ISSN 0014-3820

EVOLUTION

INTERNATIONAL JOURNAL OF ORGANIC EVOLUTION
VOL. 60 FEBRUARY 2006 NO. 2

Darwin's mockingbirds: left to right, Nesomimus parvulus, N. macdonaldi, N. trifasciatus, and N. melanotis. • *See "The Origin and Diversification of Galapagos Mockingbirds," p. 370. Graphite drawing by H. Douglas Pratt, North Carolina Museum of Natural Sciences.*

CONTENTS

(Continued on back cover)

PUBLISHED BY THE SOCIETY FOR THE STUDY OF EVOLUTION

Evolution, 60(2), 2006, pp. 370–382

THE ORIGIN AND DIVERSIFICATION OF GALAPAGOS MOCKINGBIRDS

BRIAN S. ARBOGAST,[1,2,3] SERGEI V. DROVETSKI,[2,4] ROBERT L. CURRY,[5] PETER T. BOAG,[6] GILLES SEUTIN,[7] PETER R. GRANT,[8] B. ROSEMARY GRANT,[8] AND DAVID J. ANDERSON[3,9]

[1]*Department of Biological Sciences, Humboldt State University, Arcata, California 95521*
[2]*Department of Zoology and the Burke Museum, University of Washington, Seattle, Washington 98195*
[3]*Department of Biology, Wake Forest University, Winston-Salem, North Carolina 27109*
[5]*Department of Biology, Villanova University, Villanova, Pennsylvania 19085*
[6]*Department of Biology, Queen's University, Kingston, Ontario K7L 3N6, Canada*
[7]*National Parks Directorate, Parks Canada, Gatineau, Quebec K1A 0M5, Canada*
[8]*Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey 08544*
[9]*E-mail: da@wfu.edu*

Abstract.—Evolutionary radiations of colonists on archipelagos provide valuable insight into mechanisms and modes of speciation. The apparent diversification of Galapagos mockingbirds (*Nesomimus*) provoked Darwin's initial conception of adaptive radiation, but the monophyly of this historically important exemplar has not been evaluated with molecular data. Additionally, as with most Galapagos organisms, we have a poor understanding of the temporal pattern of diversification of the mockingbirds following colonization(s) from source populations. Here we present a molecular phylogeny of Galapagos and other mockingbird populations based on mitochondrial sequence data. Monophyly of Galapagos mockingbirds was supported, suggesting a single colonization of the archipelago followed by diversification. Our analyses also indicate that *Nesomimus* is nested within the traditional genus *Mimus*, making the latter paraphyletic, and that the closest living relatives of Galapagos mockingbirds appear to be those currently found in North America, northern South America, and the Caribbean, rather than the geographically nearest species in continental Ecuador. Thus, propensity for over-water dispersal may have played a more important role than geographic proximity in the colonization of Galapagos by mockingbirds. Within Galapagos, four distinct mitochondrial DNA clades were identified. These four clades differ from current taxonomy in several important respects. In particular, mockingbirds in the eastern islands of the archipelago (Española, San Cristóbal, and Genovesa) have very similar mitochondrial DNA sequences, despite belonging to three different nominal species, and mockingbirds from Isabela, in the west of the archipelago, are more phylogenetically divergent than previously recognized. Consistent with current taxonomy is the phylogenetic distinctiveness of the Floreana mockingbird (*N. trifasciatus*) and close relationships among most mockingbirds from the central and northern region of the archipelago (currently considered conspecific populations of *N. parvulus*). Overall, phylogeographic patterns are consistent with a model of wind-based dispersal within Galapagos, with colonization of more northerly islands by birds from more southern populations, but not the reverse. Further radiation in Galapagos would require coexistence of multiple species on individual islands, but this may be prevented by relatively limited morphological divergence among mockingbirds and by lack of sufficient habitat diversity in the archipelago to support more than one omnivorous mimid.

Key words.—Allopatric speciation, history of science, *Mimodes, Mimus, Nesomimus.*

Received December 18, 2003. Accepted November 21, 2005.

The endemic mockingbirds of the Galapagos Islands (genus *Nesomimus*) played a now-famous role in triggering Charles Darwin's initial insights into evolutionary diversification and natural selection, beginning with his field observations in 1835 during his epic voyage around the world on board the *Beagle* (Sulloway 1982). Darwin's ''attention was first thoroughly aroused, by comparing together the various specimens . . . of the mocking-thrush'' from the Galapagos (Darwin 1845); while still at sea, Darwin realized that the mockingbirds he had studied and collected on four islands represented three allopatric forms that, while clearly allied to mainland mockingbirds he had observed in Argentina and Chile, differed markedly in plumage and morphology among the islands (Darwin 1836 [1963]). The mockingbirds thus helped prompt Darwin to consider mechanisms that could produce geographic variation, leading ultimately to his conception of natural selection.

Despite the pivotal role of Galapagos mockingbirds in the development of evolutionary theory, our understanding of the variation that inspired Darwin is rudimentary. Early treatments of Galapagos mockingbird diversity recognized three species collected by Darwin and his shipmates, based principally on plumage variation in five *Beagle* specimens (Gould 1837), plus a fourth species described in 1888, six years after Darwin's death (Swarth 1931). Gould originally placed the *Beagle* mockingbirds in *Orpheus* but, because of nomenclatural priority, Gray (1841) reclassified them using the epithet *Mimus*; this genus also includes 10 mockingbird species in North and South America and the Caribbean. The Galapagos populations are now placed by most workers within the endemic genus *Nesomimus* (Ridgway 1890; Swarth 1931). The southeast quadrant of the archipelago contains three species, each endemic to a single large island (Fig. 1A): the San Cristóbal mockingbird (*N. melanotis*); the Floreana mockingbird (*N. trifasciatus*), now restricted to two islets adjacent to Floreana; and the Española mockingbird (*N. macdonaldi*). The fourth species, the Galapagos mockingbird (*N. parvulus*), inhabits most other islands in the archipelago.

Darwin came to suspect that the distinctive populations of mockingbirds in Galapagos were the product of a single colonization of the archipelago by a continental ancestor, such as the mockingbirds that he had observed in Argentina and

[4] Present address: Department of Biological Sciences, University of Alaska, 3211 Providence Drive, Anchorage, Anchorage, Alaska 99508.

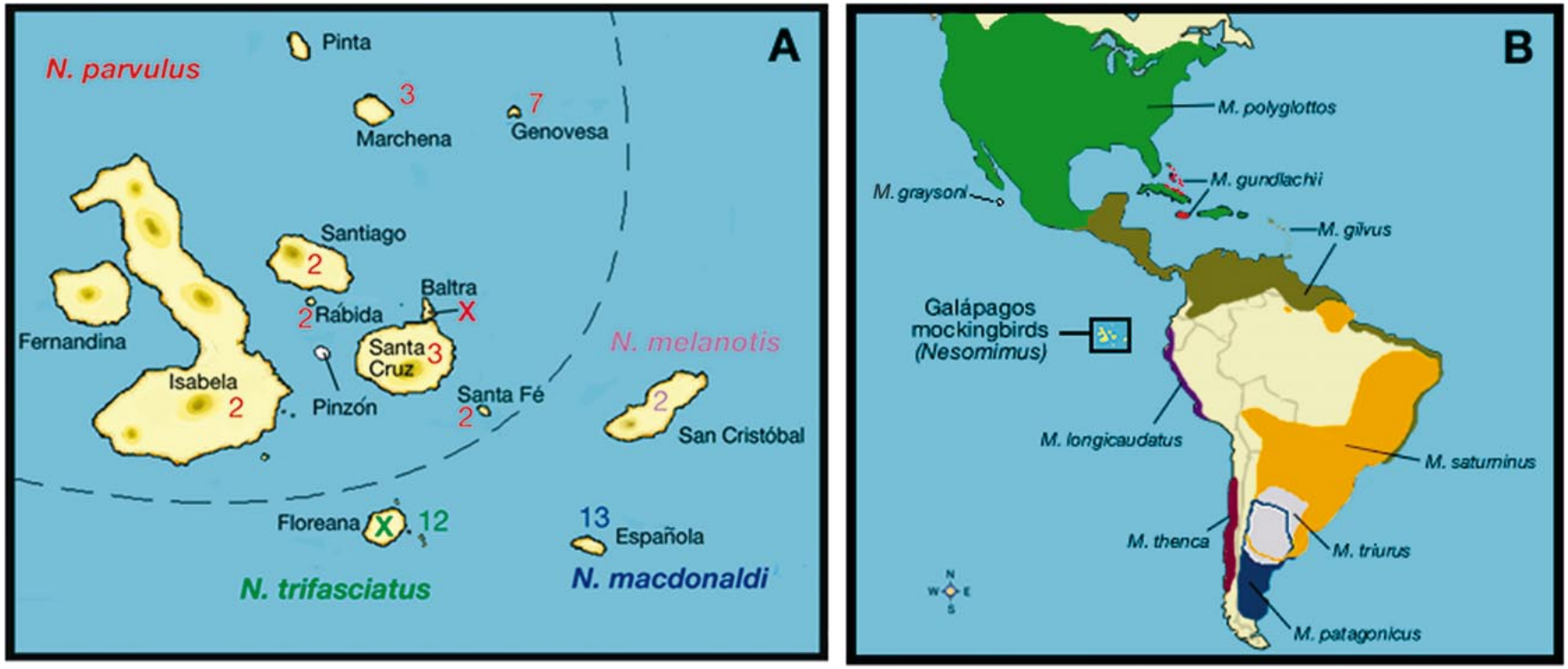

FIG. 1. Breeding distributions and sampling of mockingbirds. (A) Galapagos mockingbirds (*Nesomimus* spp.), presenting conventional plumage-based taxonomy. (B) Generalized distribution map of all New World mockingbirds (Mimidae). Numbers in (A) refer to sample sizes from each island; ''X'' refers to extirpated populations. Samples of *N. trifasciatus* were collected from Gardner-by-Floreana and Champion islets. *Nesominus parvulus* lives on all the major islands north and west of the dashed line (except Pinzón) and on two islands, Wolf and Darwin, northwest of the area shown. In (B) *Mimus triurus* and *M. patagonicus* are Austral migrants, with wintering ranges extending to northern and southern Bolivia, respectively (not shown). One species (brown-backed mockingbird, *M. dorsalis*, of Bolivia and north-eastern Argentina; range not shown), and one well-differentiated subspecies (large-billed mockingbird, *M. gilvus magnirostris*, of San Andrés Island, Colombia) were not sampled. The distributions of *M. saturninus*, *M. triurus*, and *M. patagonicus* overlap in south-central South America.

