ORIGINAL ARTICLE

The Central American land bridge as an engine of diversification in New World doves

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ABSTRACT

Aim The closure of the Central American land-bridge connection between North and South America 3.5 million years ago was a major biogeographic event that allowed considerable interchange of the previously isolated faunas of these continents. However, the role that this connection may have had in diversification of North and South American faunas is less well understood. The goal of this study was to evaluate the potential role of the formation of this land connection in generating diversity, through repeated rare dispersal events followed by isolation.

Location North and South America.

Methods We evaluated the role of the Central American land-bridge connection in avian diversification using a molecular phylogeny based on four gene regions for mid-sized New World doves. Diversification events were dated using a Bayesian relaxed clock analysis and internal calibration points for endemic island taxa with known island ages.

Results The reconstructed phylogenetic tree was well supported and recovered monophyly of the genera *Leptotila* and *Zenaida*, but the quail-doves (*Geotrygon*) were paraphyletic, falling into three separate lineages. The phylogeny indicated at least nine dispersal-driven divergence events between North and South America. There were also five dispersal events in the recent past that have not yet led to differentiation of taxa (polymorphic taxa).

Main conclusions Most of these dispersal-driven diversification events occurred at the time of or after the formation of the Central American land bridge, indicating that this land connection played a role in facilitating divergence via dispersal of doves between continents.

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INTRODUCTION

For organisms with high dispersal capabilities, new opportunities for colonization across biogeographic barriers might promote speciation for successfully dispersing populations. The formation of volcanic islands, for example, provides new habitat for terrestrial taxa, but these taxa must disperse across water. Once successful colonization has occurred, the inherent isolation of islands can lead to differentiation and eventual speciation (Mayr, 1942). Although the opportunities presented by newly formed islands for promoting speciation are relatively well understood, the role of dispersal in generating species diversity in other biogeographic settings is less well documented.

In particular, the continents of North America and South America, which had been separated since about 175 Ma, came into contact again through the formation of the Central American land bridge approximately 3.5 Ma. This provided a new opportunity for organisms to disperse between these regions, a phenomenon that is particularly well documented in

the mammalian fossil record (Simpson, 1940; Webb, 1991; Brown & Lomolino, 1998). For birds, which have the potential to fly across water, it is possible that the increased proximity of the North and South American land masses before the closure of the isthmus provided increasing frequency of dispersal between these continents, with potential isolation following. Thus dispersal events between continents in both directions potentially provided a mechanism whereby species diversity may have been generated. A lineage may disperse from one continent to another, become isolated and speciate, and then disperse back to the original continent of origin. If such a process is repeated between continents over time, species diversity could accumulate.

Another possibility is that dispersal between North and South America occurred only after the closure of the isthmus. Such dispersal events may have led to a dramatic range expansion either north or south. Because of the narrow land bridge, there may be restricted gene flow between populations on either side, leading to differentiation. Alternatively, a later vicariance event, such as range contraction with changing climate, may have isolated a species that previously underwent a range expansion across the isthmus after closure. In either case, the formation of the land bridge could have provided a new opportunity for dispersal and range expansion followed by isolation.

Here we explore the role of the formation of the Central American land bridge for processes of diversification in mid-sized New World doves. Doves in the genera *Geotrygon*, *Leptotila* and *Zenaida* form a well-supported monophyletic group within the avian order Columbiformes (Johnson & Clayton, 2000a; Johnson, 2004; Pereira *et al.*, 2007). All three of these genera have multiple species in North and South America, with a concentration of diversity around the isthmus between these continents (Gibbs *et al.*, 2001). We tested the role that inter-continental dispersal may have played in generating species diversity in this group of doves by reconstructing changes in continental distribution over a molecular phylogeny. We evaluated the timing of these changes with respect to the final closure of the Central American land bridge 3.5 Ma using calibration points independent of this event and a Bayesian relaxed clock analysis of the molecular data.

MATERIALS AND METHODS

Total genomic DNA was extracted from muscle tissue from 39 individuals belonging to the order Columbiformes (Table 1) using a Qiagen DNeasy Tissue Kit (Qiagen Inc., Valencia, CA, USA) and following the manufacturer's protocols. One nuclear gene and three mitochondrial genes were sequenced for 32 individuals of *Geotrygon*, *Leptotila* and *Zenaida* (Table 1) which represented 24 species and included multiple subspecies for four of these (taxonomy follows Gibbs *et al.*, 2001; GenBank accession numbers AF182663–667, 669, 671, 696, 698–699, 702, 704; AF251530–32, 34, 36–39, 41–42, 44–46; AF258321–24; AF279705–08, 10, 11, 15–18, 20–21, 25–32, 35, 37; AF353401, 14–15, 17, 21, 32, 34, 42; AY443658–62, 80–84; FJ175697; FJ899160; HQ993502–70). Seven outgroup species

