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RESEARCH ARTICLE

Patterns of diversification in small New World ground doves are consistent with major geologic events

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ABSTRACT

South America has undergone many dramatic changes during the past 60 million years, which has had a major impact on the patterns of biological speciation and diversity in the region. Birds have been particularly affected, and major geologic events have been an important factor in generating avian diversity in the New World. Here we investigate the impact of two geologic events, Andean uplift and the Panamanian land bridge formation, on the speciation and diversification patterns of birds in the New World using a broadly dispersed clade, the small New World ground doves (Aves: Columbidae). Using complete species-level sampling for the clade (barring 2 possibly extinct species), we used sequences of 4 mitochondrial genes and 1 nuclear gene to infer a phylogenetic tree for the group. To address historical biogeographic questions, we estimated divergence times and reconstructed ancestral ranges. The phylogenetic analysis resulted in a well-supported tree. Divergence time estimates and historical biogeographic reconstruction indicated a South American origin for the clade, with several speciation events coinciding with either Andean uplift events or the land bridge formation. These results indicate how major geologic events affected the diversification of this group of birds, and lead to a broader understanding of the impact of these events on patterns of speciation in New World birds.

Keywords: ground doves, phylogeny, biogeography, Andean uplift, Panamanian land bridge

Los patrones de diversificación de las palomas terrestres pequeñas del Nuevo Mundo son consistentes con los grandes eventos geológicos

RESUMEN

América de Sur ha sufrido muchos cambios dramáticos a lo largo de los últimos 60 millones de años, lo que ha tenido un gran impacto en los patrones de especiación biológica y de diversidad en la región. Las aves han sido particularmente impactadas, y los grandes eventos geológicos han sido un factor importante para generar diversidad de aves en el Nuevo Mundo. Aquí investigamos el impacto de dos eventos geológicos, la elevación de los Andes y la formación del puente terrestre de Panamá, sobre los patrones de especiación y diversificación de las aves en el Nuevo Mundo, usando un clado ampliamente disperso, las palomas terrestres pequeñas del Nuevo Mundo (Aves: Columbidae). Usando un muestreo completo a nivel de especie para el clado (salvo dos especies posiblemente extintas), empleamos secuencias de cuatro genes mitocondriales y un gen nuclear para inferir un árbol filogenético para el grupo. Para abordar preguntas de biogeografía histórica, estimamos los tiempos de divergencia y reconstruimos los rangos ancestrales. El análisis filogenético resultó en un árbol filogenético con buen soporte. Las estimaciones del tiempo de divergencia y la reconstrucción biogeográfica histórica indicaron un origen sudamericano del clado, con varios eventos de especiación coincidentes con los eventos de elevación de los Andes o con la formación del puente terrestre. Estos resultados indican como los grandes eventos geológicos impactaron en la diversificación de este grupo de aves, permitiendo un entendimiento más amplio del impacto de estos eventos en los patrones de especiación de las aves del Nuevo Mundo.

Palabras clave: biogeografía, elevación de los Andes, filogenia, palomas terrestres, puente terrestre de Panamá

INTRODUCTION

Since breaking off from the Gondwanan supercontinent 140–160 mya (Jokat et al. 2003, Upchurch 2008), South America has undergone several major geologic events that have helped define the diversity of the continent's biota. Speciation and diversification patterns in New World birds have historically been the foci of many studies (Wallace 1889, Chapman 1917, Chesser 2004), which is largely attributable to the high concentration of species in the area (~35% of all bird species are endemic to the Neotropics). Because of their diversity and geographic range, birds are excellent organisms for studying how major New World geologic events have influenced regional diversification

patterns. Two events that have particularly affected New World avian diversity are Andean uplift and the formation of the Panamanian land bridge.