Chile, followed by dispersal and subsequent diversification within the archipelago (Darwin 1859). It has been suggested frequently that the closest relative—and indeed, the ancestor—of all Galapagos mockingbirds is the long-tailed mockingbird (*Mimus longicaudatus*) of the geographically proximate western coast of Ecuador and Peru (Fig. 1B; Bowman and Carter 1971; Abbott and Abbott 1978; Steadman 1986). However, other candidates for the closest relative that are equally plausible based on phenetic similarity, such as the Bahama mockingbird (*M. gundlachii*), have been suggested (Gulledge 1975). Furthermore, Darwin's hypothesis of a monophyletic origin of *Nesomimus* has never been tested using phylogenetic approaches or molecular markers, so we cannot reject the possibility that several colonizations underlie the modern diversity of Galapagos mockingbirds.

In this study, we use mitochondrial DNA (mtDNA) sequence data to infer a phylogeny of Galapagos mockingbirds and their non-Galapagos relatives. We use this phylogeny to evaluate the monophyly of *Nesomimus*, to identify the closest non-Galapagos relative(s) of *Nesomimus*, to evaluate the current taxonomy of *Nesomimus*, and to infer biogeographic and evolutionary histories within *Nesomimus* and within the mockingbirds (*Mimus* spp. of North America, South America, the Caribbean, and Socorro Island, Mexico) as a group.

Materials and Methods

Our phylogenetic analyses are based on two overlapping datasets. We first conducted a detailed phylogeographic survey of *Nesomimus* from throughout Galapagos using complete sequences of the mitochondrial ND2 gene (1041 bp). Then, we collected additional mtDNA sequence data for a representative sample of mockingbird lineages to improve resolution of the phylogeny's basal nodes. This larger dataset comprised 2658 bp from the ND2, COI, COII, and tRNA-Lysine (tRNA-Lys)/ATP-synthase 6-ATP-synthase 8 (ATPase6, 8) regions for all taxa except *M. graysoni*, for which only ND2 data were available.

Laboratory Methods and Sampling

We examined complete sequences of the ND2 gene from 48 Galapagos mockingbirds representing all four recognized species of *Nesomimus* and 11 islands/islets (Fig. 1; Appendix 1, available online only at http//:dx.doi.org/10.1554/03-749.1.s1). Homologous sequences from nine of the 10 extant species of *Mimus* (including the Socorro mockingbird, *M. graysoni*, formerly placed in *Mimodes* but recently found to be embedded within *Mimus*; Barber et al. 2004; Banks et al. 2005), were also examined, for a total of 65 individuals. We generated sequence data for 60 samples (GenBank accession numbers AY311528–AY311587), including all 48 from Galapagos. The remaining five sequences were published previously (Hunt et al. 2001; Barber et al. 2004). The Galapagos samples, plus those of *M. longicaudatus* that we collected from Isla de la Plata, Ecuador ($n = 3$), consisted of blood collected in the field. The remaining samples consisted of heart, liver, or kidney tissue obtained from museum collections (voucher specimen information given in Appendix 1). We extracted DNA from blood or tissue using either Chelex (Bio-Rad, Hercules, CA) or the Qiagen DNeasy tissue kit (Qiagen, Valencia, CA) amplified the ND2 gene via polymerase chain reaction (PCR), and sequenced the gene in both directions using an ABI 377 automated sequencer (Applied Biosystems, Foster City, CA). Primers, PCR conditions, and sequence alignment are described elsewhere (Drovetski et al. 2004).

For the extended phylogenetic analysis, we examined an additional 1617 bp of mtDNA sequence data including representative lineages of *Nesomimus*, *Mimus*, the sage thrasher (*Oreoscoptes montanus*), and two members of the genus *Toxostoma* (thrashers; Appendix 2, available online only at http://dx.doi.org/10.1554/03-749.1.s2). The COI gene was amplified using primers COIa and COIf (Palumbi 1996) and the COII/tRNA-Lys/ATPase6, 8 region was amplified using primers COIIGQL and COIIHMH (Hunt et al. 2001). Reaction mixtures and thermocycling parameters followed those described in Hunt et al. (2001), with an annealing temperature of 54°C. Sequencing was conducted using primers COIa and CO1f for the COI gene and COIIGQL, COIIHMH, and A8PWL (Hunt et al. 2001) for the COII/tRNA-Lys/ATPase6, 8 region at the San Diego State University Microchemical Core Facility. Sequence data for two species (*Toxostoma rufum* and *O. montanus*) were provided by I. Lovette (Cornell University) and E. Bermingham (Smithsonian Tropical Research Institute). The remaining sequences in this combined dataset were obtained from Genbank (Appendix 2, available online).

Data Analysis

The computer programs MODELTEST (version 3.06; Posada and Crandall 1998), PAUP (version 4.0b10, Altivec; Swofford 1998), and MrBAYES (version 3.1, Huelsenbeck and Ronquist 2001; Huelsenbeck et al. 2001) were used to determine the best-fit model of nucleotide substitution, infer phylogeny, and estimate nodal support throughout resulting trees. We analyzed the ND2 and the combined mtDNA datasets separately. For the former, we used *O. montanus* as an outgroup, and for the latter we used *O. montanus*, *T. rufum*, and *Toxostoma curvirostre*.

For each dataset we determined a best-fit model of sequence evolution using the computer program MODELTEST (Posada and Crandall 1998). Model selection was based on the Akaike information criterion (AIC; see Posada and Buckley 2004). For the combined dataset, we conducted separate runs with and without *M. graysoni* (for which only ND2 data were available) included to assess whether the missing data for this taxon had a strong influence on parameter estimation or model selection. Maximum-likelihood (ML) was used to infer phylogeny and estimate branch lengths using PAUP (Swofford 1998). We used the heuristic search option with starting trees determined via random addition of taxa and tree-bisection-reconnection (TBR) branch-swapping. A likelihood-ratio test (LRT; Huelsenbeck and Rannala 1997) was used to test for a molecular clock. Nodal support was estimated using the bootstrap (Felsenstein 1985) and posterior probabilities determined by Bayesian analysis. ML bootstrap analysis consisted of 100 full heuristic search replicates with random addition of taxa. Bayesian posterior probabilities were assessed under the best-fit model (as determined using

MODELTEST) and under partitioned models using MrBAYES (Huelsenbeck and Ronquist 2001; Huelsenbeck et al. 2001). Recent studies have shown that partitioning data (i.e., by codon position or gene region) can produce less biased posterior probability estimates and provide a better fit between model and sequence data (Castoe et al. 2004; McCracken and Sorenson 2005). For the ND2 dataset we examined a model that partitioned this protein-coding gene by codon position, and for the combined dataset we examined models that partitioned the data both by codon position (with four designated partitions: one each for the first, second, and third codon positions of coding regions, plus one for tRNA-Lys) and by gene region (with five designated partitions: ND2, COI, COII, ATPase6, 8 combined, and tRNA-Lys). The ATPase6 and ATPase8 genes share an invariant, frame-shifted, 10-bp overlap region (Hunt et al. 2001; Lovette 2005), so we added two Ns to our dataset at the end of this overlap; this alleviated the frame-shift problem for analyses requiring information on codon position. Bayesian analysis generally consisted of two runs of 1,000,000 Markov chain Monte Carlo generations (sampled every 100 generations for a total of 10,000 trees), the first 250,000 generations (2500 trees) of which were excluded as burn-in. In all but one case inspection of likelihood scores indicated that the scores had stabilized by 250,000 generations and that the two runs had converged by 1,000,000 generations. The exception was the analysis of the combined dataset under the mixed-model partitioned by codon position (see Results). In this case, we increased the number of generations to 4,000,000 with a burn-in of 400,000 generations to reach convergence of likelihood scores in the two runs. In the partitioned analyses, we unlinked the following four parameters: shape of the gamma distribution, proportion of invariant sites, character state frequencies, and the substitution rates of the GTR model; the remaining parameters that can be unlinked in MrBayes were linked across partitions. We used the AIC to determine if more parameter-rich mixed models were warranted (Castoe et al. 2004; McCracken and Sorenson 2005). Alternative topologies for important nodes in our best ML phylogeny were tested using the approximately unbiased (AU) test as implemented in the computer program CONSEL (Shimodaira 2002). These tests were based on comparing the results of constrained versus unconstrained ML searches in PAUP under the best-fit model for each dataset. Specifically, we evaluated whether the following three hypotheses could be rejected statistically within a likelihood framework: (1) the monophyly of *Nesomimus*; (2) the reciprocal monophyly of *Nesomimus* and *Mimus*; and (3) a sister relationship between *M. longicaudatus* and *Nesomimus*. Separate tests of each hypothesis were conducted for the ND2 and the combined datasets.