were sequenced among the sister clade of the mid-sized New World doves, which includes the genera *Columba*, *Patagioenas*, *Streptopelia*, *Macropygia* and *Reinwardtoena* (Johnson & Clayton, 2000a; Johnson, 2004; Pereira *et al.*, 2007). Polymerase chain reactions (PCR) and sequencing reactions for nuclear beta-fibrinogen intron 7 (FIB7) and mitochondrial cytochrome *b* (cyt *b*) used primers and reaction conditions from Johnson & Clayton (2000a). Amplification, sequencing, and primers for NADH dehydrogenase subunit 2 (ND2) followed the protocols of Johnson & Clayton (2000b). A 379 bp fragment of mitochondrial cytochrome *c* oxidase subunit I (COI) was amplified and sequenced, using primers and protocols described by Johnson *et al.* (2003). These same genes have been used in previous studies of pigeons and doves and are highly informative across a range of divergences in this group (Johnson & Clayton, 2000a,b; Johnson, 2004).

Sequences were aligned by eye using SEQUENCHER v. 3.1 (Gene Codes Corporation, Ann Arbor, MI, USA). Indels were detected in the FIB7 gene, but alignment was straightforward because of the very low homoplasy of indels in this intron for Columbiformes (Johnson, 2004). We constructed a combined data set that included 3608 aligned base pairs: FIB7 (1143 bp), cyt *b* (1045 bp), ND2 (1041 bp), and COI (379 bp). We reconstructed phylogenies from these sequences using both Bayesian Markov chain Monte Carlo (MCMC) searches (MRBAYES v. 3.1.2; Ronquist & Huelsenbeck, 2003) and parsimony reconstruction (PAUP* v. 4.0; Swofford, 2001). For Bayesian analyses we used a partitioned mixed model with GTR + G for FIB7 and GTR + I + G for the mitochondrial genes as determined using MRMODELTEST v. 2 (Nylander, 2004). We calculated posterior probabilities for nodes by sampling trees every 500 generations from a 10,000,000 generation chain. Examination of likelihood scores indicated they had stabilized prior to 250,000 generations, so we conservatively discarded trees from the first 250,000 generations as burn-in to compute posterior probabilities. We used bootstrapping (Felsenstein, 1985) to assess parsimony branch support.

To estimate the timing of divergence events we used BEAST v. 1.4.8 to perform a Bayesian relaxed clock analysis (Drummond & Rambaut, 2007). The general lack of fossil data for birds makes assigning calibration points to particular nodes in the tree difficult. However, within mid-sized New World doves there are two species endemic to islands for which the timing of formation is known: *Zenaida galapagoensis* endemic to the Galapagos Islands (formed 3.3 Ma) and *Zenaida graysoni* endemic to Socorro Island (formed 540,000 years ago), and these dates have been used in prior molecular clock calibrations for birds (Weir & Schluter, 2008). Thus, we used these dates as maximum age calibrations for these speciation events in our dating analysis. For minimum age calibrations we calculated mitochondrial divergence (GTR + I + G) between these island taxa and their sister taxa and divided these divergences by the fastest reported average mitochondrial substitution rate calculated for any avian lineage [4.31% per million years (Myr); Weir & Schluter, 2008]. This rate is over

Table 1 Details of the 39 individuals belonging to the order Columbiformes that were sampled in this study.