Andean uplift had a dramatic impact on South American geology, climate, and biogeography. Uplift in the South and Central Andes began >60 mya, with more recent uplift in the north. By 25 mya the Western Cordillera of the Central Andes was at 50% of its current elevation, but underwent a drastic increase in elevation (2,000–3,500 m) between 6 and 10 mya (Gregory-Wodzicki 2000, Garzione et al. 2008), although Garzione et al. (2014) presented evidence for two separate rapid uplift events (13–16 mya and 9–13 mya). The uplift of the Eastern Cordillera of the Northern Andes occurred more recently, with evidence of a rapid elevation increase between 2.5 and 7.0 mya (Hoorn et al. 1995, 2010). These gradual and rapid uplift events, coupled with resulting changes in weather, climate, and ecology, most likely had an incredible impact on avian diversification patterns and rates throughout the continent (Fjeldsa 1994). Many consider Andean uplift a key factor contributing to the patterns of speciation that underlie the current avifaunal diversity of the region (Vuilleumier 1969, Cracraft and Prum 1988, Bates et al. 1998, Cheviron et al. 2005, Fjeldsa and Rahbek 2006, Fjeldsa and Irestedt 2009, Quintero et al. 2012).

The dry Puna grasslands of the Central Andes' Altiplano Plateau are an example of novel habitat formed as a direct result of Andean uplift. As the Andes gradually increased in elevation, the Altiplano Plateau became separated from the surrounding lowlands, and was probably isolated ~15 mya. The plateau was at 50% of its current elevation 10 mya, and reached its current elevation of 3,200–3,700 m following a recent, rapid uplift (Vandervoort et al. 1995, Gregory-Wodzicki 2000, Hoke and Garzione 2008). Between 10 and 15 mya, climate changes in the Central Andes resulted in a drier and cooler environment, which directly altered the biota of the Puna grasslands (Simpson 1975, Ehlers and Poulsen 2009). High elevation and extreme climatic conditions created a unique, isolated environment to which specific flora and fauna adapted (Szumik et al. 2012). Avian taxa in the region would have become isolated from taxa in surrounding areas, perhaps specifically from the southern open lowlands (Fjeldsa et al. 2012). This isolation probably contributed to the currently low species overlap between the Puna–Altiplano and adjacent lowland and cloud forest habitats (Lloyd and Marsden 2008, Lloyd et al. 2010).

A second major geologic event that had a great impact on New World biogeography was the formation of the Panamanian land bridge, which occurred ~2.5–3.2 mya (Keigwin 1978, Coates et al. 1992, Coates and Obando 1996, Wegner et al. 2010, Leigh et al. 2013), although earlier formation has been proposed more recently (Farris

et al. 2011, Montes et al. 2012, Bacon et al. 2013). Before this terrestrial connection between North and South America, faunas endemic to these two continents were separated by water. With the formation of the land bridge, flora and fauna could move freely between continents, which some have dubbed the "Great American Interchange" (Simpson 1950, 1980, Stehli and Webb 1985). Mammalian fossil records from both continents indicate dispersal events close to the time of land bridge formation, with species moving between the two continents (Marshall 1988, Stehli and Webb 1985). Due to their ability to fly, avian dispersal between continents was sometimes suggested to be uninhibited by the water barrier that existed prior to land bridge formation (Voelker 1999, Lomolino et al. 2006), and the sparse avian fossil record has made it difficult to prove otherwise (Vuilleumier 1985). However, several historical biogeographic reconstructions of Neotropical and Nearctic bird species based on molecular data have indicated that many species were hindered from dispersing between continents due to the water barrier (Barker 2007, Burns and Racicot 2009, Sedano and Burns 2010, Johnson and Weckstein 2011, Pulgarin-R et al. 2013). Instead, the timing of dispersal events appears similar to that of mammals, soon after land bridge formation (Smith and Klicka 2010). Also, there are more instances of North American species successfully dispersing into South America than vice versa, perhaps because a transition from a Nearctic to a Neotropical climate is easier than the reverse (Smith and Klicka 2010).

