The Auk 118(4):874–887, 2001

A MOLECULAR PHYLOGENY OF THE DOVE GENERA *STREPTOPELIA* AND *COLUMBA*

KEVIN P. JOHNSON,[1,3,5] SELVINO DE KORT,[2] KAREN DINWOODEY,[3] A. C. MATEMAN,[4] CAREL TEN CATE,[2] C. M. LESSELLS,[4] AND DALE H. CLAYTON[3]

[1]*Illinois Natural History Survey, Champaign, Illinois 61820, USA;*
[2]*Institute of Evolutionary and Ecological Sciences, Leiden University, Leiden, The Netherlands;*
[3]*Department of Biology, University of Utah, Salt Lake City, Utah 84112, USA; and*
[4]*Netherlands Institute of Ecology, Heteren, The Netherlands*

ABSTRACT.—Evolutionary history of the dove genus *Streptopelia* has not been examined with rigorous phylogenetic methods. We present a study of phylogenetic relationships of *Streptopelia* based on over 3,600 base pairs of nuclear and mitochondrial gene sequences. To test for monophyly of *Streptopelia,* we used several other columbiform taxa, including *Columba* (Old and New World), *Macropygia, Reinwardtoena,* and the enigmatic Pink Pigeon (*Nesoenas mayeri*). On the basis of our analyses, *Streptopelia* (as currently defined) is not monophyletic; *Nesoenas mayeri* is the sister species to *S. picturata,* resulting in paraphyly of *Streptopelia.* Three main clades of *Streptopelia* are identified: (1) *S. chinensis* plus *S. senegalensis,* (2) *S. picturata* plus *Nesoenas mayeri,* and (3) all other species of *Streptopelia.* It is unclear whether those clades form a monophyletic group to the exclusion of Old World *Columba,* but several analyses produce that result. Species of Old World *Columba* are closely related to *Streptopelia,* with species of New World *Columba* clustering outside that group. Taxonomic changes suggested by our results include merging *Nesoenas* with *Streptopelia* and changing the generic name for New World *Columba* species to *Patagioenas.* Vocal similarities between *S. picturata* and *N. mayeri* are striking, given the general diversity of vocalizations in other species. *Received 20 September 2000, accepted 27 March 2001.*

SPECIES OF DOVES in the genus *Streptopelia* are important model systems for studies of physiology (Walker et al. 1983, Janik and Buntin 1985, Cheng 1986, Ramos and Silver 1992, ten Cate et al. 1993, Lea et al. 1995, Georgiou et al. 1995) and behavior (Lade and Thorpe 1964, Zenone et al. 1979, Cheng et al. 1981, Cheng 1992, Slabbekoorn and ten Cate 1998, Slabbekoorn et al. 1999). The 16 species of *Streptopelia* historically had an African and Eurasian distribution, but some species have been introduced to the New World and Australia. Several species of *Streptopelia* seem highly adaptable to human-altered environments and have expanded their ranges considerably (e.g. *S. decaocto*; Bijlsma 1988, Hengeveld and van den Bosch 1991, Hengeveld 1993, Kasparek 1996). Other species have remarkably localized distributions (e.g. *S. hypopyrrha*). An understanding of historical relationships would provide an important context for work on physiology, behavior, and biogeography of this genus.

Even though species of *Streptopelia* have been well studied in many respects, phylogenetic relationships within the genus are uncertain. Nowak (1975) examined morphological characteristics within *Streptopelia* and produced a classification that grouped species into several subgenera. However, he did not produce an explicit phylogenetic tree. Goodwin (1983) depicts a tree of ''presumed relationships'' among species of *Streptopelia,* and that tree differs from Nowak's classification, but Goodwin's tree is not based on a rigorous phylogenetic analysis. Johnson and Clayton (2000a) showed that species of Old World *Columba* form the sister group to *Streptopelia,* with species of New World *Columba* being more distantly related to both groups. However, the authors included only single representatives of *Streptopelia* and Old World *Columba* in their study. The goal of the present study is to assess monophyly of the genus *Streptopelia* and identify relationships within the genus. We also use this study to test Nowak's (1975) classification and Goodwin's (1983) proposed relationships of species within the genus. We include several representatives of New and Old World *Columba,* as well as the endangered, enigmatic Pink Pigeon (*Nesoenas mayeri*) of Mauritius. We also include represen-

[5] E-mail: kjohnson@inhs.uiuc.edu

tatives of *Macropygia* and *Reinwardtoena,* which together with *Columba* and *Streptopelia* form a distinct clade within Columbiformes (Johnson and Clayton 2000a). The entire phylogenetic analysis is rooted on *Geotrygon, Leptotila,* and *Zenaida,* which together consitute the sister group to the *Columba/Streptopelia/Macropygia* clade (Johnson and Clayton 2000a).

For our current study, we use sequences of both mitochondrial and nuclear genes to construct a phylogeny for *Streptopelia, Columba,* and related taxa. We compare relative usefulness of nuclear and mitochondrial genes for phylogenetic resolution at that level. Using the phylogeny we recommend some changes in taxonomic classification, and compare phylogeny to vocal similarities and diversity in *Streptopelia*.

Methods

Sequencing.—We obtained samples of muscle tissues, feathers, or blood from representatives of 14 of the 16 described species of *Streptopelia* (Table 1). We also sampled members of New and Old World *Columba, Macropygia, Reinwardtoena, Nesoenas, Geotrygon, Leptotila,* and *Zenaida.* We extracted DNA from those samples using a Qiagen Tissue Kit (Valencia, California) with the manufacturer's protocols. For feather samples (~2 mm of the tip of the shaft) we also added 30 μL of 10% DTT to the digestion buffer. Using PCR we amplified portions of three mitochondrial genes: cytochrome-*b* (cyt *b*), cytochrome oxidase I (COI), and NADH dehydrogenase subunit 2 (ND2). We also amplified the nuclear gene β-fibrinogen intron 7 (FIB7). Table 2 lists primers used for those reactions. Protocols for reactions follow Johnson and Clayton (2000a).

Direct sequencing of PCR products and determination of sequences was performed as described by Johnson and Clayton (2000a). We aligned sequences across species using Sequencher (GeneCodes, Madison, Wisconsin). The three mitochondrial genes totaled 2,520 bp and the nuclear intron included 1,150 aligned base pairs (GenBank accession numbers in Table 1). In the case of mitochondrial protein coding genes, alignment was straightforward. We noted several insertion–deletion (indel) events in the nuclear intron, but for those taxa, divergences were so low that manual alignment was straightforward. Gaps were treated as missing data in phylogenetic analyses. For *Streptopelia tranquebarica* and *S. bitorquata,* only partial FIB7 sequences were available because of amplification failures. Thus, we repeated analyses involving the nuclear intron both with and without those species.

For each species, we included single representatives for all sequences. However, to assess the level of individual variation within each species, we sequenced (when available) multiple individuals for the COI gene (see Table 3 for list of those multiple individuals and GenBank accession numbers). Mitochondrial genes tend to evolve at similar rates at low levels of sequence divergence in birds (Johnson and Sorenson 1998, Johnson and Lanyon 1999) and more specifically for cyt *b,* ND2, and COI in Columbiformes (Johnson and Clayton 2000b). Mitochondrial divergences are also highly correlated with divergences in FIB7 in Columbiformes (Johnson and Clayton 2000a, b). Thus, within-species variation in COI sequences is likely to be representative of other mitochondrial and nuclear genes. In general, individuals of the same species differed only slightly, if at all, in those COI sequences (see below), so single exemplar individuals are reasonable for the multigene data set.