Taxon	Voucher number	Institution	Country
Zenaida macroura	DHC98-004	No voucher	USA
Zenaida graysoni	B23847	LSUMNS	Captive
Zenaida auriculata	395842	FMNH	Argentina
Zenaida galapagoensis	KPJ97-006	No voucher	Captive
Zenaida aurita (1)	331052	FMNH	Jamaica
Zenaida aurita (2)	331053	FMNH	Jamaica
Zenaida asiatica	DHC98-001	UUMNH	USA
Zenaida meloda	B5236	LSUMNS	Peru
Geotrygon chiriquensis	B5431	NMNH	Panama
Geotrygon goldmani	B1404	LSUMNS	Panama
Geotrygon frenata frenata	B22781	LSUMNS	Bolivia
Geotrygon frenata erythropareia	B6104	LSUMNS	Ecuador
Geotrygon albifacies	343198	FMNH	Mexico
Geotrygon costaricensis	B1544	NMNH	Panama
Geotrygon lawrencii	B28364	LSUMNS	Panama
Leptotila verreauxi decipiens	B6882	NMNH	Brazil
Leptotila verreauxi chalcauchenia	B25764	LSUMNS	Paraguay
Leptotila verreauxi decolor	CCW-389	LSUMNS	Peru
Leptotila verreauxi fulviventris	B610	KUMNH	Mexico
Leptotila verreauxi angelica	UT5	UUMNH	USA
Leptotila jamaicensis	B2135	KUMNH	Mexico
Leptotila cassini cassini	B26577	LSUMNS	Panama
Leptotila cassini cerviniventris	B321	NMNH	Panama
Leptotila plumbeiceps	B2162	KUMNH	Mexico
Leptotila rufaxilla dubusi	B793	KUMNH	Peru
Leptotila rufaxilla rufaxilla	B9413	NMNH	Guyana
Leptotila megalura	395842	FMNH	Argentina
Geotrygon veraguensis	B76913	UWBMNH	Panama
Geotrygon violacea	B9655	LSUMNS	Bolivia
Geotrygon montana	B995	KUMNH	Peru
Geotrygon purpurata	B11720	LSUMNS	Ecuador
Geotrygon saphirina	B10770	LSUMNS	Peru
Streptopelia semitorquata	B34270	LSUMNS	South Africa
Streptopelia senegalensis	B34209	LSUMNS	South Africa
Columba guinea	B34209	LSUMNS	South Africa
Patagioenas speciosa	B2096	KUMNH	Mexico
Patagioenas fasciata	DHC-1	No voucher	USA
Reinwardtoena browni	B4024	NMNH	Captive
Macropygia mackinlayi	MKL-82	AMNH	Solomon Islands

LSUMNS, Louisiana State University Museum of Natural Science; KUMNH, Kansas University Museum of Natural History; FMNH, Field Museum of Natural History; UWBMNH, University of Washington Burke Museum of Natural History; NMNH, US National Museum of Natural History.

two times faster than the estimated rate for Columbiformes (Weir & Schluter, 2008) and provides a very conservative estimate for the lower bounds for the age of these calibration points. These maximum and minimum age calibrations were used to set the upper and lower bounds on a uniform prior distribution for each calibration point.

For rates, we used the uncorrelated lognormal distribution with mean (parameter ucld.mean) following a uniform distribution between 0.005 and 0.025 substitutions/site/branch/Myr (s/s/b/Myr). The standard deviation for this lognormal prior distribution (parameter ucld.stdev) was also set as uniform and bounded by 0.0 and 10.0 s/s/b/Myr. For the

relaxed clock analysis we used the Bayesian tree as a starting tree and divided the data into two partitions (mitochondrial DNA and FIB7). Each partition had its own model, as determined using MrModeltest and the parameters for each of the models were estimated separately. The positions of all nodes recovered with ≥ 95% posterior probability in the Bayesian phylogenetic analysis were fixed between partitions and the positions of the remaining nodes were allowed to vary. Non-calibrated nodes were assigned a Yule prior with default parameters. We ran beast for 40,000,000 generations sampling output every 1000 generations, and assessed stationarity of the MCMC analysis, parameter effective sample sizes (ESSs), and

posterior intervals using TRACER v. 1.4.1 (Rambaut & Drummond, 2008).

Distributional changes of lineages between North and South America are the result of these continents coming into proximity and connection rather than separation. Thus methods that posit dispersal are appropriate for this biogeographic reconstruction (Johnson & Sorenson, 1999; DaCosta & Klicka, 2008). Note that vicariance might be involved in later separation of populations that expanded their range between North and South America; however, in this case dispersal is still the primary mechanism by which lineages changed their distributional range. We used both parsimony and maximum likelihood reconstructions of biogeographic region (Brooks, 1990) over the Bayesian tree to identify dispersal events between these two major biogeographic regions using MACCLADE v. 3.08 (Maddison & Maddison, 1999) and MESQUITE v. 1.11 (Maddison & Maddison, 2006). The Isthmus of Panama (Canal Zone) was used as the dividing line between coding of North versus South American distributions for each taxon. Two taxa restricted to islands were coded according to the continental affiliation of those islands (Socorro Island – North America; Galapagos Islands – South America). Taxa that have a substantial distribution on either side of the isthmus were coded as polymorphic (Gibbs *et al.*, 2001; Table 1). Some species in our study also have distributions in the Caribbean. All species had a large majority of their distribution in North America, with the exception of the Zenaida dove (*Zenaida aurita*). However, we performed an additional analysis where the Caribbean was coded as a third biogeographic region (using data from Gibbs *et al.*, 2001) and this alternate coding produced largely the same results as strictly binary coding. For maximum likelihood reconstruction we used both Mk1 and Mk2 models as implemented in MESQUITE (Maddison & Maddison, 2006). Because changes in distribution are likely to occur at divergence events, we used an equal branch lengths assumption for the likelihood analyses. Maximum likelihood models cannot account for polymorphic taxa, so these were treated as two terminal taxa coded with alternate character states for the analysis.

