population expansion following an increase in suitable habitat since deglaciation awaits detailed phylogeographic analysis.

The alternative, that expansion follows upon favorable intrinsic changes, is embodied in the concept of the taxon cycle (Wilson 1959, 1961; Ricklefs and Cox 1972; Ricklefs and Bermingham 2002). Previous studies on the Lesser Antillean avifauna have shown nonequilibrium dynamics consistent with taxon cycles (Ricklefs and Bermingham 2001). The presently quiescent state of some populations is indicated by the absence of *Myadestes* from Puerto Rico, which has habitat suitable for *Myadestes* and would have been a likely intermediary in any stepping-stone model of dispersal between the modestly differentiated populations of *M. genibarbis* on Hispaniola and the Lesser Antilles. Whether Puerto Rico supported a population of *Myadestes* in the past or not, the island is currently not occupied by *Myadestes*, despite the proximity of Hispaniola. It is worth noting that vagrant individuals are known only in the migratory North American *M. townsendi*. If *M. genibarbis* is representative of the genus, then not only is dispersal too infrequent to prevent divergence, but it is also too infrequent to effect colonization of currently unoccupied areas of suitable habitat that would have been reached during phases of population expansion.

Taxonomic note—Our study revealed significant phylogenetic differentiation below the species level in *M. genibarbis* and *M. ralloides*. In the case of *M. genibarbis*, the deepest phylogeographic break separates the Jamaican population from the rest of the sampled West Indian islands. One taxonomic solution would be to follow Ridgway (1907) and recognize the Jamaican Solitaire, *Myadestes solitarius* Baird, as specifically distinct from other populations of *M. genibarbis*.

Given the genetic divergence among *M. melanops*, *M. coloratus*, and *M. ralloides*, continued recognition of these three species appears to be warranted. Furthermore, the mtDNA divergence between populations of *M. ralloides* on either side of the Marañon valley is greater than the divergence between *M. melanops* and *M. coloratus*, indicating that additional species descriptions in the group may be appropriate.

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