Where possible, we used tissue or feather samples to avoid risk of nuclear copies of mitochondrial genes (Sorenson and Quinn 1998). In cases where blood samples were used, we verified sequences for COI using multiple individuals. We also checked chromatograms for signs of double peaks, as well as checking for indels and stop codons. By sequencing several mitochondrial genes, we were also able to test for any incongruence in phylogenies resulting from those gene regions, which would likely occur if some of the sequences represented nuclear copies. We found no evidence of nuclear copies in our sequences.

Phylogenetic analysis.—Relative rates of substitution can be examined by plotting pairwise sequence divergences for various substitution types and genes. For the nuclear gene (FIB7), we estimated the ''native'' transition:transversion ratio by plotting pairwise transition differences against pairwise transversion differences. Slope of the linear portion of that curve estimates the transition:transversion ratio (Sturmbauer and Meyer 1992). We do not fit regressions through those points because they are nonindependent, rather we use slopes as a rough indicator of relative rates. For mitochondrial genes, we plotted transition difference at third positions against transversions at third positions to estimate that ratio. To estimate relative rates of mitochondrial versus nuclear substitution, we plotted pairwise divergences for mitochondrial genes against those for FIB7. We also plotted pairwise divergences for individual mitochondrial genes against each other and against FIB7 to determine which genes are more subject to multiple substitution.

PAUP* (Swofford 2000) was used for all phylogenetic analyses. We used the partition homogeneity test (Farris et al. 1994, 1995; Swofford 2000) to examine whether the gene regions could be considered samples of the same underlying phylogeny, or whether there was evidence for different phylogenetic signal between gene regions. Even though that

TABLE 1. Samples sequenced for all genes.

Species	Locality	Sample number	Tissue type	GenBank accession numbers			
				Cyt *b*	ND2	COI	FIB7
Streptopelia decaocto	Netherlands	SDK 4	Muscle	AF353398	AF353418	AF353469	AF353449
Streptopelia roseogrisea	Cameroon	SDK 1	Feather	AF353399	AF353419	AF353470	AF353450
Streptopelia decipiens	Cameroon	SDK 1	Feather	AF353400	AF353420	AF353471	AF353451
Streptopelia semitorquata	South Africa	LSUMNS B34270[a]	Muscle	AF353401	AF353421	AF353472	AF353452
Streptopelia capicola	South Africa	LSUMNS B34271[a]	Muscle	AF279709	AF353422	AF279734	AF279719
Streptopelia vinacea	Cent. Afr. Rep.	AMNH PRS-2168[a]	Muscle	AF353402	AF353423	AF353473	AF353453
Streptopelia hypopyrrha	Cameroon	SDK 4	Muscle	AF353403	AF353424	AF353474	AF353454
Streptopelia turtur	Kazakhastan	UWBM DAB-236[a]	Muscle	AF353404	AF353425	AF353475	AF353455
Streptopelia orientalis	Russia	UWBM 47282[a]	Muscle	AF353405	AF353426	AF353476	AF353456
Streptopelia bitorquata	Captive	SDK 1	Feather	AF353406	AF353427	AF353477	AF353457
Streptopelia tranquebarica	Captive	SDK 2	Feather	AF353407	AF353428	AF353478	AF353458
Nesoenas (*Streptopelia*) *mayeri*	Captive	Tracy Aviary	Feather	AF353408	AF353429	AF353479	AF353459
Streptopelia picturata	Madagascar	CC 1	Feather	AF353409	AF353430	AF353480	AF353460
Streptopelia chinensis	Philippines	FMNH DW-4712[a]	Muscle	AF182695	AF353431	AF353481	AF182662
Streptopelia senegalensis	South Africa	LSUMNS B34209[a]	Muscle	AF279710	AF353432	AF279735	AF279720
Columba liva	Utah	423	Muscle	AF182694	AF353433	AF279733	AF182661
Columba rupestris	Mongolia	UWBM 59755[a]	Muscle	AF353410	AF353434	AF353482	AF353461
Columba guinea	South Africa	LSUMNS B34209[a]	Muscle	AF279708	AF353435	AF279732	AF279718
Columba palumbus	Captive	Tracy Aviary	Muscle	AF353411	AF353436	AF353483	AF353462
Columba arquatrix	South Africa	CC 2	Feather	AF353412	AF353437	AF353484	AF353463
Columba pulchrichollis	Captive	SDK 1	Muscle	AF353413	AF353438	AF353485	AF353464
Columba plumbea	Brazil	FMNH ATP86-136[a]	Muscle	AF182691	AF251547	AF279736	AF182658
Columba subvinacea	Peru	FMNH SML-1045[a]	Muscle	AF182692	AF353439	AF353486	AF182659
Columba oenops	Peru	FMNH AJB-556[a]	Muscle	AF182690	AF353440	AF353487	AF182657
Columba leucocephala	Florida	KUMNH B1798[a]	Muscle	AF182689	AF353441	AF353488	AF182656
Columba speciosa	Mexico	KUMNH B2096[a]	Muscle	AF279711	AF353442	AF279737	AF279721
Columba fasciata	Utah	DHC 1[a]	Muscle	AF353414	AF353443	AF353489	AF353465
Macropygia mackinlayi	Solomon Islands	AMNH MKL-82[a]	Muscle	AF353415	AF353444	AF353490	AF353466
Macropygia tenurirostris	Philippines	FMNH SEA-074[a]	Muscle	AF353416	AF353445	AF353491	AF353467
Reinwardtoena browni	Captive	NMNH B4024[a]	Muscle	AF353417	AF353446	AF353492	AF353468
Zenaida asiatica	Arizona	KPJ 5	Muscle	AF251533	AF251543	AF279731	AF258324
Zenaida macroura	Arizona	KPJ 5	Muscle	AF251530	AF251535	AF353493	AF258321
Geotrygon montana	Peru	KUMNH B995[a]	Muscle	AF182696	AF353447	AF279728	AF182663
Leptotila rufaxilla	Peru	KUMNH B793[a]	Muscle	AF182698	AF251546	AF353494	AF182665
Leptotila verreauxi	Texas	DHC 5[a]	Muscle	AF279705	AF353448	AF279725	AF279715

[a] Indicates samples that have a corresponding museum skin voucher.

TABLE 2. Primers used in study.

Gene	Primer name	Source
cyt *b*	L14841	Kocher et al. (1989)
	H4a	Harshman (1996)
	H15299	Kocher et al. (1989)
	L15517	Johnson and Sorenson (1998)
ND2	L5215	Hackett (1996)
	H6313	Johnson and Sorenson (1998)
	L5758	Johnson and Sorenson (1998)
COI	L6625	Hafner et al. (1994)
	H7005	Hafner et al. (1994)
FIB7	FIB-BI7L	Prychitko and Moore (1997)
	FIB-BI7U	Prychitko and Moore (1997)
	FIB-DOVEF	Johnson and Clayton (2000a)
	FIB-DOVER	Johnson and Clayton (2000a)

test indicated no significant incongruence between any of the gene regions (see below), we also conducted several analyses with mitochondrial and nuclear genes separately. We did this because of the slow rate and lack of informative sites in the nuclear gene and because we wanted to identify what nodes were common to trees derived from independently sorting gene regions.

We conducted parsimony analyses with a range of transversion weighting schemes from 1:1 (unordered parsimony) to 20:1. For each weighting scheme, we used 50 random addition replicates with heuristic searches. For each analysis, we also performed 1,000 bootstrap replicates (Felsenstein 1985) to assess relative support for various branches in the phylogeny.

We used one of the combined unordered parsimony trees to estimate parameters for maximum-likelihood searches. We used likelihood ratio tests to estimate the best fit model that could not be rejected in favor of a simpler model (Huelsenbeck and Crandall 1997). Using the estimated model parameters, we conducted 50 heuristic maximum-likelihood searches with nearest neighbor interchange (NNI) branch swapping. We used bootstrapping (100 replicates with NNI branch swapping) to evaluate relative support for nodes in maximum-likelihood topologies.