We were most interested in portions of the tree where the distribution changed between North and South America and thus identified contrasts in the tree where reconstructions inferred state changes in the geographic distribution (i.e. an inferred dispersal event or range expansion event). Because both the parsimony and maximum likelihood reconstructions revealed that confidence in ancestral state reconstructions for many deeper nodes was very low, we also repeated this assessment using two additional reconstructions. First, we forced any node that was ambiguous under maximum likelihood reconstruction to be reconstructed as South America. We performed a second reconstruction, where we forced these nodes to be reconstructed as North America. These reconstructions, in combination with the equally weighted parsimony reconstructions, provide the range of possibilities for evaluating the timing of dispersal events. Using the Bayesian tree and calibrated chronogram, we estimated the time of divergence for each inferred inter-continental dispersal event, to evaluate when it occurred with respect to the closure of the Isthmus of Panama.

RESULTS

The tree from the Bayesian MCMC searches was well supported with posterior probabilities above 95% for 26 of 31 ingroup nodes (Fig. 1). The parsimony tree was identical to the Bayesian tree except for two branch rearrangements and 23 of 31 ingroup nodes had bootstrap support over 75% (Fig. 1). These analyses supported monophyly for the genera *Leptotila* (100% bootstrap and posterior probability) and *Zenaida* (63% bootstrap, 100% posterior probability). However, the genus *Geotrygon* was paraphyletic. In particular, the species *Geotrygon veraguensis* was recovered as the sister taxon of the genus *Leptotila* (96% bootstrap, 100% posterior probability). Furthermore, a clade of mainly montane species of *Geotrygon* was recovered as the sister taxon of *Zenaida* (100% bootstrap and posterior probability). A third clade of lowland *Geotrygon* species was identified, although support for monophyly of this clade was not as strong (< 90% posterior probability). In the Bayesian tree, this lowland *Geotrygon* clade was recovered as sister to the clade containing the remaining *Geotrygon*, *Leptotila* and *Zenaida*; however, the parsimony tree placed the lowland *Geotrygon* clade as sister to the *G. veraguensis* + *Leptotila* clade. These same paraphyletic relationships of *Geotrygon* were also recovered from separate analyses of mitochondrial versus nuclear genes, revealing support from independent loci for these results. Relationships among species within these clades were generally very well supported (Fig. 1).

Reconstructing biogeographic history over this tree revealed at least fourteen changes in distribution (i.e. inferred dispersal events) between North and South America (Fig. 2). In nine of these cases these dispersal events are associated with differentiation (either a speciation event or subspecific divergence). Using unordered parsimony, there are twenty equally parsimonious reconstructions of biogeographic region, indicating considerable uncertainty in the inferred ancestral distribution, and this uncertainty results from the large number of changes in distribution that occur over the history of this group. These reconstructions range from eight inferred dispersal events from South to North America and one event from North to South America (Fig. 2) to eight dispersal events from North to South America and one from South to North America (Fig. 3). There are also five cases of inferred dispersal from South to North America that has not yet led to differentiation, and these may represent very recent changes in distribution (i.e. polymorphic taxa). Likelihood reconstruction of distributional changes using the Mk1 and Mk2 models revealed a similar number of changes and again there was little certainty regarding the inferred ancestral states and direction of dispersal because of the large number of changes in species distributions across the phylogeny.

Bayesian relaxed molecular clock dating methods (BEAST) revealed that the timing of all (all nine dispersal-driven

divergence events) or nearly all (eight of the nine dispersal-driven divergence events) of these events were approximately at or after the closure of the Isthmus of Panama (Figs 2 & 3). Most of the inter-continental dispersal events appear to have occurred well after the closure of the isthmus and over a range of times. Six nodes could be unequivocally (using parsimony) associated with a change in distribution between continents, and all six of these events occurred after the formation of the land bridge (Table 2).

When nodes that were ambiguous under a maximum likelihood reconstruction were forced to be all North America or all South America the number of changes in distribution was higher than unordered parsimony (15 for North America ancestral and 13 for South America ancestral). All of the inferred reconstruction events from these alternative reconstructions occurred at the time of or after the closure of the isthmus. Thus, even though uncertainty exists regarding the ancestral distribution of these lineages, changes in intercontinental distribution, regardless of direction, are inferred to have occurred mainly after the formation of the isthmus.