Results

ND2 Sequence Data

Alignment of the ND2 sequences was unambiguous as all sequences were of equal length. Replicated sequences for the same individual were always identical, and none of the sequences showed evidence of being a nuclear pseudogene of mtDNA (numt): there were no unexpected stop codons and inspection of sequence chromatograms did not reveal double-peaks characteristic of coamplification of mtDNA and nuclear pseudogenes (Sorenson and Quinn 1998). The best-fit model of evolution for the ND2 dataset was a GTR + Γ model (Rodriguez et al. 1990; Goldman 1993). The ML phylogeny inferred under this model had a −ln likelihood score of 3834.53 (Fig. 2). Based on AIC scores, partitioning of the data by codon position under the GTR + Γ model provided a much better fit to the ND2 data than did the non-partitioned GTR + Γ model (harmonic mean −ln likelihood of two Bayesian runs = 3618.97 for the former vs. 3855.59 for the latter; 27 vs. versus nine parameters; ΔAIC = 437.24). All methods of phylogenetic reconstruction (ML and both Bayesian analyses) resulted in similar trees. All methods recovered a monophyletic *Nesomimus* (node E) nested within *Mimus* and sister to a monophyletic clade comprising *M. polyglottos*, *M. gilvus*, *M. gundlachii*, and *M. graysoni* (nodes A, D). All analyses also supported a monophyletic clade comprising *M. saturninus*, *M. triurus*, *M. thenca*, and *M. patagonicus*. The position of *M. longicaudatus* was not well resolved in any of the analyses. ML bootstrap and posterior probability scores were high for many nodes (Fig. 2); however, some important nodes (i.e., nodes A, D, E) were not well supported, and AU tests failed to reject a variety of alternative topologies, including some in which *Nesomimus* is not monophyletic (Table 1).

Among the mockingbirds in the Galapagos, four distinct mtDNA lineages were recovered (Fig. 2). One lineage includes populations on Española, San Cristóbal, and Genovesa (node I); *N. trifasciatus*, endemic to Floreana and its islets (node F), is a second lineage; *N. parvulus* on Isabela (node G) is a third; and *N. parvulus* populations from the remainder of that species' range except Genovesa (node H) is a fourth. In all but one of the population sampled, mockingbirds had mtDNA more similar to birds from the same location than to any others. The exception was an individual from Rábida, a small island in central Galapagos (Fig. 1A), whose ND2 haplotype (Fig. 2) resembled more closely that of birds from Santa Cruz, 25 km to the southeast, than that of another mockingbird from Rábida, whose mtDNA was closer to that of the population on Santiago, 8 km to the north.

A LRT failed to reject clocklike evolution among the 13 unique ND2 haplotypes of *Nesomimus* (best-fit model for this reduced data set was the TIM + I model; −ln likelihood with molecular clock enforced = 2037.5895 and without clock enforced = 2032.7272; $\chi^2 = 9.7246$, df = 11, $P = 0.56$), and in the clade consisting of the northern mockingbird taxa and *Nesomimus* (i.e., the clade defined by node D, Fig. 2; best-fit model for this reduced dataset was the TIM + I model; −ln likelihood with molecular clock enforced = 2572.6400 and without clock enforced = 2566.6488; $\chi^2 = 11.9824$, df = 16, $P = 0.75$). However, a LRT rejected a molecular clock for the full ND2 data set (−ln likelihood with molecular clock enforced = 3863.30262 and without clock enforced = 3834.53303; $\chi^2 = 57.53918$, df = 29, $P = 0.001$). Systematic removal of individual taxa from the full ND2 dataset revealed failure to reject clocklike behavior in all cases except those in which *M. graysoni* was included. The best-fit model for the ND2 dataset with *M. graysoni* removed was the GTR + Γ model (−ln likelihood with molecular clock enforced =

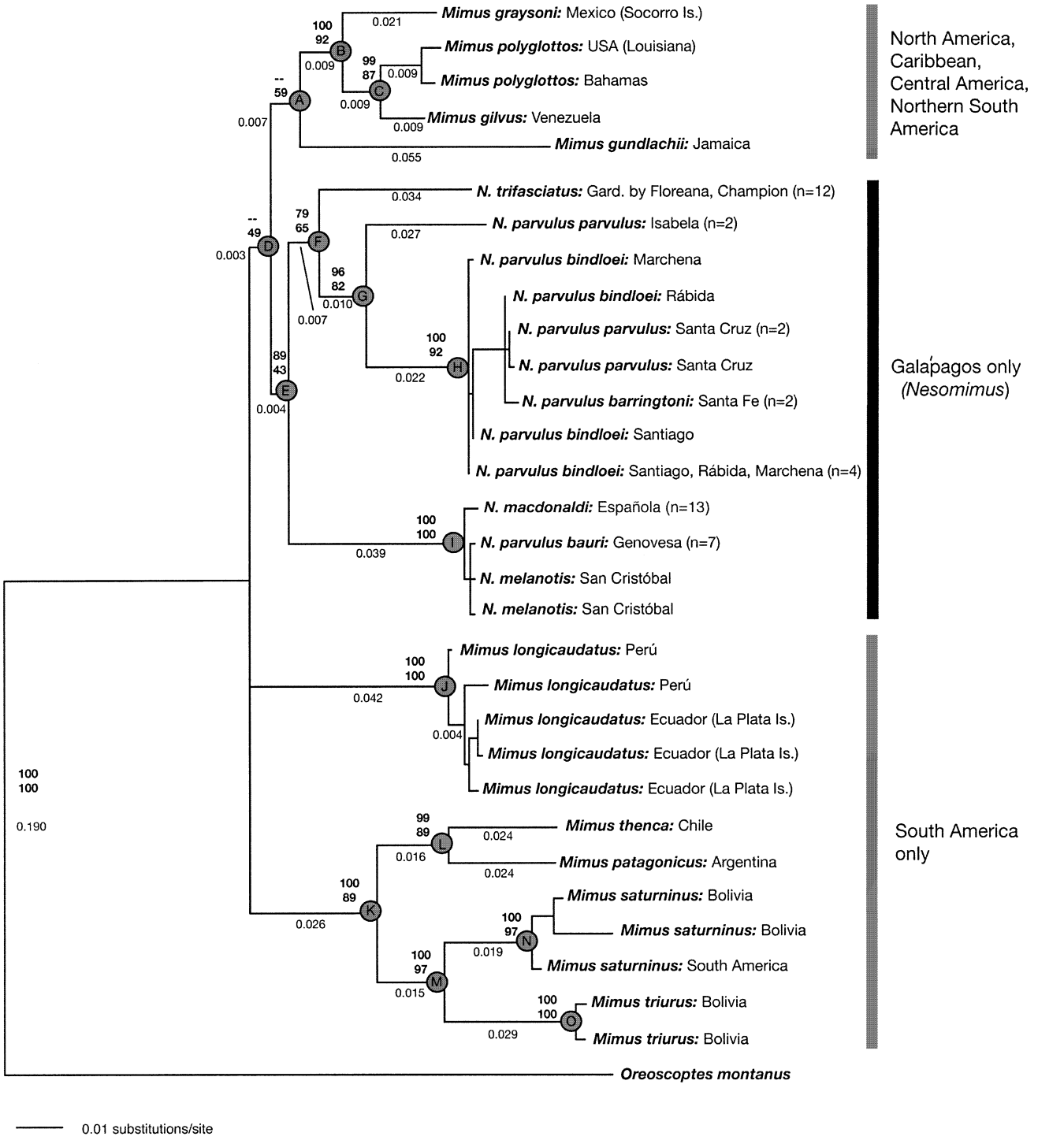

FIG. 2. Rooted maximum-likelihood (ML) phylogeny of mockingbirds based on complete sequences of the ND2 gene of the mitochondrial DNA. Shown is the ML tree estimated under the best-fit model (GTR + Γ model, alpha = 0.1392; see Materials and Methods) with the sage thrasher (*Oreoscoptes montanus*) designated as the outgroup. Taxon labels for *Nesomimus* spp. correspond to those in Figure 1A; for *N. parvulus*, subspecies designation is also shown. Nodal support based on Bayesian probability scores (under the mixed GTR + Γ model partitioned by codon position) and ML bootstrap values are shown above branches at each node (top and bottom numbers, respectively). Estimated branch lengths are shown under each branch. For haplotypes that were not unique, numbers of birds per haplotype are indicated in parentheses. Information on localities, voucher specimens, tissue samples, and GenBank accession numbers is provided in Appendix 1 (available online only).

TABLE 1. Comparison of alternative phylogenetic hypotheses under maximum-likelihood criterion. Tree topologies were constrained to be consistent with each alternative hypothesis and compared to the maximum-likelihood tree using the approximately unbiased test of Shimodaira (2002).

Hypothesis	ND2			Combined data		
	−ln L	Δ in L	*P*-value	−ln L	Δ in L	*P*-value
Maximum-likelihood tree	3834.53	—	—	10,315.89	—	—
Nonmonophyletic *Nesomimus*	3835.65	1.12	0.399	10,317.52	1.63	0.297
Reciprocal monophyly of *Mimus* and *Nesomimus*	3837.36	2.83	0.154	10,321.65	5.76	0.174
Mimus longicaudatus sister to *Nesomimus*	3838.17	3.64	0.144	10,321.10	5.21	0.277

3759.1303 and without clock enforced = 3744.6508; χ^2 = 28.9590; df = 28; P = 0.41).

Combined Analysis

Our combined mtDNA analysis consisted of 2658 bp from the ND2, CO1, COII, tRNA-Lys, and ATPase 6, 8 regions. The molecular characterization and phylogenetic content of these regions for mimids was detailed by Hunt et al. (2001). We did not detect numts in any of these regions (Sorenson and Quinn 1998). Our data aligned with those from Hunt et al. (2001) and with the sequences provided by I. Lovette and E. Bermingham without any insertions, deletions, or unexpected stop codons. Separate analysis of the regions revealed similar relative levels of sequence divergence between taxa (not shown) and double-peaks characteristic of coamplification of mitochondrial and nuclear pseudogenes were not observed.