RESULTS

Sequence variation.—Mitochondrial genes were similar in the fraction of sites that were variable and potentially phylogenetically informative, but ND2 showed the most variation, followed by cyt *b,* then COI (Table 4). FIB7 showed a much smaller fraction of variable and phylogenetically informative sites (Table 4). Within *Streptopelia,* mitochondrial sequence divergences ranged from 1.9 to 12.4%. For those

TABLE 3. Samples sequenced for COI only.

Species	Locality	Sample number	Tissue type	GenBank number
Streptopelia decaocta	Netherlands	SDK 1	Feather	AF353495
Streptopelia decaocto	Netherlands	SDK 2	Feather	AF353496
Streptopelia roseogrisea	Cameroon	SDK 2	Blood	AF353497
Streptopelia roseogrisea	Cameroon	SDK 3	Feather	AF353498
Streptopelia decipiens	Cameroon	SDK 2	Feather	AF353499
Streptopelia semitorquata	Cameroon	SDK 1	Feather	AF353500
Streptopelia capicola	South Africa	LSUMNS B34205[a]	Muscle	AF353501
Streptopelia vinacea	Cameroon	SDK 1	Feather	AF353502
Streptopelia hypopyrrha	Cameroon	SDK 2	Feather	AF353503
Streptopelia turtur	Cameroon	SDK 1	Feather	AF353504
Streptopelia turtur	Cameroon	SDK 2	Feather	AF353505
Streptopelia orientalis	Captive	SDK 2	Feather	AF353506
Streptopelia tarnquebarica	Captive	SDK 3	Feather	AF353507
Streptopelia picturata	Captive	SDK 1	Feather	AF353508
Streptopelia chinensis	Singapore	AMNH PRS-678[a]	Fuscle	AF353509
Streptopelia senegalensis	Cameroon	SDK 1	Feather	AF353510

[a] Indicates samples that have a corresponding museum skin voucher.

TABLE 4. Variable and phylogenetically informative sites for each gene region.

Gene	Number of sites	Percent variable	Percent information
cyt *b*	1070	39.0%	33.1%
ND2	1067	48.7%	39.8%
COI	383	34.2%	30.0%
FIB7	1150	19.6%	7.9%

same comparisons, FIB7 showed much less divergence (0.0 to 1.4%). Plots of third position transitions against third position transversions for mitochondrial genes (Fig. 1) indicated considerable multiple substitution of third position transitions with an estimated transition: transversion ratio of approximately 10:1. Divergences of mitochondrial genes were similar, but comparisons of those divergences indicated that ND2 was less subject to multiple substitution than was cyt *b* or COI, because plots of ND2 divergence against FIB7 or the other mitochondrial genes indicated continuing accumulation of substitutions at high divergences. The estimated transition:transversion ratio for FIB7 was approximately 1.5:1 (Fig. 3), with no evidence of multiple substitution of transitions compared to transversions. Plots of divergences for the mitochondrial genes against FIB7 divergence indicated a 5 to 10× higher rate of substitution in the mitochondrial genes (Fig. 4).

Several indels occurred in FIB7. One of those is a 166 bp deletion shared by *Streptopelia, Nesoenas,* and Old World *Columba.* Other columbiform taxa do not show that deletion. Other indels in FIB7 ranged from 1 to 125 bp, but only two others were potentially phylogenetically informative (one uniting *Streptopelia, Nesoenas,* Old World *Columba,* and *Macropygia* the other uniting clade A of *Streptopelia* [Fig. 5]).

Within species, little sequence variation was evident. For the COI gene, within-species variation ranged from 0.0% (for 6 of 13 species with multiple samples) to 1.0% (for comparisons of *Streptopelia semitorquata* between South Africa and Cameroon). The low within-species variation for mitochondrial genes suggests that single species exemplars are suitable for species-level phylogenetic analysis, given that between-species divergences all exceeded 2.5%.

Phylogeny.—Partition homogeneity tests comparing congruence among the three mitochondrial genes indicate that those genes could be considered samples of the same underlying phylogeny ($P = 0.44$). Similarly, trees derived from FIB7 alone compared to trees for mitochondrial genes combined were not significantly incongruent ($P = 1.0$).

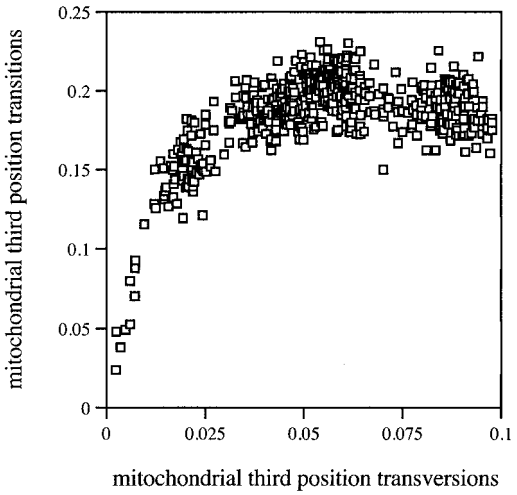

FIG. 1. Plot of pairwise percentage divergence for transitions against transversions for third positions of all mitochondrial genes combined.

Unordered parsimony analysis of all three mitochondrial genes combined produced three equally parsimonious trees (not shown, but see Fig. 5 for reference). Those trees indicated that *Streptopelia* is not monophyletic. *Nesoenas mayeri* is the sister taxon to *S. picturata* with high bootstrap support. In addition, two groups of *Streptopelia* are sister to Old World *Columba,* but that result has only weak bootstrap support (49%). One large group of *Streptopelia* is monophyletic (clade A) with strong support (100%).

Transversion weighting of 2:1 to 5:1 produced identical tree topologies (one tree) that were completely resolved (not shown). Analysis of mitochondrial genes with those low transversion weights also produced a paraphyletic *Streptopelia,* both with respect to *Nesoenas* and with respect to Old World *Columba.* However, transversion weighting of 10:1 and higher produced a single tree showing monophyly of *Streptopelia* with respect to Old World *Columba. Nesoenas* was still sister to *S. picturata,* again with high bootstrap support.

Unordered parsimony analysis of the nuclear intron alone produced 32,020 trees (not shown). The high number of trees was not sim-