To understand the impact of these two major New World geologic events on avian evolutionary history, an ideal study group would be one having representatives in both North and South America, as well as in lowland and Andean zones. One such group is the small New World ground dove clade (Aves: Columbidae). This group of 17 species and 45 subspecies contains the genera *Metriopelia*, *Claravis*, *Uropelia*, and *Columbina*. Two species have often been placed within a fifth genus, *Scardafella* (e.g., Goodwin 1983, del Hoyo et al. 1997, Gibbs et al. 2001), but are otherwise included within *Columbina* (American Ornithologists' Union 1998). Two of the 17 species have not been detected recently (*Columbina cyanopis* and *Claravis godefrida*) and may be extinct. The overall geographic range of this group covers the southern United States, Central America (including the Caribbean Islands), and most of South America. Several phylogenies have indicated that this group forms a monophyletic clade, although the placement of the clade within Columbidae is still unclear. Some phylogenies have placed the small New World ground doves as sister to the rest of the family (Johnson and Clayton 2000, Johnson 2004, Johnson et al. 2010), but other work has placed the group as nested within the family (Shapiro et al. 2002, Pereira et al. 2007, Gibb and Penny 2010). Relationships among the species within this

clade, however, have yet to be addressed in detail. Furthermore, given the widespread distribution of this clade throughout Central and South America, this group could provide great insight into how past geologic events in this region have influenced current biological patterns of distribution and speciation. Here, we reconstruct the phylogeny of the small New World ground dove clade based on several gene regions. We then use this phylogeny in a molecular dating analysis to evaluate the effects of Andean uplift and the appearance of the Panamanian land bridge on the timing of divergence in this group. If Andean uplift events did not have a major effect on the speciation patterns of these clades, then our estimated timing of relevant speciation events would not be expected to correlate with the timing of these events. In particular, we would not expect high-Andean species nor sister taxa currently separated by the Andean range to have divergence estimates correlated with Andean uplift events. Similarly, if land bridge formation did not have a significant effect on the speciation patterns of small New World ground doves, then our results would not be expected to indicate dispersal events consistent with the timing of land bridge formation. More specifically, we would expect the discovery of dispersal events occurring before the estimated formation of the land bridge.

MATERIALS AND METHODS

DNA Sequencing

Using a Qiagen Blood and Tissue Kit (Qiagen, Valencia, California, USA; catalogue # 69506), we extracted DNA from tissues and feather samples of 15 extant species of the small New World ground dove clade, including 16 subspecies from 10 species, for a total of 26 in-group samples (Table 1). The remaining 10 samples were either from monotypic species or were duplicate samples of a subspecies. Using PCR (polymerase chain reaction), we amplified portions of 4 mitochondrial loci—cytochrome b (Cytb), NADH dehydrogenase subunit 2 (ND2), cytochrome oxidase subunit 1 (CO1), and ATP synthase 8 (ATP8)—and 1 nuclear locus, beta-fibrinogen intron (FIB7), which have been used successfully in previous studies of the phylogeny of Columbiformes (Johnson and Clayton 2000, Johnson et al. 2001, Periera et al. 2007). For Cytb we used the primers L14841 and H4a to amplify the gene, along with the sequencing primers L15517 and H15299 (Kocher et al. 1989, Harshman 1996). To amplify ND2 we used the primers L5215 and H6313 (Johnson and Sorenson 1998), and used L5758s and H5766s (Price et al. 2004) internally for sequencing. To amplify and sequence CO1 we used the primers L6625 and H7005 (Hafner et al. 1994). To amplify and sequence ATP8 we used the primers CO2GQL and A6MNH (Lovette et al. 1998). We amplified the nuclear intron FIB7 with the primers FIBB17U and FIBB17L (Prychitko and Moore 1997) and the internal sequencing primers FIBDOVEF and FIBDOVER (Johnson and Clayton 2000). We amplified selected loci using PCR according to previously used protocols for each locus (Johnson 2004, Pereira et al. 2007). Resulting amplified products were purified with a Qiagen PCR Purification Kit (catalogue # 28106) and sequenced using ABI Prism BigDye Terminators (Applied Biosystems, Foster City, California, USA) and Sanger DNA sequencing on an AB 3730xl DNA Analyzer (Applied Biosystems, Foster City, California, USA) at the University of Illinois Roy J. Carver Biotechnology Center, Champaign, Illinois, USA. We reconciled resulting complementary chromatograms and trimmed primer sequences by eye using Sequencher version 5.0.1 (Gene Codes, Ann Arbor, Michigan, USA). For out-groups, we selected representatives outside the New World ground dove clade from 2 genera in each of 5 monophyletic clades within Columbidae identified in Pereira et al. (2007), using previously published sequences (Table 1). In one case we were unable to amplify and sequence a gene for one extract, and this was coded as missing data.