The best-fit model of evolution for the combined dataset (both with and without *M. graysoni* included) was a GTR + Γ + I (inclusion/exclusion of *M. graysoni* had little influence on parameter estimation or model selection in MODELTEST; Posada and Crandall 1998). The −ln likelihood of the ML phylogeny inferred under the best-fit model was 10315.89 (Fig. 3). As with the ND2 data, partitioning of the combined data by codon position resulted in a large improvement in likelihood compared to the nonpartitioned GTR + Γ + I model. The −ln likelihood scores (harmonic mean of two Bayesian runs) were 9557.15 for the former versus 10354.30 for the latter (43 vs. 10 parameters; ΔAIC = 1484.48). Partitioning of the data by gene resulted in only a modest improvement in fit (ΔAIC = 7) over the nonpartitioned GTR + Γ + I model (mean −ln likelihood score = 10335.81 for the former vs. 10354.30 for the latter; 54 vs. 10 parameters).

All phylogenetic analyses of the combined data resulted in a similar phylogeny (Fig. 3). All methods of tree reconstruction recovered a monophyletic *Nesomimus* (node E) nested within *Mimus*. The additional sequence data included in the combined analysis resulted in a higher ML bootstrap score for this node compared to that based on the ND2 data alone (Figs. 2, 3). All analyses of the combined data also strongly supported a sister relationship between *M. saturninus* and *M. triurus* (node M) and between *M. thenca* and *M. patagonicus* (node L).

The results of the combined analysis were largely consistent with those based on the ND2 data (cf. Figs. 2 and 3). Regardless of tree-reconstruction methodology or dataset, a monophyletic *Nesomimus* (node E) was recovered in every case. The one major topological difference between analyses was the position of *Mimus gundlachii;* this species was sister to *Nesomimus* in the combined analyses, rather than a member of the *M. polyglottos*/*M. gilvus*/*M. graysoni* clade, as recovered using ND2 only. However, this relationship did not receive high nodal support in the combined analysis. Although the position of *M. longicaudatus* was not well resolved, a sister relationship between this species and members of *Nesomimus* was not recovered in any of the analyses. AU tests based on the combined dataset failed to reject alternative topologies constrained to make *Nesomimus* nonmonophyletic, *Nesomimus* and *Mimus* reciprocally monophyletic, and *M. longicaudatus* sister to *Nesomimus* (Table 1).

Examination of the ML phylogram based on the combined dataset (Fig. 3) showed that the mtDNA regions we examined, as a group, evolved at similar rates across mockingbirds; however, the branches leading to the *Toxostoma* outgroups were relatively long. Nonetheless, a LRT failed to reject a molecular clock for the combined dataset (−ln likelihood with molecular clock enforced = 10329.42 and without clock enforced = 10315.89; χ^2 = 27.06, df = 17, P = 0.057) with all taxa included.

DISCUSSION

Phylogeny of Mockingbirds

Phylogenetic relationships of mockingbirds show a high degree of consistency across the methods of phylogenetic reconstruction and datasets we examined. However, the relatively short internodes separating the major lineages of mockingbirds (Figs. 2, 3) made it challenging to resolve some relationships with high nodal support. In addition, several alternate hypotheses could not be rejected within a likelihood framework (Table 1). For example, the monophyly of *Nesomimus*, although recovered in every analysis, received only moderately high nodal support, even in the combined analysis of more than 2600 bp (Fig. 3). Taken as a whole, however, our phylogenetic analyses were most consistent with the simplest explanation for the origin of *Nesomimus*—that these taxa diversified in Galapagos from a common ancestor after a single colonization event—than with alternative hypotheses involving multiple colonizations. Our results also supported an origin of Galapagos mockingbirds from within *Mimus*, such that *Mimus* as currently recognized is paraphyletic. This result supports the suggestion made many times previously that the Galapagos mockingbirds are not sufficiently distinct, based on morphological criteria, to merit recognition as an endemic genus (e.g., Rothschild and Hartert 1899; Bowman and Carter 1971; Abbott and Abbott 1978; Steadman 1986)

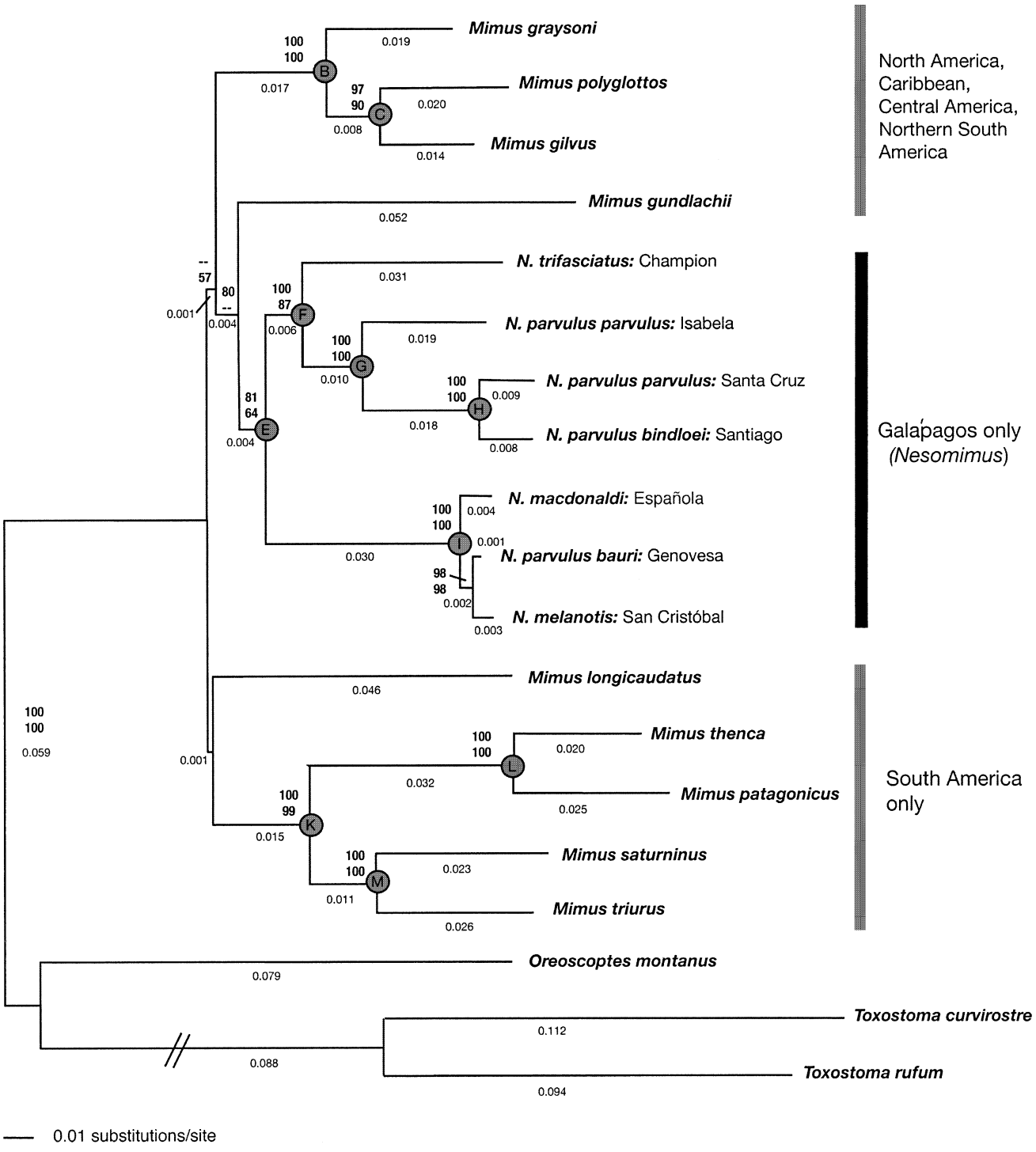

FIG. 3. Rooted maximum-likelihood (ML) phylogeny of mockingbirds based on the combined ND2, COI, COII, and tRNA-Lys/ATPase 6, 8 mitochondrial DNA sequences. Shown is the ML tree estimated under the best-fit model (GTR + Γ + I; alpha = 1.1415; pinvar = 0.6024; −ln likelihood = 10315.89; see Materials and Methods) with the sage thrasher (*Orescoptes montanus*) and two species of thrasher (*Toxostoma curvirostre* and *T. rufum*) designated as outgroups. Taxon labels correspond to those in Figures 1 and 2. Nodal support based on Bayesian probability scores (under the mixed GTR + Γ + I model partitioned by codon position) and ML bootstrap values are shown above branches at each node (top and bottom numbers, respectively). Estimated branch lengths are shown under each branch. Note that all branches are proportional except those leading to the two *Toxostoma* outgroup taxa. Information on voucher specimens, tissue samples, and GenBank accession numbers are provided in Appendix 2 (available online only).

and that *Nesomimus* therefore should be subsumed within *Mimus*.

The several short internodes characterizing the mockingbird phylogeny also suggest that the current diversity of this group is the result of a relatively rapid diversification (Figs. 2, 3). The sum of the branch lengths separating members of *Nesomimus* from *M. polyglottos*, *M. gilvus*, *M. gundlachii*, and *M. graysoni* are estimated to be 0.079–0.110 substitutions per site (equivalent to 7.9–11.0% corrected sequence divergence) based on the ND2 data (values are similar for the combined dataset). Estimated rates of evolution for mtDNA coding regions in birds typically range from 0.01 to 0.025 substitutions per site per lineage per million years (equivalent to a divergence rate of 2–5% per million years; for reviews see Arbogast et al. 2002; and Lovette 2004). Application of these rates to our taxa suggests that the ancestors of *Nesomimus* colonized the Galapagos archipelago approximately 1.6–5.5 million years ago. The extant above-water islands in southeast Galapagos are thought to be about 2–6 million years in age (minimum and maximum age estimates for Española and San Cristóbal are 2.8–5.6 million years and 2.3–6.3 million years, respectively; Geist 1996). Therefore, colonization of older, presently submerged islands (as has been suggested for some other Galapagos taxa; Christie et al. 1992; Rassmann 1997; see also Grehan 2001) need not be invoked in the case of the mockingbirds.