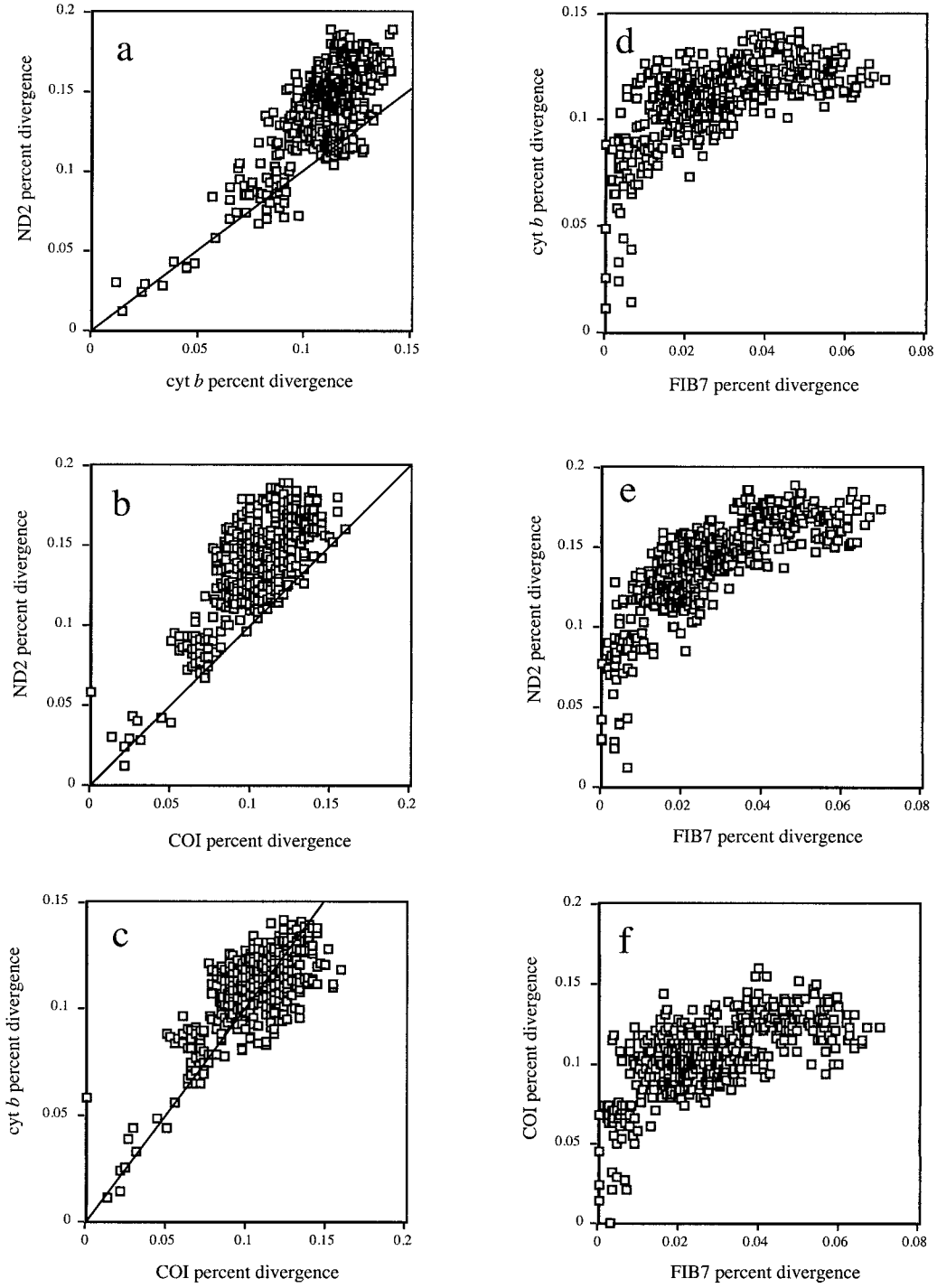

FIG. 2. Plot of pairwise percentage divergence for (A) ND2 versus cyt *b*, (B) ND2 versus COI, (C) cyt *b* versus COI, (D) cyt *b* versus FIB7, (E) ND2 versus FIB7, (F) COI versus FIB7. Lines for the mitochondrial gene plots (A–C) indicate expectation if rates are equal.

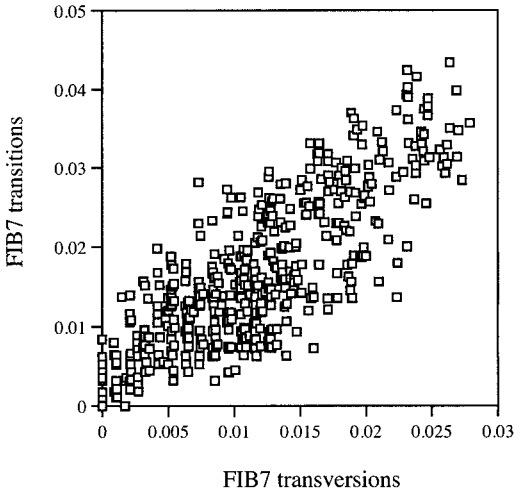

FIG. 3. Plot of pairwise percentage divergence for transitions against transversions for all positions of nuclear FIB7.

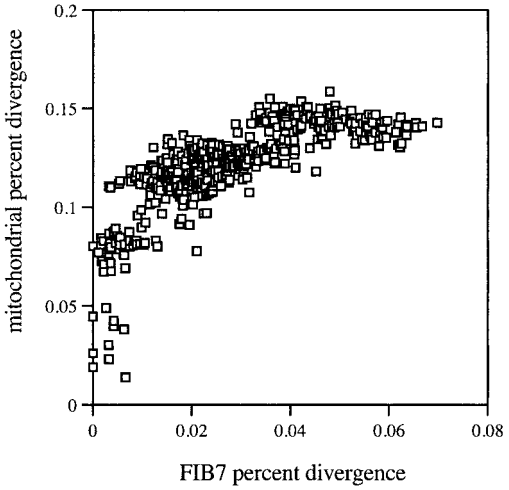

FIG. 4. Plot of overall percentage divergence for all mitochondrial genes combined against percentage divergence for nuclear FIB7.

ply an artifact of incomplete sequences for *Streptopelia bitorquata* and *S. tranquebarica.* Exclusion of those sequences from phylogenetic analyses produced 4,236 trees, the consensus of which was identical to the consensus of trees with those taxa included. FIB7 trees did not resolve relationships among major *Streptopelia* lineages plus Old World *Columba.* However, New World *Columba* is placed outside *Streptopelia* and Old World *Columba* (bootstrap support 100%). Monophyly of both clades B and C of *Streptopelia* (see Fig. 5 for reference) was strongly supported in parsimony analyses of FIB7 alone, as was monophyly of Old World *Columba.*

Unordered parsimony analysis of combined gene regions (mitochondrial and nuclear) produced two trees (Fig. 5). Strict consensus of those trees, like unordered parsimony analysis of mitochondrial genes alone, does not recover a monophyletic *Streptopelia* with respect to Old World *Columba.* However, in most respects that tree is very similar to trees produced by separate analysis. Increasing transversion weighting of combined gene regions (in excess of 10: 1) produced trees with a monophyletic *Streptopelia* with respect to Old World *Columba* (not shown, see Fig. 6 for reference).

Likelihood ratio tests indicated that models incorporating unequal base frequencies, six substitution types, and rate heterogeneity were statistically better justified than simpler models. Maximum-likelihood searches on mitochondrial genes alone produced a tree very similar to parsimony trees, and that tree indicated monophyly for *Streptopelia* with respect to Old World *Columba.* Likelihood analysis of the intron alone identifies monophyly for the three main clades of *Streptopelia* and Old World *Columba,* but does not resolve relationships among those groups. There is also little resolution within the large *Streptopelia* clade A. Maximum-likelihood trees for combined gene regions (Fig. 6) are well resolved and indicate monophyly for *Streptopelia* (inclusive of *Nesoenas*) with moderate support (bootstrap 64%). The three main clades of *Streptopelia* identified by combined parsimony analysis are also recovered in that tree with strong support (100% in each case), as is paraphyly of *Columba* (100% bootstrap support for sister relationship between Old World *Columba* and *Streptopelia*). In fact, support for a sister relationship between New World *Columba* and Old World *Columba* + *Streptopelia* is relatively poor (51%). Most other branches are identical to those recovered by unordered parsimony analysis (Fig. 5).