Phylogenetic Analysis

We aligned the edited sequences for each of the five loci using the default gap opening and gap extend parameters in program MUSCLE (Edgar 2004), and checked each alignment by eye using SeaView version 4 (Gouy et al. 2010). To check for major discordance between individual gene trees, we created neighbor-joining and majority-rule maximum parsimony trees (100 random sampling replicates, tree bisection and reconnection [TBR] branch swapping, 100 bootstrap replicates) for each gene alignment in program PAUP* (Swofford 2003). Since these gene trees did not have any nodes that strongly conflicted in bootstrap support (>75%), we concatenated the data using SeaView version 4. We also computed the pairwise distance values for the mitochondrial data using PAUP* (Supplementary Material Table S1).

Using the concatenated dataset, we performed Bayesian and Maximum Likelihood (ML) analyses using mixed models. We determined the appropriate substitution model for each gene partition by calculating AIC (Akaike's Information Criterion; Akaike 1974) values for 88 different models in program jModelTest2 (Darriba et al. 2012). Based on the AIC results, we applied a general time reversible model with a proportion of invariant sites and a four-category gamma distribution (GTR + I + G model) to the mitochondrial loci (CO1, Cytb, ND2, ATP8), and a GTR + G model to the nuclear locus (FIB7).

We performed our ML analysis on the concatenated dataset using program GARLI 2.0 (Zwickl 2006), applying the appropriate models for each gene partition and running 500 bootstrap replicates. We obtained a 50%

TABLE 1. Samples included in our study of small New World ground dove phylogeny. GenBank accession numbers are indicated for the 4 mitochondrial loci—cytochrome b (Cytb), NADH dehydrogenase subunit 2 (ND2), cytochrome oxidase subunit 1 (CO1), and ATP synthase 8 (ATP8)—and 1 nuclear locus, beta-fibrinogen intron (FIB7), that we sequenced. Voucher indicates location and museum accession number of each sample. Locality is the collection location.