Two rate calibrations based on relatively young islands suggest that mockingbirds may have colonized the Galapagos even more recently. Socorro Island, Mexico, is thought to be less than 1 million years in age (Brattstrom 1990), yet the sum of the branch lengths separating *M. graysoni* from its closest relatives (*M. polyglottos* and *M. gilvus*) range from 0.040 to 0.043 substitutions per site based on the ND2 data (Fig. 2). This suggests a minimum rate for ND2 of ≥0.020–0.022 substitutions per site per lineage per million years (equivalent to a rate of divergence of approximately 4.0–4.3% per million years). Similarly, Isabela is thought to be no more than 0.4 million years old (Geist 1996), but the sums of the branch lengths separating mockingbirds of this island from their closest relatives to the east are ≥0.049 substitutions per site (Fig. 2). This suggests a rate of evolution for the ND2 gene of at least 0.061 substitutions per site per lineage per million years (or a divergence rate of approximately 12.3% per million years). Although these calibrations require several assumptions (Fleischer et al. 1998; Warren et al. 2003), they parallel recent estimates from Indian Ocean sunbirds (divergence rates of approximately 5.6–9.5% per million years; Warren et al. 2003) and grouse (divergence rates of approximately 4.5–12.5% per million years; Drovetski 2003) in suggesting a rate of mtDNA evolution in birds that is higher than that typically recognized. However, given the relatively young ages of our calibration points, some of the discrepancy we observed might be due to the effects of purifying selection (Ho et al. 2005). This may be especially true for the Isabela calibration, which is considerably younger than most published calibration points (see Garcia-Moreno 2004; Ho et al. 2005). On the other hand, rate estimates based on recent divergences are less likely to be influenced by sequence saturation (a phenomenon that can lead to the underestimation of rates of molecular evolution; Arbogast et al 2002). Regardless of the exact rate of evolution applied to our data, the entire radiation of mockingbirds appears to have been rapid (as evidenced from the branching patterns of Figs. 2 and 3) and relatively recent (beginning within the last 0.6–5.5 million years), with the colonization of the Galapagos occurring shortly after the beginning of the mockingbird radiation.

Apart from inferences focusing on Galapagos mockingbirds, our results also suggest novel interpretations of relationships among South American mockingbirds. Our phylogeny strongly supports a closer relationship of *M. thenca*, a species endemic to central Chile (Fig. 1; Ridgely and Tudor 1989; Brewer 2001; Jaramillo 2003), to *M. patagonicus* of southern Argentina than to any other member of the genus (Figs. 2 and 3, node L). The mtDNA tree also strongly supports a close relationship between *M. saturninus* and *M. triurus* (Figs. 2 and 3, node M), species that are sympatric in northern Argentina (Fig. 1). *Mimus longicaudatus* of coastal Ecuador and northwestern Peru is apparently more distantly related to these South American species. These suggested relationships differ markedly from previous treatments, based on distribution, morphology, and plumage, that link *M. thenca* with *M. longicaudatus* and *M. patagonicus* with *M. saturninus* as allopatric sibling species pairs (Darwin 1845; Sibley and Monroe 1990). Further examination of these relationships, with analysis that includes *M. dorsalis* (a probable sister taxon to *M. triurus*; Sibley and Monroe 1990), is merited.

Ancestor of Galapagos Mockingbirds

Our results suggest that the geographically closest taxa upwind of Galapagos (the long-tailed mockingbird, *M. longicaudatus*, and the Chilean mockingbird, *M. thenca*) are not the Galapagos birds' closest relatives. In fact, none of our analyses suggested the above arrangement. Rather, Galapagos mockingbirds appear to be most closely related to a northern group of mockingbirds, including: the northern mockingbird (*M. polyglottos*) of North America (including Mexico) and the northern Caribbean; the tropical mockingbird (*M. gilvus*) of northern South America, parts of Central America, and Mexico, and the Lesser Antilles; the Bahama mockingbird (*M. gundlachii*) of the northern Caribbean; and the Socorro mockingbird (*M. graysoni*) endemic to the Pacific island of Socorro, Revillagigedos Archipelago, Mexico. Of these species, the combined analysis (Fig. 3) suggested that *M. gundlachii* is the closest living relative to Galapagos mockingbirds, although this relationship was not strongly supported. Our ND2 dataset (Fig. 2) placed *M. gundlachii* in a clade with *M. polyglottos*, *M. gilvus*, and *M. graysoni*. Additional sequence data for the latter species (for which only ND2 were available) may help clarify the position of *M. gundlachii* relative to other members of the *M. polyglottos*/*M. gilvus*/*M. graysoni* clade and to Galapagos mockingbirds.

Our mtDNA phylogenies (Figs. 2, 3) challenge prior hypotheses of mockingbird relationships on two levels. First, they do not support the frequently stated suggestion that *M. longicaudatus* is the closest relative of the Galapagos mockingbirds based on their geographic proximity, shared preference for xeric habitats, and phenotypic similarity including a long bill, presence of a pale nuchal collar, and dorsal streak-

ing (Gulledge 1975; Abbott and Abbott 1978; Steadman 1986). Although this possibility could not be statistically rejected within a likelihood framework (Table 1), a sister relationship between *M. longicaudatus* and *Nesomimus* was not recovered in any of our analyses. Second, previous analyses, based on morphometric, skeletal, and plumage data, have not indicated a close evolutionary relationship between *M. gundlachii* and the *M. polyglottos*/*gilvus* species pair. That *M. polyglottos* and *M. gilvus* are closely allied has never been questioned; these parapatrically distributed species hybridize in southern Mexico and have sometimes been considered conspecific (Davis and Miller 1960). Previous molecular analyses also support a closer relationship between *M. polyglottos* and *M. gilvus* than between either and *M. gundlachii* (Hunt et al. 2001). The finding of Barber et al. (2004) that *M. graysoni* is sister to *M. polyglottos*/*gilvus*, further supported in our analysis, strengthens the case for a close affinity among the northern forms.

The sister relationship between *M. graysoni* and *M. polyglottos*/*gilvus* (Barber et al. 2004; this study) suggests similar processes of colonization by mockingbird ancestors of Socorro, 1000 km west of the Mexican mainland, and of Galapagos. We propose that an ancestral mockingbird centered in Central America or the Caribbean displayed a tendency to wander widely and an ability to become established on oceanic islands. Such traits would have promoted dispersal to Caribbean and Pacific islands, including Galapagos, and a continental expansion throughout the Americas. Indeed, all of the northern species of mockingbirds (*M. gundlachii*, *M. polyglottos*, *M. gilvus*, and *M. graysoni*) have demonstrated an ability to colonize oceanic islands; several have also shown that they can become established on islands following introduction. For example, *M. polyglottos* became established in the Hawaiian Islands and on Socorro Island (in both instances following arrival assisted by human settlers; Jehl and Parkes 1983; Derrickson and Breitwisch 1992; Martínez-Gómez and Curry 1996), and *M. gilvus* has spread northward through the Lesser Antilles from Dominica to Antigua and inhabits remote islands elsewhere in the Caribbean (numerous islands north of Venezuela; Cozumel). The presence of the endemic large-billed *M. gilvus magnirostris* on San Andrés indicates both long-distance colonization and morphological divergence from typical *M. gilvus* after establishment. Furthermore, while not truly migratory, *M. polyglottos* tends to wander widely, with individuals being reported well beyond the normal range limits of the species (Derrickson and Breitwisch 1992), including cases where travel across large stretches of ocean was required (three independent sightings in Great Britain, and a single individual observed in 1933 on Isla Clarión in the Revillagigedos Archipelago, many years before human-assisted establishment of the same species on nearby Socorro; Swarth 1933; Jehl and Parkes 1983).

The Bahama mockingbird, *M. gundlachii*, appears to be more sedentary than either *M. polyglottos* or *M. gilvus*. This nonmigratory species is restricted to southern Jamaica and islands of the Bahama Bank, where it inhabits dry forest habitats (Raffaele et al. 1998); strays sometimes reach the Florida Keys (Sibley 2000). However, the present disjunct distribution of *M. gundlachii* suggests a wider distribution during the Pleistocene, when lower sea level and a drier climate produced greater expanses of lowland, xeric habitats throughout the Caribbean Basin (Lack 1976). If the range of an ancestor of *M. gundlachii*, or of a common ancestor between *M. gundlachii* and the *M. polyglottos*/*M. gilvus*/*M. graysoni* clade, extended into Central America or northern South America at about the same time as the closing of the Isthmus of Panama, it could have supplied a colonist to Galapagos consistent with arrival dates supported by our mtDNA analyses. Likewise, drier conditions of the past might have allowed an ancestral lineage of the northern clade to extend further to the south than any current member (i.e., *M. gilvus*) does presently, enhancing its ability to provide colonists to Galapagos.

While northern species of mockingbirds have characteristics that make them likely colonists, the same could also be true of remaining members of *Mimus*. However, the geographic configuration of South America offers few opportunities for tests, because few islands exist to which any of the continental mockingbirds could have dispersed. An endemic subspecies (*M. longicaudatus platensis*) of the long-tailed mockingbird on Isla de la Plata, 25 km off the west coast of Ecuador, probably represents one case of over-water dispersal (followed by selection for increased size and bill length in the island birds), because La Plata originated in the middle Pleistocene through emergence of an uplifted section of the continental shelf (Cantalamessa and Di Celma 2004).

Evidence of a close evolutionary and biogeographic connection between mockingbirds of Galapagos and those of the Caribbean (i.e., *M. gundlachii*) is noteworthy given evidence of a similar connection suggested for Darwin's finches, which appear to be most closely related to grassquits of the genus *Tiaris* and their allies, a group with a center of radiation in the Caribbean (Baptista and Trail 1988; Sato et al. 2001; Burns et al. 2002). Several other organisms in Galapagos (e.g., flamingos, *Phoenicopterus ruber*; isopods, *Nesophiloscia*; snakes, *Antillophis*; moths, *Oxydia*,) similarly show phylogeographic affinities with populations in the Caribbean (Thornton 1971; Grehan 2001).