DISCUSSION

Phylogeny.—A phylogeny based on 2,530 bp of mitochondrial and 1,150 bp of nuclear DNA sequences is generally well resolved and well supported for the dove genus *Streptopelia* and

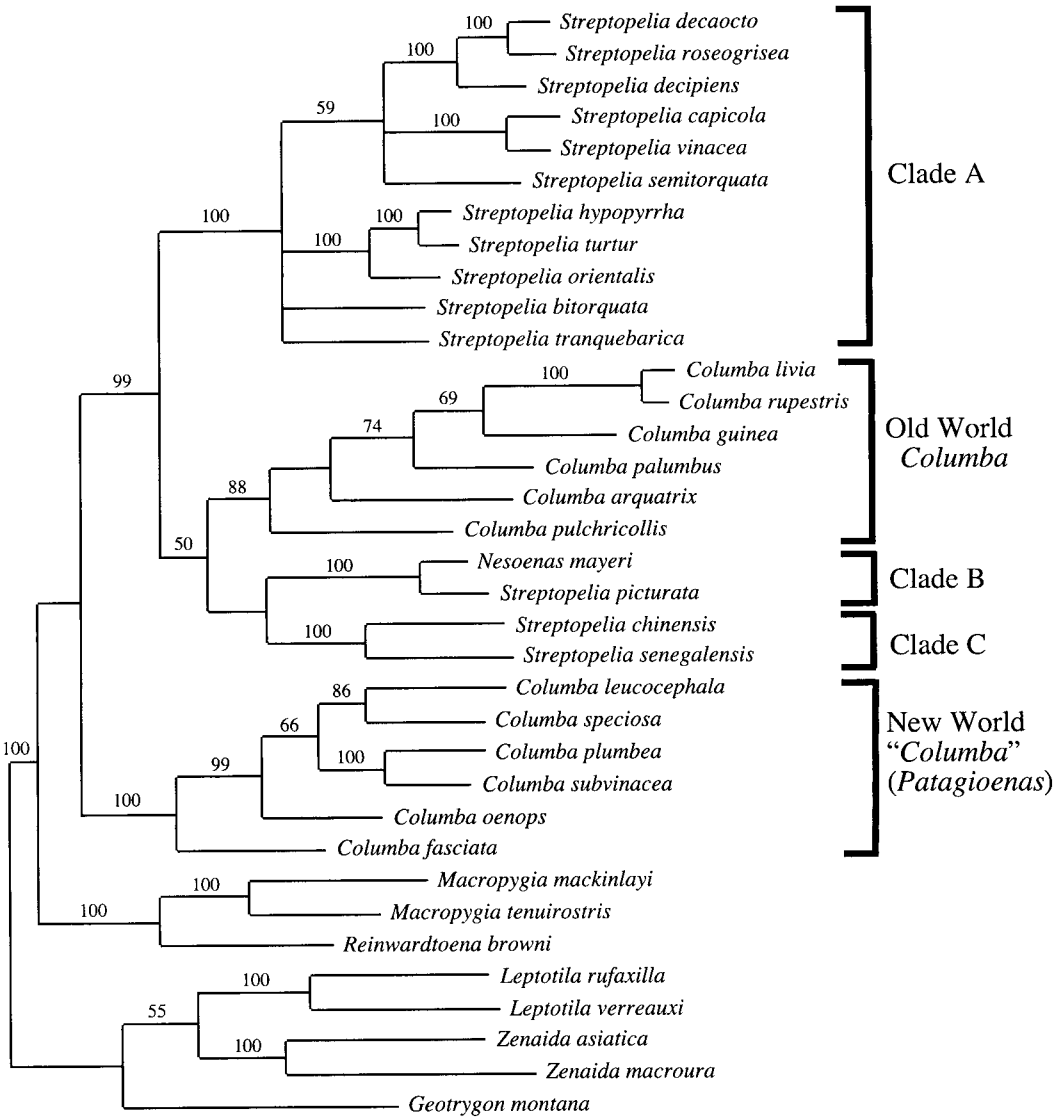

FIG. 5. Strict consensus of two trees (length = 4470, RC = 0.200) from unordered parsimony analysis of combined mitochondrial (cyt *b*, ND2, COI) and nuclear (FIB7) genes. Numbers above branches indicate bootstrap support from 1,000 full heuristic replicates. Unlabelled nodes received <50% bootstrap support. Branch lengths are proportional to reconstructed changes using parsimony. Indicated groups are clades referred to in text.

outgroup taxa. However, even given the relatively large amount of DNA sequence data, some aspects of the tree are still weakly supported. Primary among those uncertainties is whether or not *Streptopelia* is monophyletic with respect to Old World *Columba.*

Despite the lower homoplasy present in the FIB7 sequences, mitochondrial genes provided better resolution for the phylogeny of *Streptopelia.* Mitochondrial genes have around a 5 to 10× higher substitution rate (Fig. 4), and thus variation can accumulate in mitochondrial DNA between closely related species. For several closely related species of *Streptopelia,* sequences of FIB7 were identical, preventing resolution of species level relationships. Importantly for this study,

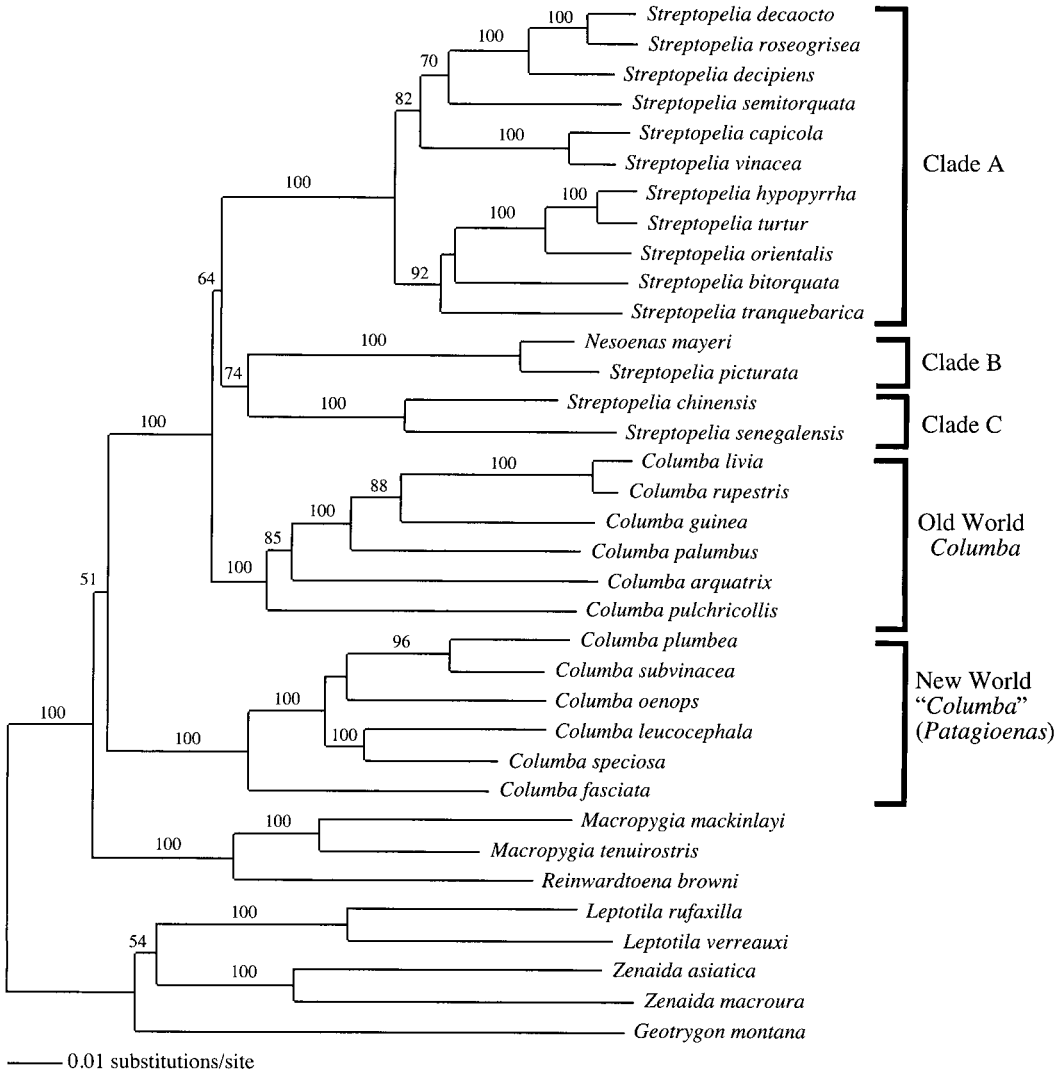

FIG. 6. Tree resulting from maximum likelihood searches using combined mitochondrial (cyt *b*, ND2, COI) and nuclear (FIB7) genes (ln likelihood = −25,202; model parameters: gamma shape parameter = 0.209 with eight rate categories, transition matrix: A–C = 1.41, A–G = 17.96, A–T = 1.22, C–G = 0.54, C–T = 16.77, G–T = 1.0). Numbers above branches indicate bootstrap support from 100 heuristic search replicates. Unlabelled nodes received <50% bootstrap support. Branch lengths are proportional to likelihood estimated branch lengths (scale indicated). Indicated groups are clades referred to in text.