Under the most parsimonious reconstructions, the directionality of dispersal is generally uncertain. However, within *Leptotila* dispersal is inferred with more confidence to occur in both directions. The oldest divergence in this genus (3.4 Ma) was inferred as a dispersal speciation event from South America to North America and more recently (0.87 Ma) the northern clade (*Leptotila verreauxi* taxa) radiated back into South America in a north–south direction (Figs 2 & 3). For example, the oldest divergence within *Leptotila verreauxi* is between the northernmost subspecies (*L. v. angelica*) and the subspecies immediately to the south (*L. v. fulviventris*). Divergence appears to have continued in a stepping-stone fashion south across the isthmus and into South America with the most recently diverged subspecies (*L. v. decipiens* and *L. v. chalcauchenia*) being the southernmost in distribution. Conversely, the other clade of *Leptotila* appears to have radiated in the same time frame but in a south–north direction, with the oldest divergences among the southernmost taxa and dispersal events north across this isthmus in the recent past (maximum 0.12 Ma).

Figure 1 Phylogeny of mid-sized New World doves based on Bayesian analysis of the nuclear beta-fibrinogen intron 7 (FIB7) (1143 bp) and mitochondrial cytochrome *b* (cyt *b*; 1045 bp), NADH dehydrogenase subunit 2 (ND2; 1041 bp), and cytochrome *c* oxidase subunit I (COI; 379 bp) genes. Branches are proportional to substitutions per site over the Bayesian consensus tree. Numbers above branches are bootstrap support from parsimony analysis and numbers below branches are posterior probabilities from Markov chain Monte Carlo (MCMC) analysis 10,000,000 generations long. Trees are rooted on a composite outgroup of *Streptopelia*, *Columba*, *Patagioenas*, *Reinwardtoena* and *Macropygia*.
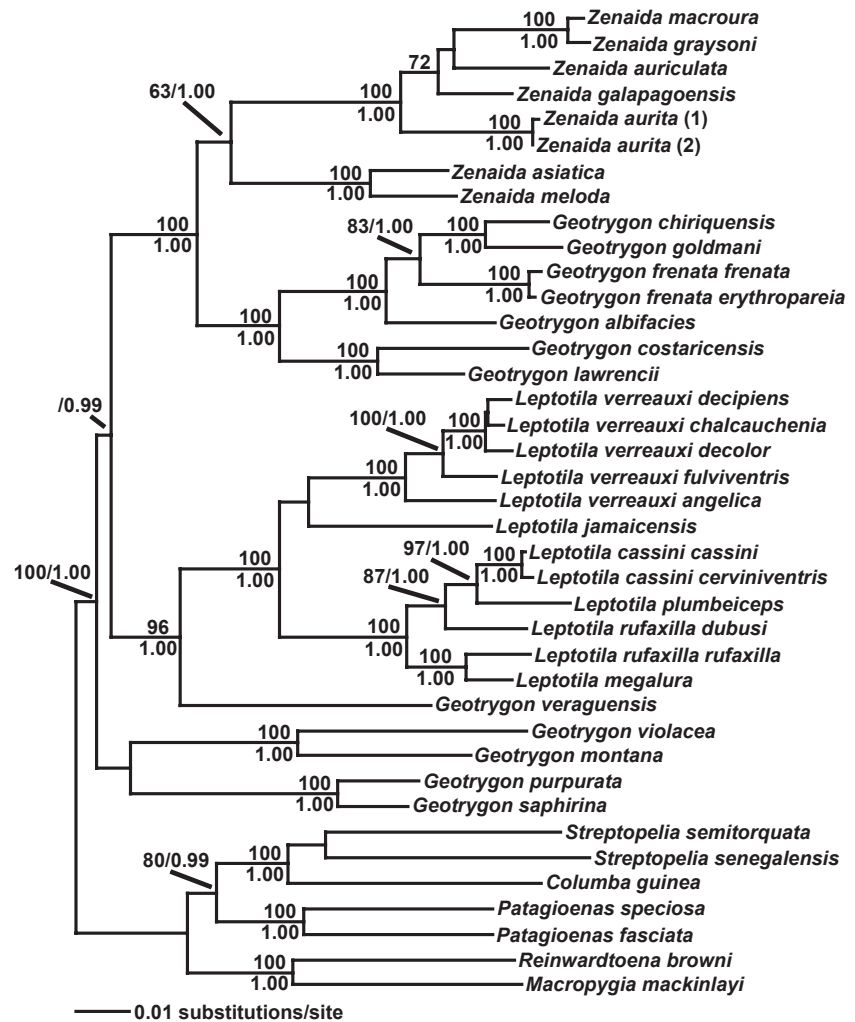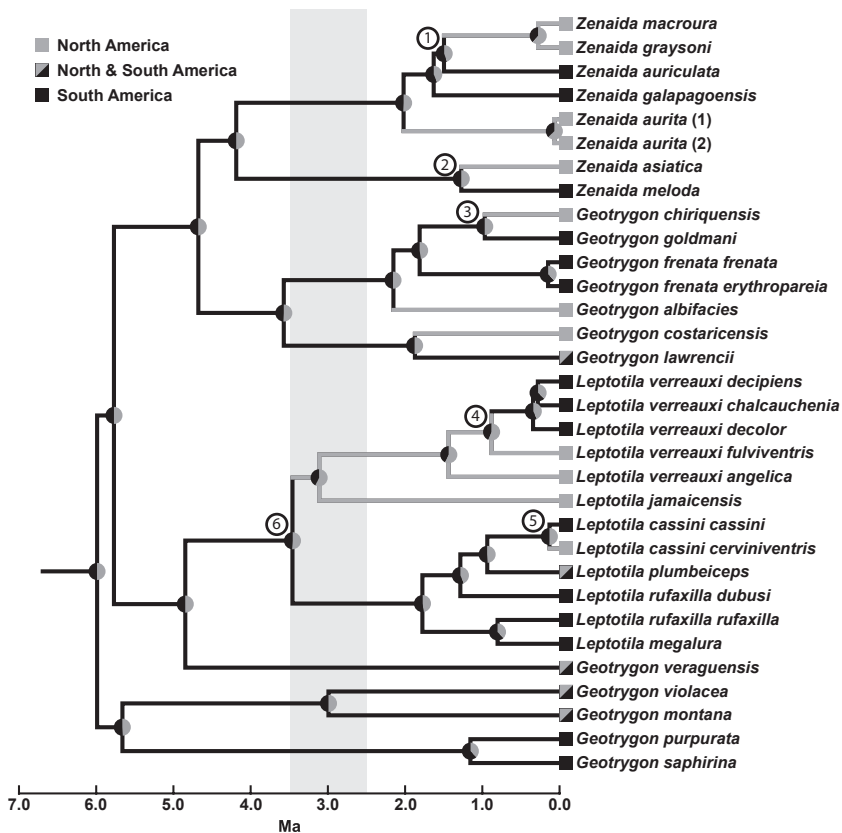
Figure 2 Chronogram from BEAST analysis of DNA sequences for mid-sized New World doves. Number scale indicates million years ago (Ma). The grey vertical shaded bar indicates the timing of the closure of the Isthmus of Panama. Branch shading indicates geographic distribution inferred by 1 of 20 most parsimonious reconstructions showing the highest fraction of *south to north* dispersal events. Changes between North America and South America are inferred dispersal-driven divergence events, and numbered nodes indicate six unambiguous events (see Table 2). Pie charts indicate relative proportional likelihoods under the Mk1 model for North and South America (grey and black, respectively).
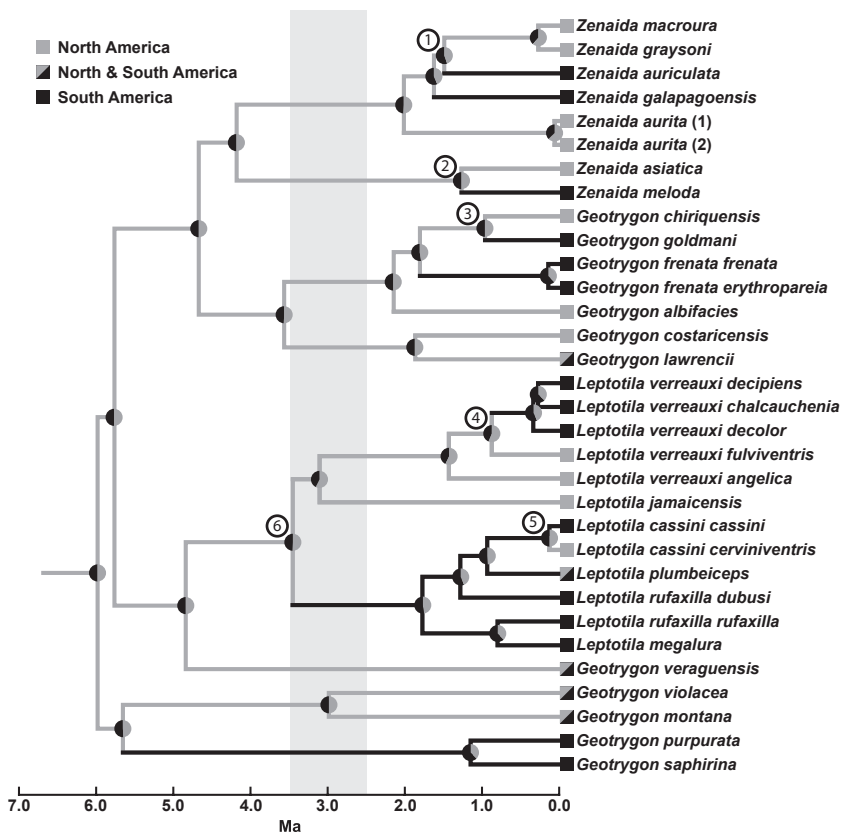