Diversification among Mockingbirds in Galapagos

We identified four lineages of mockingbirds in Galapagos that could be considered distinct at the level of species, based on reciprocal monophyly and estimated levels of mtDNA sequence divergence (Figs. 2, 3). However, these four lineages do not correspond to the four phenotypically defined species (Figs. 1–3; Swarth 1931). One of the four mtDNA lineages (defined by node I) contains birds from Genovesa, San Cristóbal, and Española. Birds from these islands share closely related mtDNA haplotypes ($<0.6\%$ corrected sequence divergence in the ND2 dataset; $<1.0\%$ in combined dataset), yet the three populations are phenotypically distinct and have been considered different species (*N. parvulus*, *N. melanotis*, and *N. macdonaldi*, respectively). A close relationship between *N. melanotis* and *N. macdonaldi* has been suggested previously based on shared plumage characteristics, including in particular a band of dark feathers across the breast of adults that is absent in *N. parvulus* on Genovesa and elsewhere (Swarth 1931; Grant 1999). A close link between the endemic subspecies of mockingbird from Gen-

ovesa, *N. parvulus bauri,* with *N. melanotis* and *N. macdonaldi* is therefore surprising.

The close mtDNA relationship observed between the Genovesa mockingbirds and *N. macdonaldi* and *N. melanotis* (Figs. 2, 3) seems to imply extensive convergence of plumage and other traits of mockingbirds on Genovesa with those of *N. parvulus* on all other islands. Phenotypic convergence (especially in plumage traits) is well documented in other passerines such as orioles (*Icterus* spp.; Allen and Omland 2003), wagtails (*Motacilla* spp.; Pavlova et al. 2003), and woodwarblers (*Phaeothlypis* spp.; Lovette 2005). The discrepancies noted above between the traditional taxonomic arrangement of southern South American *Mimus* and relationships inferred from our mtDNA data suggest that it may also be common in mimids. However, in the case of the Genovesa mockingbirds, the apparent mismatch between mtDNA and phenotypic affinities could also reflect plumage symplesiomorphy; under this hypothesis, the lack of a breast band in *N. parvulus* on Genovesa and elsewhere is the ancestral condition, and the presence of the breast band in the San Cristóbal and Española populations is a recently derived trait. Factors other than plumage convergence or symplesiomorphy, such as differential introgression of mitochondrial and nuclear genes, might also be responsible for this pattern. For example, nuclear loci affecting plumage might have entered the Genovesa population via male-mediated dispersal from central or western populations without a corresponding influx of maternal mtDNA. However, this seems unlikely given that female birds typically disperse farther, on average, than males do (Greenwood and Harvey 1982), a contrast that is reinforced in *Nesomimus* by their cooperative breeding (males act as helpers and are typically more sedentary than females; Curry and Grant 1990). Nonetheless, examples exist of both males and females of island species breeding on islands other than their natal site (e.g., Grant et al. 2001), and there is clear evidence for both hybridization (Grant et al. 2005) and contrasting nuclear and mtDNA phylogenies in Darwin's finches (Petren et al. 1999, 2005; Sato et al. 2001). Finally, it is possible that ancestral mtDNA lineages in the Genovesa population were replaced by a selective sweep after introgression of a lineage arriving with a dispersing female from San Cristóbal, such that the nuclear genome of the Genovesa birds is similar to that of other *N. parvulus* populations. Perhaps, multilocus data (i.e., from single nucleotide polymorphisms, microsatellites, amplified fragment length polymorphisms) from the nuclear genome could help to rule out such possibilities for mockingbirds and to test interpretations based on the mtDNA tree.

Based on the mtDNA data, populations of *N. parvulus* from Isabela are much more divergent from other populations of *N. parvulus* than previously recognized (sums of branch lengths $\geq$0.049 substitutions per site based on ND2 data, $\geq$0.045 substitutions per site based on combined data; Figs. 2, 3). Swarth (1931) assigned mockingbirds from Isabela and Santa Cruz to *N. p. parvulus* (a subspecies that also inhabits Fernandina to the west and Seymour Norte to the east), whereas birds from Rábida, Santiago, and Marchena have been assigned to *N. p. bindloei*. The mtDNA distinctiveness of the Isabela birds could reflect early colonization of that large island from one of the eastern islands, prior to diversification throughout the rest of the range of *N. parvulus*. Among the remaining populations of *N. parvulus*, our data recovered some additional structure matching traditional treatments: mockingbirds from Rábida, Santiago, and Marchena had similar haplotypes, with the exception of the single bird from Rábida; the latter may reflect downwind immigration from Santa Cruz.

The mtDNA data strongly support previous classifications in recognizing the Floreana mockingbird (*N. trifasciatus*) as a distinct evolutionary lineage (Figs. 2, 3). This taxon is one of the rarest birds in the world; it inhabited the large island of Floreana until a few decades after the *Beagle* visit (Curry 1985), but now persists on only two satellite islets (Champion and Gardner-by-Floreana), where it numbers fewer than 200 individuals and is at high risk of extinction (Grant et al. 2000). These mockingbirds display several unique phenotypic traits, including predominantly brown dorsal plumage, dark brown patches on the sides of the upper breast, and white auricular areas (Gould 1837; Darwin 1841; Swarth 1931). The seal-brown iris color of this mockingbird also differs from the yellowish irides of all other Galapagos mockingbirds (Rothschild and Hartert 1899). The sister relationship between *N. trifasciatus* and most populations of *N. parvulus* supported by our results has not been suggested previously.

The mtDNA data suggest that diversification of mockingbirds within Galapagos proceeded primarily along two independent tracks, both generally south or southeast to north or northwest. An early split within *Nesomimus* (Figs. 2, 3) separated two clades (nodes F and I), each with southern and northern populations. The clade defined by node F contains *N. trifasciatus* and most of the populations corresponding to *N. parvulus*. The earliest split within this clade appears to have divided *N. trifasciatus* (the southeastern most population in this clade) from the rest, consistent with a southern origin of the extant taxa and later dispersal to the north and northwest. The clade defined by node I contains populations of *N. macdonaldi* from Española, *N. melanotis* from San Cristóbal, and the population of *N. parvulus* from Genovesa that lie on a south–north axis. The close relationship of the haplotypes from these three islands suggests that the more recent diversification within this clade may have proceeded in a south–north direction. In both cases, the postulated directionality of colonization matches that of prevailing winds. The asymmetry of aerially formed palagonitic volcanic cones in Galapagos, with heavier deposits on the northern and northwestern slopes than on the southern and southeastern slopes, indicates that the prevailing winds have come consistently from the south-southeast for at least 1 million years (Geist 1992); present-day winds come mostly from the south-southeast also (Colinvaux 1984). The distribution of the large cactus ground finch (*Geospiza conirostris*; Grant 1999) and mtDNA sequence analyses of giant tortoises (*Geochelone nigra*; Caccone et al. 1999, 2002) also show phylogeographic connections between northern populations (i.e., Pinta, Marchena, or Genovesa) and those of Española. The position of these islands along a general southeast–northwest axis suggests that prevailing wind patterns, and associated ocean currents in the case of the tortoises, have influenced diversification of several vertebrate groups in Galapagos. This inter-

pretation is also consistent with the geological evidence of greater age of the southeastern islands (Geist 1996).

Adaptive Radiation of Galapagos Mockingbirds

Along with 14 species of mockingbird (*Mimus* and *Nesomimus*), the Mimidae also includes 10 typical thrashers (*Toxostoma* spp.), the sage thrasher (*Oreoscoptes*), two blue mockingbirds (*Melanotis* spp.), two catbirds (*Dumetella* and *Melanoptila*), and five Caribbean endemics (two *Margarops* thrashers, two *Cinclocerthia* tremblers, and *Ramphocinclus*, the white-breasted thrasher). Morphological variation in the family as a whole is considerable, involving body size, bill length, bill curvature, leg length, and plumage color, especially among genera (Gulledge 1975; Brewer 2001). Among *Mimus* mockingbirds, morphological evolution has been comparatively limited. Plumage features that vary in this genus include presence of dorsal streaking, presence of spots on the ventral flanks, presence of a malar streak, extent of white in the outer tail feathers, and prominence of white wing bars (Gulledge 1975; Brewer 2001).

The mockingbirds of Galapagos exhibit variation in size and shape, plumage color and pattern, and behavior that matches or exceeds variation among all other mockingbirds (Bowman and Carter 1971; Gulledge 1975; Curry and Grant 1990; Brewer 2001). Thus, branching evolution in Galapagos mockingbirds has likely been associated with adaptive radiation. However, diversification has not proceeded to the point where morphologically distinctive mockingbird species live sympatrically in Galapagos, as in Darwin's finches (Grant 1999). The natural history of mockingbirds on islands, including especially their omnivorous foraging behavior, may constrain adaptive radiation by limiting the number of species that can occur together. Relative to variation in the Mimidae as a whole, mockingbirds have moderately sized and unspecialized bills, albeit lengthened in some Galapagos populations (presumably through selection associated with terrestrial habits and digging behavior; Bowman and Carter 1971).

Most regions of the New World are inhabited by only a single representative of *Mimus* (Brewer 2001). In some areas, two *Mimus* species exist sympatrically (Fig. 1B; also the Bahamas, where *M. polyglottos* and *M. gundlachii* overlap); in these locations, the species usually segregate to some degree by habitat preference, rather than morphological divergence. Three members of *Mimus* overlap only in small regions of southern South America: *M. triurus*, *M. saturninus*, and *M. dorsalis* in Bolivia and *M. triurus*, *M. saturninus*, and *M. patagonicus* in northern Argentina. In both areas, however, one species is migratory, so only two congeners are sympatric for much of the year.