trees based on FIB7 identified the same major clades that were identified by analyses of mitochondrial genes. In addition, there was no significant conflict between nuclear and mitochondrial data sets, suggesting that trees recovered in our analyses estimate the species' phylogeny rather than simply gene trees.

All analyses identify three major clades within *Streptopelia* (Figs. 5 and 6). Two of those groups involve only two species: *S. chinensis* + *S. senegalensis* (clade C) and *S. picturata* + *Nesoenas* (*Streptopelia*) *mayeri* (clade B). The other clade (A) includes all other species of *Streptopelia.* Monophyly of each of those clades is generally well supported, but relationships among those groups and Old World *Columba* is less clear. Analyses that take into account large transition:transversion biases (transversion-weight-

ed parsimony and maximum likelihood) tend to recover monophyly for *Streptopelia* (inclusive of *Nesoenas*).

Phylogenetic relationships within *Streptopelia* do not correspond in a strong way to either Nowak's (1975) classification or Goodwin's (1983) hypothesized evolutionary relationships. However, similarities with both are evident. Nowak (1975) unites *S. decipiens, capicola, vinacea, tranquebarica, semitorquata, roseogrisea,* and *decaocto* into a subgenus. We find support for a similar clade (excluding *tranquebarica*). Goodwin (1983) outlines a similar group, but places *tranquebarica* outside of it and puts *bitorquata* close to *decaocto.* In our phylogenetic analyses, *S. tranquebarica* and *S. bitorquata* consistently fall at the base of a clade containing those two species plus *S. orientalis, turtur,* and *hypopyrrha.* Like many species of *Streptopelia, tranquebarica* and *bitorquata* possess a ''ring-neck,'' unlike *orientalis, turtur,* and *hypopyrrha* that have a dark patch on the side of the neck. Our results suggest that the ring-neck (a dark bar running around the back of the neck) is the ancestral condition in group A of *Streptopelia,* having been lost in the ancestor of *S. orientalis, turtur,* and *hypopyrrha.* Species of *Streptopelia* outside group A tend to have spotting on the neck. The close relationship of *S. chinensis* and *S. senegalensis* was recognized by Goodwin (1983) and to some extent by Nowak (1975).

A novel finding of our study is the sister relationship between the Pink Pigeon (*Nesoenas mayeri*), which is endemic to Mauritius, and the Madagascan Turtle Dove (*Streptopelia picturata*), endemic to Madagascar. In most classifications, *Nesoenas* is united with species of Old World *Columba* whereas the Madagascan Turtle Dove is considered to be an aberrant *Streptopelia.* On the basis of the close relationship of those two species, we suggest that the common ancestor of the Pink Pigeon and the Madagascan Turtle Dove colonized Mauritius from Madagascar and subsequently speciated. Percentage divergence for mitochondrial genes between the Pink Pigeon and the Madagascan Turtle Dove is only 3.0%. On the basis of mitochondrial molecular clock calibrations for birds (Klicka and Zink 1997), that represents a colonization time of ~1.5 Mya, much younger than the age of Mauritius (Proag 1995). Mitochondrial divergence between the Madagascan Turtle Dove and other species of *Streptopelia* ranges from 11.1 to 11.9%, whereas the maximum mitochondrial divergences within clade A of *Streptopelia* range to 8.4%.

Streptopelia vinacea and *S. capicola* are a pair of allopatric sister taxa of particular interest. Those taxa are distributed in sub-Saharan northern Africa and in southeastern Africa, respectively. Another pair of dove taxa with a similar distribution is *Turtur abyssinicus* and *T. chalcospilos.* Mitochondrial sequence divergence between *S. vinacea* and *S. capicola* is 2.5% and that between *T. abyssinicus* and *T. chalcospilos* is 1.7% (K. P. Johnson unpubl. data). Similarity in geographic distributions and genetic divergences suggests some common biogeographic factor underlying speciation between those species of *Streptopelia* and *Turtur,* perhaps ~1 Mya.

Taxonomic implications.—The Pink Pigeon, in the monotypic genus *Nesoenas* Salvadori 1893, is sister to *Streptopelia picturata.* That result is evidenced by two independent gene regions and receives strong support in all analyses. The sister relationship between *Nesoenas mayeri* (Mauritius) and *S. picturata* (Madagascar) is not surprising, given the geographic proximity of those two islands. In light of those results, we recommend transferring *N. mayeri* to the genus *Streptopelia* Bonaparte 1855.

Regarding the generic status of *Streptopelia,* our results do not conclusively demonstrate monophyly of *Streptopelia.* However, in analyses that take into account rate heterogeneity and transition biases, *Streptopelia* (as redefined to include *Nesoenas mayeri*) is monophyletic. On the basis of those results, we suggest retaining the name *Streptopelia* for all species currently in the genus. An alternative would be to recognize the three main clades (A–C) as separate genera, but we feel a more conservative approach, minimizing name changes, is prudent.

All of our analyses indicated that Old World *Columba* species are sister to, or imbedded within, *Streptopelia.* That phylogenetic position results in paraphyly for *Columba.* Our current study confirms preliminary results of Johnson and Clayton (2000a), which also indicated that relationship. Because *Columba* for Old World species has priority, we recommend transferring all species of New World *Columba* into the genus *Patagioenas* (as partially suggested by Johnston 1962). Johnston (1962) suggested that the Band-tailed Pigeon (*Columba fasciata*) is a

close relative of Old World *Columba*; however, our results strongly supported monophyly of New World ''*Columba*,'' inclusive of *fasciata.* Further analysis is needed to determine if all New and Old World ''*Columba*'' species cluster by biogeographic distribution, but we suspect that will be the case.

Vocal evolution.—Streptopelia vocalizations have been studied extensively (Lade and Thorpe 1964, Gaunt et al. 1982, Cheng 1992, Ballintijn and ten Cate 1997, Slabbekoorn and ten Cate 1998, Slabbekoorn et al. 1999), making that genus an important group for comparative studies of vocalizations. Slabbekoorn et al. (1999) compared acoustic similarity of *Streptopelia* perch-coos with Goodwin's ideas on taxonomy (1983). They concluded that, at the species level, there is little congruence between similarity in perch-coos and phylogenetic relatedness, suggesting that environmental or social factors promote the relatively rapid diversification of perch-coo vocalizations. Although a formal reanalysis is beyond the scope of this paper, an informal comparison of acoustic similarity in relation to our phylogeny does not contradict Slabbekoorn et al.'s (1999) conclusions.