Genus	Species	Extract code	Voucher	Locality	Cytb	ND2	CO1	ATP8	FIB7
In-groups									
Columbina	passerina	Copas.1.26.1998.1	KUMNH B1755	USA: Missouri	KJ639102	KJ645745	KJ630887	KJ630861	KJ668695
Columbina	passerina	CopasTX.9.8.1998.10	176	USA: Texas	KJ639082	KJ645725	KJ630867	KJ630841	KJ668676
Columbina	passerina	Copas1878.10.28.1998.1	KUMNH B1878	Mexico	KJ639097	KJ645740	KJ630882	KJ630856	KJ668690
Columbina	passerina	Copas8166.8.1.2006.9	ANSP8166	Ecuador	KJ639095	KJ645738	KJ630880	KJ630854	KJ668688
Columbina	passerina	Copas16864.8.1.2006.10	LSU B16864	Bahamas	KJ639091	KJ645734	KJ630876	KJ630850	KJ668684
Columbina	minuta	Comin.5.6.1998.3	DFS92-210	Brazil	KJ639100	KJ645743	KJ630885	KJ630859	KJ668693
Columbina	buckleyi	Cobuc956.6.8.2001.4	LSU RCF956	Peru	KJ639079	KJ645722	KJ630864	KJ630838	KJ668673
Columbina	talpacoti	Cotal1504.10.28.1998.8	FMNH SML86-107	Bolivia	KJ639088	KJ645731	KJ630873	KJ630847	KJ668681
Columbina	talpacoti	Cotal9763.10.6.1998.3	NMNH B09763	Guyana	KJ639101	KJ645744	KJ630886	KJ630860	KJ668694
Columbina	picui	Copic.1.26.1998.5	KUMNH B153	Paraguay	KJ639094	KJ645737	KJ630879	KJ630853	KJ668687
Columbina	picui	Copic458.8.1.2006.5	KGM458	Argentina	KJ639080	KJ645723	KJ630865	KJ630839	KJ668674
Columbina	cruziana	Cocru154.11.26.2003.5	REW154	Peru	KJ639084	KJ645727	KJ630869	KJ630843	KJ668678
Columbina	cruziana	Cocru85.8.1.2006.11	REW85	Peru	KJ639089	KJ645732	KJ630874	KJ630848	KJ668682
Claravis	pretiosa	Clpre.1.26.1998.3	KUMNH B85	Paraguay	KJ639096	KJ645739	KJ630881	KJ630855	KJ668689
Claravis	pretiosa	Clpre2154.10.28.1998.2	KUMNH B2154	Mexico	KJ639087	KJ645730	KJ630872	KJ630846	KJ668680
Claravis	mondetoura	Clmon16221.8.1.2006.4	LSU B16221	Costa Rica	KJ639093	KJ645736	KJ630878	KJ630852	KJ668686
Metriopelia	ceciliae	Mecec.4.23.1998.4	LSU B23851	Captive	KJ639085	KJ645728	KJ630870	KJ630844	KJ668679
Metriopelia	ceciliae	Mecec382.6.8.2001.3	LSU CCW382	Bolivia	KJ639081	KJ645724	KJ630866	KJ630840	KJ668675
Metriopelia	morenoi	Memor.10.6.1998.5	NMNH B05812	Argentina	KJ639083	KJ645726	KJ630868	KJ630842	KJ668677
Metriopelia	melanoptera	Memel273.5.15.2003.15	REW273	Peru	KJ639086	KJ645729	KJ630871	KJ630845	—
Metriopelia	melanoptera	Memel443.8.1.2006.6	KGM443	Argentina	KJ639092	KJ645735	KJ630877	KJ630851	KJ668685
Metriopelia	aymara	Meaym432.8.1.2006.12	KGM432	Argentina	KJ639099	KJ645742	KJ630884	KJ630858	KJ668692
Columbina	inca	Coinc1.9.16.1997.1	1	USA: Arizona	KJ639103	KJ645746	KJ630888	KJ630862	KJ668696
Columbina	inca	CoincTX.9.8.1998.8	123	USA: Texas	KJ639090	KJ645733	KJ630875	KJ630849	KJ668683
Columbina	squammata	Scsqu.5.6.1998.11	SML88-153	Venezuela	KJ639104	KJ645747	KJ630889	KJ630863	KJ668697
Uropelia	campestris	Urcam925.6.8.2001.5	LSU CCW925	Bolivia	KJ639098	KJ645741	KJ630883	KJ630857	KJ668691
Out-groups									
Columba	livia	Coliv423	UT 423	USA: Utah	AF182694	AF353433	EF373367	EF373446	AF182661
Chalcophaps	stephani	Chste	NMNH B4013	Papua New Guinea	AY443673	EF373328	EF373365	EF373439	EF373477
Ducula	bicolor	Dubic	LSU B19214	Captive	AF182705	KF446740	KJ630891	AY443632	AF182672
Geopelia	cuneata	Gecun	KUMNH B1586	Captive	AF182711	KC484595	KJ630890	AY443645	AF182678
Goura	cristata	Gocri	KUMNH B1588	Captive	AF182709	EF373336	EF373374	EF373453	AF182676
Leucosarcia	melanoleuca	Lemel	LSU B20539	Captive	AF182712	EF373341	EF373379	EF373458	AF182679
Oena	capensis	Oecap	FMNH SMG-4180	Madagascar	AF182707	EF373345	EF373383	EF373462	AF182674
Phapitreron	amethystinus	Phame	FMNH ATP92-109	Philippines	AF182706	EF373349	EF373387	EF373466	AF182673
Treron	calvus	Trcal	AMNH ALP80	Central African Republic	AY443674	EF373354	EF373392	EF373471	AY443696
Zenaida	macroura	Zemac5	UT 5	USA: Arizona	AF182703	EF373359	EF373397	EF373476	AF258321