Figure 3 Chronogram from BEAST analysis of DNA sequences for mid-sized New World doves. Number scale indicates million years ago (Ma). The grey vertical shaded bar indicates the timing of the closure of the Isthmus of Panama. Branch shading indicates geographic distribution inferred by 1 of 20 most parsimonious reconstructions showing the highest fraction of *north to south* dispersal events. Changes between North America and South America are inferred dispersal-driven divergence events and numbered nodes indicate six unambiguous events (see Table 2). Pie charts indicate relative proportional likelihoods under the Mk1 model for North and South America (grey and black, respectively).

Table 2 Mean Bayesian divergence times (in million years ago) and 95% highest posterior density (HPD) interval for the six nodes unequivocally (using parsimony) associated with a change in distribution of mid-sized New World doves between North and South America.

Node number*	Mean divergence time (Ma)	95% HPD (lower – upper) (Ma)
1	1.4815	0.8669–2.4763
2	1.2578	0.6003–2.2037
3	0.9531	0.4761–1.6748
4	0.8656	0.4347–1.5133
5	0.1156	0.0363–0.2267
6	3.4436	1.9033–5.8697

*Node numbers are associated with node labels in Figs 2 & 3.

DISCUSSION

Dispersal of mid-sized New World doves between North and South America appears to have been a major factor in their diversification. For these taxa, at least nine dispersal-driven divergence events were detected between the two continental regions. Dispersal between continents accounts for around 30% of the species or subspecies level divergence events in our phylogeny. Furthermore, recent dispersal between North and South America that has not yet resulted in species or subspecies level divergence appears to have occurred in some taxa (five undifferentiated taxa with current distribution in both North and South America). All (or at least the vast majority) of these events occurred after the closure of the Isthmus of Panama connecting these two continents. However, given the large number of changes in distribution, the directionality of most of these events could not be inferred with confidence using parsimony or likelihood approaches. At least some events are inferred in both directions under all of the most parsimonious reconstruction scenarios. If dispersal between continents can occur in either direction, this sets the stage for allopatrically driven radiation. A lineage may colonize one continent from the other, but then experience sufficient geographic and genetic isolation such that it speciates. This could either happen at the time of the dispersal event or by a subsequent vicariance event after dispersal-driven range expansion. This has happened repeatedly in both directions for the mid-sized New World doves, suggesting that once a lineage colonizes and speciates, it may also back colonize its original continent of origin. Based on the timing of these events, the closure of the Isthmus of Panama appears to have facilitated this dispersal-driven speciation. The broad range in timing of these divergences is evidence against a single vicariance event causing isolation of widespread taxa.

If one examines in detail the geographic distribution of taxa in the two *Leptotila* clades, the directionality of these dispersal events is particularly striking. Among the subspecies of *Leptotila verreauxi*, which are as genetically divergent from each other as many other species level taxa in mid-sized doves,

the earliest divergences occurred in the northern part of the range in North America. Divergence then appears to have occurred in a stepping stone fashion down through Central America, across the isthmus, and down into southern South America, with the most terminal divergences being among South American subspecies. This diversification occurred well after the closure of the isthmus. Interestingly, the other major clade of *Leptotila* appears to have diversified in the opposite direction, with the earliest divergences occurring in South America and the most recent divergences occurring northwards across the Isthmus of Panama.