The close phylogenetic relationship between *Streptopelia picturata* and *S.* ''*Nesoenas*'' *mayeri* is somewhat surprising on the basis of morphological characters, but is supported by vocal characteristics. First, the relationship in general between *Streptopelia* and ''*Nesoenas*'' is supported by similarities in the Excitement Cry (Baptista 1997). More dramatically, the perch-coos of *S. picturata* and *S. mayeri* are very similar (Fig. 7), unlike comparisons of many other sister pairs of *Streptopelia.* Two other sister species pairs also show some similarity in vocalizations as compared to other *Streptopelia* species: *vinacea–capicola* and *turtur–hypopyrrha.* Although those species pairs group together in a similarity analysis, they can be separated unambiguously on the basis of acoustic parameters (Slabbekoorn et al. 1999). Thus perch-coos of other sister species pairs show structural acoustic differences (e.g. Fig. 7), which is not the case between *S. mayeri* and *picturata.* The latter instead show considerable divergence in morphological features, including a lack of any neck pattern and a reddish bill in *S. mayeri.* Those features, among others, are the reasons that *S. mayeri* has often been placed in a monotypic genus. In contrast, most other species of

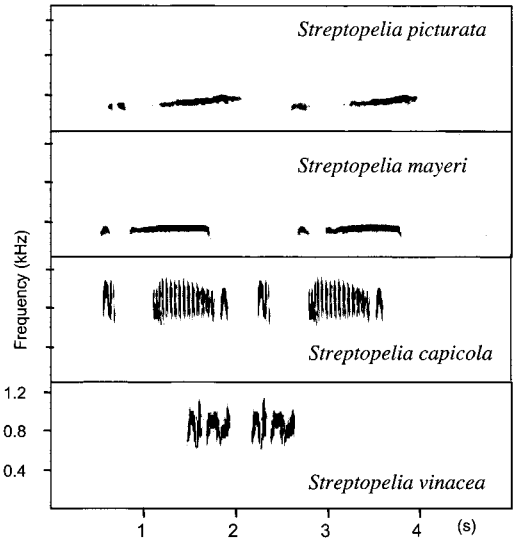

FIG. 7. Sonograms of selected *Streptopelia* perch-coos. Note the similarity between *S. picturata* and *S. mayeri.* Sonograms of *S. capicola* and *S. vinacea* represent two sister species of smaller genetic divergence, but greater divergence in perch-coo vocalizations.

Streptopelia are quite homogeneous in morphological characteristics. In fact, often the most reliable way to discriminate species in the field is by their distinctive perch-coos. Generally speaking, vocalizations in *Streptopelia* seem to be evolutionarily labile compared to morphological characteristics.

Two hypotheses explain why *Streptopelia picturata* and *S. mayeri* show the greatest degree of vocal similarity within *Streptopelia* (Slabbekoorn et al. 1999). First, selection may favor divergence between vocalizations of sympatric species, because of a need to use a signal that can be distinguished from that of closely related species (Nelson and Marler 1990). Unlike other *Streptopelia* species, *S. picturata* and *S. mayeri* are allopatric with all other congeners, perhaps reducing need for divergence in signal structure. Second, environment and habitat often play important roles in evolution of avian signals (Morton 1975, Wiley and Richards 1978, Marchetti 1993, Endler and Théry 1996, Johnson 2000, Johnson and Lanyon 2000). Both *S. picturata* and *S. mayeri* predominantly inhabit densely forested habitats through which their low-pitched vocalizations should propagate further than high-pitched vocalizations (Morton 1975, Wiley and Richards 1978, Ryan and

Brenowitz 1985, McCracken and Sheldon 1997). Further evidence for potential stabilizing selection on the perch-coos of those two species comes from examination of the relationship between body size and sound frequency. In New World pigeons, a negative correlation exists between body weight and perch-coo frequency (Tubaro and Mahler 1998). That relationship is not apparent in the perch-coos of *S. picturata* and *S. mayeri,* because *S. mayeri* is nearly twice as heavy as *S. picturata,* yet sound frequencies of the perch-coos are very similar (Fig. 7). One or both of these factors may have caused vocalizations of those two species to remain relatively unchanged since speciation.

One other unexpected phylogenetic relationship is also supported by careful examination of vocalizations. Exclusion of *Streptopelia bitorquata* and *S. tranquebarica,* despite similarity in plumage characteristics, from the group of typical ring-necked doves (*decaocto* through *vinacea* clade) is somewhat surprising. The Excitement or Flight Call is a conspicuous characteristic for the true ring-necked species (as defined above). That display, in the same context, is absent in *S. bitorquata* and *S. tranquebarica.* Absence of that display is shared with *S. hypoppyrha, turtur,* and *orientalis,* the close relatives of *bitorquata* and *tranquebarica.* Likewise the bow-coo of those two species is very similar to that of *S. hypoppyrha, turtur,* and *orientalis* (S. de Kort unpubl. data). In sum, despite the overall diversity and rapid evolution of vocalizations in *Streptopelia,* some behaviors reflect phylogenetic relationships.

Acknowledgments

We are grateful to the following individuals and institutions (and curators thereof) who were instrumental in providing samples: American Museum of Natural History, Field Museum of Natural History, University of Kansas Museum of Natural History, Louisiana State University Museum of Natural Science, U.S. National Museum, University of Washington Burke Museum, the Tracy Aviary, and Charlie Collins. The following individuals and organizations provided field assistance in collecting specimens: Sarah Al-Tamimi, Jason Weckstein, Rob Moyle, Nigella Hilgarth, Tony Jones, Aldolfo Navarro, A. Townsend Peterson, Mark Robbins, Moussa Barka, Imar Moussa, Wil Silkens, Arizona Fish and Game, Texas Parks and Wildlife, and the U.S. Fish and Wildlife Service. M. Griekspoor provided sound recordings. Dave Enstrom, Larry Page, Fred Sheldon, and two anonymous reviewers provided helpful comments on this manuscript. We thank the DNA Sequencing Facility at the University of Utah, supported in part by National Cancer Institute grant #5p30CA42014. This work was supported by NSF-CAREER award DEB-9703003 to D.H.C.

Literature Cited

Ballintijn, M. R., and C. ten Cate. 1997. Sex differences in vocalizations and syrinx of the Collared Dove (*Streptopelia decaocto*). Auk 114:22–39.

Baptista, L. 1997. Family Columbidae (Pigeons and Doves). Pages 60–243 *in* Handbook of the Birds of the World, vol. 4. Sandgrouse to Cuckoos (J. del Hoyo, A. Elliott, and J. Sargatal, Eds.). Lynx Edicions, Barcelona, Spain.

Bijlsma, R. G. 1988. Population growth in the Collared Dove *Streptopelia decaocto* in the Netherlands. Limosa 61:41–42.

Cheng, M. F. 1986. Female cooing promotes oviarian development in Ring Doves (*Streptopelia risoria*). Physiology and Behavior 37:371–374.

Cheng, M. F. 1992. For whom does the female dove coo? A case for the role of vocal self-stimulation. Animal Behaviour 43:1035–1044.

Cheng, M. F., M. Porter, and G. Ball. 1981. Do Ring Doves copulate more than necessary for fertilization? Physiology and Behavior 27:659–662.

Endler, J. A., and M. Théry. 1996. Interacting effects of lek placement, display behavior, ambient light, and color patterns in three Neotropical forest-dwelling birds. American Naturalist 148: 421–452.

Farris, J. S., M. Kallersjo, A. G. Kluge, and C. Bult. 1994. Testing significance of congruence. Cladistics 10:315–320.

Farris, J. S., M. Kallersjo, A. G. Kluge, and C. Bult. 1995. Constructing a significance test for incongruence. Systematic Biology 44:570–572.

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

Gaunt, A. S., S. L. L. Gaunt, and R. M. Casey. 1982. Syringeal mechanisms reassessed: Evidence from *Streptopelia.* Auk 99:474–494.