In the family as a whole, morphological diversification has progressed further than among the mockingbirds alone, with up to seven species overlapping in some regions (Brewer 2001). Large and functionally significant differences in bill morphology among the typical thrashers (Engels 1940; Zink et al. 1999) and among Caribbean lineages (Hunt et al. 2001) may facilitate this sympatry. Only a few pairs of forms within *Nesomimus* differ morphologically to a comparable degree. Therefore, the potential for further adaptive radiation in Galapagos through repeated cycles of recolonization, reinforcement, and divergence (Lack 1947; Grant 2001; Grant and Grant 2002; Ricklefs 2004) is limited: the process likely would require the coming together of particular combinations (e.g., large, long-billed, and terrestrial *N. macdonaldi* and small, short-billed, and arboreal forms of *N. parvulus*) on islands with sufficient habitat diversity to support both.

The preceding conclusion largely parallels current understanding of the relative lack of diversification among Hawaiian thrushes (Turdidae: *Myadestes* spp.) when compared to the extensive adaptive radiation of the same archipelago's endemic honeycreepers (Fringillidae: Drepanidinae) especially with respect to bill morphology (Lovette et al. 2002; Pratt 2005). For these Hawaiian taxa, estimated dates of colonization are similar, so contrasting degrees of diversification cannot be attributed to evolution over different amounts of time; instead, limited differentiation among the thrushes is associated with a diet high in insects, soft fruits, and flower products, whereas traits associated with the granivorous ecology of honeycreeper cardueline relatives appears to have predisposed the latter group to rapid and extensive diversification (Lovette et al. 2002; Pratt 2005). For Galapagos birds, a corresponding comparison is between the mockingbirds and Darwin's finches. Morphological diversification among the latter is pronounced (Grant 1999) and parallels extensive variation in bill size and shape among mainland and Caribbean relatives (Burns et al. 2002). Comparatively limited differentiation among Galapagos mockingbirds probably cannot be attributed to time, because available evidence suggests a date of arrival in Galapagos similar to that for the finches (Vincek et al. 1997; Grant 1999; Petren et al. 2005; this study). While lagging Darwin's finches in the extent of their adaptive radiation, Galapagos mockingbirds nonetheless have diversified to a relatively greater degree than have the Hawaiian thrushes, such that morphological variation in *Nesomimus* encompasses more variation than among *Mimus* species and a relatively large proportion of the range exhibited by all other mimids (Gulledge 1975; Abbott and Abbott 1978; Hunt et al. 2001). However, further radiation of mockingbirds in Galapagos would require coexistence of different species on existing islands (or, over the longer term, appearance of new islands for novel colonizations). Coexistence is impeded in Galapagos mockingbirds and facilitated in Darwin's finches by the degree of divergence in allopatry (low in omnivorous mockingbirds, high in granivorous finches), providing a striking parallel to the conclusions drawn for the Hawaiian bird community.

Acknowledgments

We thank the Galapagos National Park Service and the Machalilla National Park Service for permission to work in those parks, and the Charles Darwin Research Station and TAME airlines for logistical support; J. Hunt, E. Bermingham, B. R. Barber, J. E. Martínez-Gómez, and A. Townsend Peterson for providing sequences; and the following museums for providing tissue samples: the LSU Museum of Natural Sciences, Baton Rouge; the Museo Nacional Historia Natural de Chile (and M. Marin), Santiago; and the Marjorie Barrick Museum of Natural History, Las Vegas. We thank K. Kron, Wake Forest University, and S. Birks, the Burke

Museum, University of Washington, for laboratory support, and A. Jaramillo for notes regarding Chilean distributions. We thank I. Lovette (Cornell University) and E. Bermingham (Smithsonian Tropical Research Institute) for providing sequence information and critical laboratory advice. We thank A. J. Schwandt-Arbogast for assistance in preparing figures, and especially M. Sorenson for extensive help with phylogenetic analyses and valuable comments on the text. The cover artwork was drawn by H. Douglas Pratt, Curator of Birds, North Carolina Museum of Natural Sciences, from photographs taken by the artist and David A. Wiedenfeld, formerly Director of Vertebrate Ecology at the Charles Darwin Institute in Galapagos. Financial support was provided by grants to BSA from the American Museum of Natural History, Sigma Xi, and the Humboldt State University Foundation, and by US National Science Foundation award 98-06606 to DJA, and Wake Forest University. DJA and BSA conceived the study, and DJA, PTB, GS, PRG, and BRG collected the Galapagos samples. BSA located continental samples and, together with SVD, conducted sequencing and phylogenetic reconstruction analyses. DJA, BSA, and RLC were the principal writers of the paper.

Literature Cited

Abbott, I., and L. K. Abbott. 1978. Multivariate study of morphometric variation in Galapagos and Ecuadorean mockingbirds. Condor 80:302–308.

Allen, E. S., and K. E. Omland. 2003. Novel intron phylogeny supports plumage convergence in orioles (*Icterus*). Auk 120: 961–969.

Arbogast, B. S., S. V. Edwards, J. Wakely, P. Beerli, and J. B. Slowinski. 2002. Estimating divergence times from molecular data on phylogenetic and population genetic timescales. Annu. Rev. Ecol. Syst. 33:707–740.

Banks, R. C., C. Cicero, J. L. Dunn, A. W. Kratter, P. C. Rasmussen, J. V. Remsen Jr., J. D. Rising, and D. F. Stotz. 2005. Forty-sixth supplement to the American Ornithologists' Union checklist of North American birds. Auk 122:1026–1031.

Baptista, L. F., and P. W. Trail. 1988. On the origins of Darwin's finches. Auk 105:663–671.

Barber, B. R., J. E. Martínez-Gómez, and A. T. Peterson. 2004. Systematic position of the Socorro mockingbird *Mimodes graysoni*. J. Avian Biol. 35:195–198.

Bowman, R. I., and A. Carter. 1971. Egg-pecking behavior in Galapagos mockingbirds. Living Bird 10:243–270.

Brattstrom, B. 1990. Biogeography of the Islas Revillagigedo, Mexico. J. Biogeogr. 17:177–183.

Brewer, D. 2001. Wrens, dippers, and thrashers. Yale Univ. Press, New Haven, CT.

Burns, K. J., S. J. Hackett, and N. J. Klein. 2002. Phylogenetic relationships and morphological diversity in Darwin's finches and their relatives. Evolution 56:1240–1252.

Caccone, A., J. P. Gibbs, V. Ketmaier, E. Suatoni, and J. R. Powell. 1999. Origin and evolutionary relationships of giant Galapagos tortoises. Proc. Natl. Acad. Sci. USA 96:13223–13228.

Caccone, A., G. Gentile, J. P. Gibbs, T. H. Fritts, S. H. L., J. Betts, and J. R. Powell. 2002. Phylogeography and history of giant Galapagos tortoises. Evolution 56:2052–2066.

Cantalamessa, G., and C. Di Celma. 2004. Origin and chronology of Pleistocene marine terraces of the Isla de la Plata and of flat, gently dipping surfaces of the southern coast of Cabo San Lorenzo (Manabı, Ecuador). J. S. Am. Earth Sci. 16:633–648.

Castoe, T. A., T. M. Doan, and C. L. Parkinson. 2004. Data partitions and complex models in Bayesian analysis: the phylogeny of *Gymnophthalmid* lizards. Syst. Biol. 53:448–469.

Christie, D. M., R. A. Duncan, A. R. McBirney, M. A. Richards, W. M. White, K. S. Harpp, and C. G. Fox. 1992. Drowned islands downstream from the Galapagos hotspot imply extended speciation times. Nature 355:246–248.

Colinvaux, P. A. 1984. The Galapagos climate: past and present. Pp. 55–69 *in* R. Perry, ed. Galapagos (Key Environments). Pergamon, Oxford, U.K.

Curry, R. L. 1985. Whatever happened to the Floreana mockingbird? Noticias de Galapagos 43:13–15.

Curry, R. L., and P. R. Grant. 1990. Galapagos mockingbirds: territorial cooperative breeding in a climatically variable environment. Pp. 290–331 *in* P. B. Stacey and W. D. Koenig, eds. Cooperative breeding in birds: long-term studies of ecology and behavior. Cambridge Univ. Press, Cambridge, U.K.

Darwin, C. R. 1836 [1963]. Darwin's ornithological notes (ed. by N. Barlow). Bull. Brit. Mus. Nat. Hist. Ser. 2:201–278.

———. 1841. Zoology of the Voyage of *H. M. S. Beagle*, under the command of Captain FitzRoy, R. N., during the years 1832–1836. Part III: Birds. Smith Elder, London.

———. 1845. Journal of researches into the natural history and geology of the countries visited during the voyage of H.M.S. Beagle round the world under the command of Capt. FitzRoy, R.N. John Murray, London.

———. 1859. On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. John Murray, London.

Davis, J., and A. H. Miller. 1960. Family Mimidae. Pp. 440–458 *in* E. Mayr and J. C. Greenway, eds. Check-list of birds of the world. Museum of Comparative Zoology, Cambridge, U.K.

Derrickson, K. C., and R. Breitwisch. 1992. Northern mockingbird. No. 7 *in* A. Poole, P. Stettenheim, and F. Gill, eds. The birds of North America. The Academy of Natural Sciences, Philadelphia, PA.

Drovetski, S. V. 2003. Plio-Pleistocene climatic oscillations, Holarctic biogeography and speciation in an avian subfamily. J. Biogeogr. 30:1173–1181.

Drovetski, S. V., R. M. Zink, I. V. Fadeev, E. V. Nesterov, E. A. Koblik, Y. A. Red'kin, and S. Rohwer. 2004. Mitochondrial phylogeny of *Locustella* and related genera. J. Avian Biol. 35: 105–110.

Engels, W. L. 1940. Structural adaptations in thrashers (Mimidae: genus *Toxostoma*) with comments on interspecific relationships. Univ. Calif. Pub. Zool. 43:341–400.

Felsenstein, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39:783–791.

Fleischer, R. C., C. E. McIntosh, and C. L. Tarr. 1998. Evolution on a volcanic conveyor belt: using phylogeographic reconstructions and K-Ar-based ages of the Hawaiian Islands to estimate molecular evolutionary rates. Mol. Ecol. 7:533–545.