Although the considerable fossil record of mammals has allowed detailed documentation of the direction and timing of dispersal of mammalian lineages across the Isthmus of Panama, birds in general lack such a detailed fossil record and thus uncertainty in the role of the isthmus for avian diversification exists. However, recent studies of wrens (Barker, 2007) and trogons (DaCosta & Klicka, 2008) have indicated a Central American origin for these avian taxa with multiple dispersal events into South America. Studies of other avian lineages have shown that South to North American dispersal is more common (Burns & Racicot, 2009: tanagers; Weir *et al.*, 2009: antbirds, woodcreepers, tanagers, and blackbirds). These dispersal events were repeated within each clade and inferred to have occurred after the formation of the Isthmus of Panama, highlighting the role that this event may have played in generating diversity. Our study of New World doves also indicated that numerous diversification events occurred across the isthmus after its formation, and that dispersal is occurring in both directions.

REFERENCES

Barker, F.K. (2007) Avifaunal interchange across the Panamanian isthmus: insights from *Campylorhynchus* wrens. *Biological Journal of the Linnean Society*, **90**, 687–702.

Brooks, D.R. (1990) Parsimony analysis in historical biogeography and coevolution: methodological and theoretical update. *Systematic Zoology*, **39**, 14–30.

Brown, J.H. & Lomolino, M.V. (1998) *Biogeography*, 2nd edn. Sinauer Associates Inc., Sunderland, MA.

Burns, K.J. & Racicot, R.A. (2009) Molecular phylogenetics of a clade of lowland tanagers: implications for avian participation in the Great American Interchange. *The Auk*, **126**, 635–648.

DaCosta, J.M. & Klicka, J. (2008) The Great American Interchange in birds: a phylogenetic perspective with the genus *Trogon*. *Molecular Ecology*, **17**, 1328–1343.

Drummond, A.J. & Rambaut, A. (2007) Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology*, **7**, 214.

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

Gibbs, D., Barnes, E. & Cox, J. (2001) *Pigeons and doves: a guide to the pigeons and doves of the world*. Yale University Press, New Haven, CT.

Johnson, K.P. (2004) Deletion bias in avian introns over evolutionary timescales. *Molecular Biology and Evolution*, **21**, 599–602.

Johnson, K.P. & Clayton, D.H. (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. & Clayton, D.H. (2000b) A molecular phylogeny of the dove genus *Zenaida*: mitochondrial and nuclear DNA sequences. *The Condor*, **102**, 864–870.

Johnson, K.P. & Sorenson, M.D. (1999) Phylogeny and biogeography of the dabbling ducks (genus: *Anas*): a comparison of molecular and morphological evidence. *The Auk*, **116**, 792–805.

Johnson, K.P., Adams, R.J., Page, R.D.M. & Clayton, D.H. (2003) When do parasites fail to speciate in response to host speciation? *Systematic Biology*, **52**, 37–47.

Maddison, W.P. & Maddison, D.R. (1999) *MacClade: analysis of phylogeny and character evolution, v. 3.08*. Sinauer Associates, Sunderland, MA.

Maddison, W.P. & Maddison, D.R. (2006) *Mesquite: a modular system for evolutionary analysis, v. 1.11*. Available at: http://mesquiteproject.org.

Mayr, E. (1942) *Systematics and the origin of species*. Columbia University Press, New York.

Nylander, J.A.A. (2004) *MrModeltest v2*. Program distributed by the author. Evolutionary Biology Centre, Uppsala University, Uppsala, Sweden.

Pereira, S.L., Johnson, K.P., Clayton, D.H. & Baker, A.J. (2007) Mitochondrial and nuclear DNA sequences support a Cretaceous origin of Columbiformes and dispersal driven radiation in the Paleogene. *Systematic Biology*, **56**, 656–672.

Rambaut, A. & Drummond, A.J. (2008) *Tracer version 1.4*. Available at: http://beast.bio.ed.ac.uk/Tracer.

Ronquist, F. & Huelsenbeck, J.P. (2003) MrBayes 3. Bayesian phylogenetic inference under mixed models. *Bioinformatics*, **19**, 1572–1574.

Simpson, G. (1940) Mammals and land bridges. *Journal of the Washington Academy of Sciences*, **30**, 137–163.

Swofford, D. (2001) *PAUP*: phylogenetic analysis using parsimony (*and other methods), version 4.0, beta*. Sinauer, Sunderland, MA.

Webb, S.D. (1991) Ecogeography and the Great American Interchange. *Paleobiology*, **17**, 266–280.

Weir, J.T. & Schluter, D. (2008) Calibrating the avian molecular clock. *Molecular Ecology*, **17**, 2321–2328.

Weir, J.T., Bermingham, E. & Schluter, D. (2009) The Great American Biotic Interchange in birds. *Proceedings of the National Academy of Sciences USA*, **106**, 21737–21742.

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