Georgiou, G. C., P. J. Sharp, and R. W. Lea. 1995. (14C) 2-Deoxyglucose uptake in the brain of the Ring Dove (*Streptopelia risoria*). II. Differential uptake at the onset of incubation. Brain Research 700:137–141.

Goodwin, D. 1983. Pigeons and Doves of the World, 3rd ed. Cornell University Press, Ithaca, New York.

Hackett, S. J. 1996. Molecular phylogenetics and biogeography of tanagers in the genus *Ramphocelus* (Aves). Molecular Phylogenetics and Evolution 5:368–382.

HAFNER, M. S., P. D. SUDMAN, F. X. VILLABLANCA, T. A. SPRADLING, J. W. DEMASTES, AND S. A. NADLER. 1994. Disparate rates of molecular evolution in cospeciating hosts and parasites. Science 365: 1087–1090.

HARSHMAN, J. 1996. Phylogeny, evolutionary rates, and ducks. Ph.D. dissertation. University of Chicago, Chicago.

HENGEVELD, R. 1993. What to do about the North American invasion by the Collared Dove? Journal of Field Ornithology 64:477–489.

HENGEVELD, R., AND F. VAN DEN BOSCH. 1991. The expansion velocity of the Collared Dove *Streptopelia decaocto* population in Europe. Ardea 79: 67–72.

HUELSENBECK, J. P., AND K. A. CRANDALL. 1997. Phylogeny estimation and hypothesis testing using maximum likelihood. Annual Review of Ecology and Systematics 28:437–466.

JANIK, D. S., AND J. D. BUNTIN. 1985. Behavioral and physiological effects of prolactin in incubating doves (*Streptopelia risoria*). Journal of Endocrinology 105:201–210.

JOHNSON, K. P. 2000. The evolution of courtship display repertoire size in the dabbling ducks (Anatini). Journal of Evolutionary Biology 13:636–644.

JOHNSON, K. P., AND D. H. CLAYTON. 2000a. Nuclear and mitochondrial genes contain similar phylogenetic signal for pigeons and doves (Aves: Columbiformes). Molecular Phylogenetics and Evolution 14:141–151.

JOHNSON, K. P., AND D. H. CLAYTON. 2000b. A molecular phylogeny of the dove genus *Zenaida*: Mitochondrial and nuclear DNA sequences. Condor 102:864–870.

JOHNSON, K. P., AND S. M. LANYON. 1999. Molecular systematics of the grackles and allies, and the effect of additional sequence (cyt *b* and ND2). Auk 116:759–768.

JOHNSON, K. P., AND S. M. LANYON. 2000. Evolutionary change in color patches of blackbirds are associated with marsh nesting. Behavioral Ecology 11:515–519.

JOHNSON, K. P., AND M. D. SORENSON. 1998. Comparing molecular evolution in two mitochondrial protein coding genes (cytochrome *b* and ND2) in the dabbling ducks (Tribe: Anatini). Molecular Phylogenetics and Evolution 10:82–94.

JOHNSTON, R. F. 1962. The taxonomy of pigeons. Condor 64:69–74.

KASPAREK, M. 1996. Dispersal and range extension of the Collared Dove (*Streptopelia decaocto*) in Europe. Journal für Ornithologie 137:1–33.

KLICKA, J. T., AND R. M. ZINK. 1997. The importance of recent ice ages in speciation: A failed paradigm. Science 277:1666–1669.

KOCHER, T. D., W. K. THOMAS, A. MEYER, S. V. EDWARDS, S. PÄÄBO, F. X. VILLABLANCA, AND A. C. WILSON. 1989. Dynamics of mitochondrial DNA evolution in animals: Amplification and sequencing with conserved primers. Proceedings of the National Academy of Sciences USA 86: 6196–6200.

LADE, B. I., AND W. H. THORPE. 1964. Dove songs are innately coded patterns of specific behaviour. Nature 202:366–368.

LEA, R. W., G. C. GEORGIOU, Q. LI, R. J. STERLING, AND P. J. SHARP. 1995. (14C) 2-Deoxyglucose uptake in the brain of the Ring Dove (*Streptopelia risoria*). I. Prolactin-induced uptake. Brain Research 700:129–136.

MARCHETTI, K. 1993. Dark habitats and bright birds illustrate the role of environment in species divergence. Nature 362:149–152.

MCCRACKEN, K. G., AND F. H. SHELDON. 1997. Avian vocalizations and phylogenetic signal. Proceedings of the National Academy of Science USA 94: 3833–3836.

MORTON, E. S. 1975. Ecological sources of selection on avian sounds. American Naturalist 108:17–34.

NELSON, D. A., AND P. MARLER. 1990. The perception of bird song and an ecological concept of signal space. Pages 443–478 *in* Comparative Perception, vol. 2: Complex Signals (W. C. Stebbins and M. A. Berkeley, Eds.). John Wiley and Sons, New York.

NOWAK, E. 1975. Zur Systematik der Gattung *Streptopelia* (Columbiformes, Aves). Bonner Zoologische Beitraege 26:135–154.

PROAG, V. 1995. The Geology and Water Resources of Mauritius. Mahatma Gandhi Institute, Moka, Mauritius.

PRYCHITKO, T. M., AND W. S. MOORE. 1997. The utility of DNA sequences from an intron from the β-fibrinogen gene in phylogenetic analysis of woodpeckers (Aves: Picidae). Molecular Phylogenetics and Evolution 8:193–204.

RAMOS, C., AND R. SILVER. 1992. Gonadal hormones determine sex differences in timing of incubation by doves. Hormones and Behavior 26:586–601.

RYAN, M. J., AND E. A. BRENOWITZ. 1985. The role of body size, phylogeny, and ambient noise in the evolution of bird song. American Naturalist 126: 87–100.

SLABBEKOORN, H., S. DE KORT, AND C. TEN CATE. 1999. Comparative analysis of perch-coo vocalizations in *Streptopelia* doves. Auk 116:737–748.

SLABBEKOORN, H., AND C. TEN CATE. 1998. Multiple parameters in the territorial coo of the Collared Dove: Interactions and meaning. Behaviour 135: 879–895.

SORENSON, M. D., AND T. W. QUINN. 1998. Numts: A challenge for avian systematics and population biology. Auk 115:214–221.

STURMBAUER, C., AND A. MEYER. 1992. Genetic divergence, speciation, and morphological stasis in the lineage of African cichlid fishes. Nature 358:578–581.

SWOFFORD, D. L. 2000. PAUP*: Phylogenetic Analysis Using Parsimony, version 4.0. Sinauer, Sunderland, Massachusetts.

TEN CATE, C., R. W. LEA, M. R. BALLINTIJN, AND P. J. SHARP. 1993. Brood size affects behavior, interclutch interval, LH levels, and weight in Ring Dove (*Streptopelia risoria*) breeding pairs. Hormones and Behavior 27:539–550.

TUBARO, P. L., AND B. MAHLER. 1998. Acoustic frequencies and body mass in the New World doves. Condor 100:54–61.

WALKER, L. E., J. M. WALKER, J. W. PALCA, AND R. J. BERGER. 1983. A continuum of sleep and shallow torpor in fasting doves (*Streptopelia risoria*). Science 221:194–195.

WILEY, R. H., AND D. G. RICHARDS. 1978. Physical constraints on acoustic communication in the atmosphere: Implications for the evolution of animal vocalizations. Behavioral Ecology and Sociobiology 3:69–94.

ZENONE, P. G., M. E. SIMS, AND C. J. ERICKSON. 1979. Male Ring Dove (*Streptopelia risoria*) behavior and the defense of genetic paternity. American Naturalist 114:615–626.

Associate Editor: F. Sheldon