Garcia-Moreno, J. 2004. Is there a universal mtDNA clock for birds? J. Avian Biol. 35:465–468.

Geist, D. J. 1992. Pyroclastic rocks as paleoclimate indicators, Galapagos Islands. Pp. 18 *in* R. P. Turco, ed. Abstracts and Program, Chapman Conference on Climate, Volcanism and Global Change. American Geophysical Union, Washington, DC.

———. 1996. On the emergence and submergence of the Galapagos Islands. Noticias de Galapagos 56:5–9.

Goldman, N. 1993. Statistical tests of models of DNA substitution. J. Mol. Evol. 36:182–198.

Gould, J. 1837. Two new species of the genus *Sterna*, a species of cormorant, and three species of the genus *Orpheus*, from the Galapagos, in the collection of Mr. Darwin. Proc. Zool. Soc. Lond. 5:26–27.

Grant, P. R. 1999. Ecology and evolution of Darwin's finches. 2nd ed. Princeton Univ. Press, Princeton, NJ.

———. 2001. Reconstructing the evolution of birds on islands: 100 years of research. Oikos 92:385–403.

Grant, P. R., and B. R. Grant. 2002. Adaptive radiation of Darwin's finches. Am. Sci. 90:130–139.

Grant, P. R., R. L. Curry, and B. R. Grant. 2000. A remnant population of the Floreana mockingbird on Champion island, Galapagos. Biol. Conserv. 92:285–290.

Grant, P. R., B. R. Grant, and K. Petren. 2001. A population founded by a single pair of individuals: establishment, expansion, and evolution. Genetica 112/113:359–382.

———. 2005. Hybridization in the recent past. Am. Nat. 166:56–67.
Gray, G. R. 1841. Birds. Part III of Zoology of the Voyage of *H. M. S. Beagle*, under the command of Captain FitzRoy, R. N., during the years 1832–1836. Smith Elder, London.
Greenwood, P. J., and P. H. Harvey. 1982. The natal and breeding dispersal of birds. Annu. Rev. Ecol. Syst. 13:1–21.
Grehan, J. 2001. Biogeography and evolution of the Galapagos: integration of the biological and geological evidence. Biol. J. Linn. Soc. 74:267–287.
Gulledge, J. L. 1975. A study of the phenetic and phylogenetic relationships among the mockingbirds, thrashers and their allies. Ph.D. diss., City University of New York.
Ho, S. Y. W., M. J. Phillips, A. Cooper, and A. J. Drummond. 2005. Time dependency of molecular rate estimates and systematic overestimation of recent divergence times. Mol. Biol. Evol. 22: 1561–1568.
Huelsenbeck, J. P., and B. Rannala. 1997. Phylogenetic methods come of age: testing hypotheses in an evolutionary context. Science 276:227–232.
Huelsenbeck, J. P., and F. Ronquist. 2001. MRBAYES: Bayesian inference of phylogenetic trees. Bioinformatics 17:754–755.
Huelsenbeck, J. P., F. Ronquist, R. Nielsen, and P. Bollback. 2001. Bayesian inference of phylogeny and its impact on evolutionary biology. Science 294:2310–2314.
Hunt, J. S., E. Bermingham, and R. E. Ricklefs. 2001. The molecular systematics and biogeography of Antillean thrashers, tremblers, and mockingbirds (Aves: Mimidae). Auk 118:35–55.
Jaramillo, A. 2003. Birds of Chile. Princeton Univ. Press, Princeton, NJ.
Jehl, J. R., Jr.,and K. C. Parkes. 1983. ''Replacements'' of landbird species on Socorro Island, Mexico. Auk 100:551–559.
Lack, D. 1947. Darwin's finches. Cambridge Univ. Press, Cambridge, U.K.
———. 1976. Island biology, illustrated by the land birds of Jamaica. Univ. of California Press, Berkeley.
Lovette, I. J. 2004. Mitochondrial dating and mixed support for the ''2% rule'' in birds. Auk 121:1–6.
———. 2005. Molecular phylogeny and plumage signal evolution in a trans Andean and circum Amazonian avian species complex. Mol. Phylogenet. Evol. 32:512–523.
Lovette, I. J., E. Bermingham, and R. E. Ricklefs. 2002. Clade-specific morphological diversification and adaptive radiation in Hawaiian songbirds. Proc. R. Soc. B 269:37–42.
Martínez-Gómez, J. E., and R. L. Curry. 1995. First description of the nest and eggs of the Socorro mockingbird. Wilson. Bull. 107:551–555.
———. 1996. Conservation status of the Socorro mockingbird *Mimodes graysoni* in 1993–94. Bird Conserv. Int. 6:271–281.
McCracken, K. G., and M. D. Sorenson. 2005. Is homoplasy or lineage sorting the source of incongruent mtDNA and nuclear gene trees in the stiff-tailed ducks (*Nomonyx-Oxyura*)? Syst. Biol. 54:33–55.
Palumbi, S. R. 1996. Nucleic acids II: the polymerase chain reaction. Pp. 205–247 *in* D. M. Hillis, C. Moritz, and B. K. Mable, eds. Molecular Systematics. Sinauer Associates, Sunderland, MA.
Pavlova, A., R. M. Zink, S. V. Drovetski, Y. Red'kin, and S. Rohwer. 2003. Phylogeographic patterns in *Motacilla flava* and *Motacilla citreola*: species limits and population history. Auk 120: 744–758.
Petren, K., B. R. Grant, and P. R. Grant. 1999. A phylogeny of Darwin's finches based on microsatellite DNA length variation. Proc. R. Soc. B 266:321–330.
Petren, K., P. R. Grant, B. R. Grant, and L. F. Keller. 2005. Comparative landscape genetics and the adaptive radiation of Darwin's finches: the role of peripheral isolation. Mol. Ecol. 14: 2943–2957.
Posada, D., and T. R. Buckley. 2004. Model selection and model averaging in phylogenetics: advantages of the Akaike information criterion and Bayesian approaches over likelihood ratio tests. Syst. Biol. 53:793–808.
Posada, D., and K. A. Crandall. 1998. MODELTEST: Testing the model of DNA substitution. Bioinformatics 14:817–818.
Pratt, H. D. 2005. The Hawaiian honeycreepers: Drepanidae. Oxford Univ. Press, New York.
Raffaele, H., J. Wiley, O. Garrido, A. Keith, and J. Raffaele. 1998. A guide to the birds of the West Indies. Princeton Univ. Press, Princeton, NJ.
Rassmann, K. 1997. Evolutionary age of the Galapagos iguanas predates the age of the present Galapagos islands. Mol. Phylogenet. Evol. 7:158–172.
Ricklefs, R. E. 2004. Cladogenesis and morphological diversification in passerine birds. Nature 430:338–341.
Ridgely, R. S., and G. Tudor. 1989. Birds of South America. Vol. I. The oscine passerines. Univ. of Texas Press, Austin.
Ridgway, R. 1890. Scientific results of explorations by the U.S. Fish Commission steamer Albatross, No. 1. Birds collected on the Galapagos Islands in 1888. Proc. US Natl. Mus. 12:101–128.
Rodriguez, F., J. L. Oliver, A. Marin, and J. Medina. 1990. The general stochastic model of nucleotide substitution. J. Theor. Biol. 142:485–501.
Rothschild, W., and E. Hartert. 1899. A review of the ornithology of the Galapagos Islands, with notes on the Webster-Harris expedition. Nov. Zool. 6:85–205.
Sato, A., H. Tichy, C. O'hUigin, P. R. Grant, B. R. Grant, and J. Klein. 2001. On the origin of Darwin's finches. Mol. Biol. Evol. 18:299–311.
Shimodaira, H. 2002. An approximately unbiased test of phylogenetic tree selection. Syst. Biology 51:492–508.
Sibley, C. G., and J. E. Ahlquist. 1984. The relationships of the starlings (Sturnidae: Sturnini) and the mockingbirds (Sturnidae: Mimini). Auk 101:230–243.
Sibley, C. G., and B. L. Monroe Jr. 1990. Distribution and taxonomy of birds of the world. Yale Univ. Press, New Haven, CT.
Sibley, D. 2000. The Sibley guide to birds. Knopf, New York.
Sorenson, M. D., and T. W. Quinn. 1998. Numts: a challenge for avian systematics and population biology. Auk 115:214–221.
Steadman, D. W. 1986. Holocene vertebrate fossils from Isla Floreana, Galapagos. Smiths. Contrib. Zool. 413:1–103.
Sulloway, F. J. 1982. Darwin's conversion: the *Beagle* voyage and its aftermath. J. Hist. Biol. 15:325–396.
Swarth, H. S. 1931. The avifauna of the Galapagos Islands. Occ. Pap. Cal. Acad. Sci. 18:1–299.
———. 1933. Off-shore migrants over the Pacific. Condor 35: 39–41.
Swofford, D. 1998. PAUP*: phylogenetic analysis using parsimony (* and other methods). Version 4.0b10. Sinauer Associates, Sunderland, MA.
Thornton, I. 1971. Darwin's islands: a natural history of the Galapagos. Natural History Press, Garden City, NY.
Vincek, V., C. O'hUigin, Y. Satta, N. Takahata, P. T. Boag, P. R. Grant, B. R. Grant, and J. Klein. 1997. How large was the founding population of Darwin's finches? Proc. R. Soc. B 264: 111–118.
Warren, B. H., E. B. Bermingham, R. C. K. Bowie, R. P. Prys-Jones, and C. Thébaud. 2003. Molecular phylogeography reveals island colonization history and diversification of western Indian Ocean sunbirds (Nectarinia: Nectariniidae). Mol. Phylogenet. Evol. 29:67–85.
Zink, R. M., D. L. Dittman, J. Klicka, and R. C. Blackwell-Rago. 1999. Evolutionary patterns of morphometrics, allozymes, and mitochondrial DNA in thrashers (genus *Toxostoma*). Auk 116: 1021–103.

Corresponding Editor: M. Sorenson