majority-rule consensus tree from the bootstrap replicates using program SumTrees version 1.0.2 (Sukumaran and Holder 2008), and edited the resulting tree in FigTree version 1.4 (Rambault 2012). We also created a concatenated dataset of the four mitochondrial loci in order to compare the resulting tree with the tree for the full dataset. We generated the mitochondrial tree in GARLI 2.0 using the same methods as for the full dataset.

For the Bayesian analysis, we used program MrBayes version 3.2 (Ronquist and Huelsenbeck 2003). As with the ML analysis, we used a mixed-model analysis and assigned appropriate models to the gene partitions based on the AIC results. We ran 4 runs with 4 chains for 20 million generations under MCMC (Markov chain Monte Carlo) sampling every 1,000 trees, and viewed the trace files in program Tracer version 1.4 (Rambaut et al. 2007) to ensure chain mixture and stationarity of the MCMC data. Based on the trace files, we discarded the first 2 million generations (10%) as burn-in and edited the resulting 50% majority-rule consensus tree in FigTree version 1.4 (Rambaut 2012).

Divergence Time Estimation

In order to estimate divergence times, we created a chronogram using program BEAST version 1.7.5 (Drummond et al. 2012). We partitioned the data into mitochondrial and nuclear loci, and applied a strict molecular clock estimate of $1.96 \pm 0.10\%$ myr^{-1} divergence between two taxa (i.e. 0.0098 ± 0.0005 $substitutions^{-1}$ $site^{-1}$ $lineage^{-1}$ myr^{-1}) under a normal distribution for the mitochondrial partition and a Yule speciation process model. This estimate was based on Weir and Schluter (2008), who showed that a molecular clock of 2% myr^{-1} accumulated pairwise divergence between lineages could be used for dating avian phylogenies. Several avian phylogenetic studies have used this estimate to infer seemingly accurate divergence estimates (Milá et al. 2009, Qu et al. 2010, Sedano and Burns 2010). In particular, Weir and Schluter (2008) determined an average rate of pairwise divergence between two taxa at $1.96 \pm 0.10\%$ myr^{-1} for Columbiformes. We ran our MCMC runs for 20 million generations in program BEAST, sampling every 1,000 trees, and discarding the first 2 million (10%) generations as burn-in based on the trace plot in Tracer version 1.4.

Biogeographic Analysis

Since one of our main historical biogeographic questions centered on the formation of the Panamanian land bridge, we reconstructed ancestral geographic ranges with a focus on whether particular species in the clade are currently found in North or South America. We primarily used both parsimony reconstruction and likelihood character mapping over the tree created using program BEAST, since our focus was on the dispersal events between North and South America after the formation of the Panamanian land bridge,

rather than vicariance events. In this biogeographic scenario, methods such as dispersal-vicariance analysis (DIVA) that assume vicariance as the null model are inappropriate. Such models are biased toward vicariance events, and could therefore incorrectly attribute a speciation event to vicariance rather than to dispersal (see Johnson and Weckstein 2011 and Bess et al. 2014 for further rationale). In this case, North America and South America came into contact, rather than separating from each other, so scenarios that posit vicariance are not biogeographically plausible. For the parsimony analysis, we coded each species as 1 of 2 character states: having a primarily North American range, or having a primarily South American range. Species that are widespread on both continents were given a polymorphic character state. For the likelihood analysis, we coded species with ranges spanning both continents as having a third character state, rather than being polymorphic (because current implementations of these maximum-likelihood reconstructions do not allow for more than two character states). We implemented the character reconstruction and mapping in Mesquite version 2.75 (Maddison and Maddison 2011). For the purpose of comparison, we analyzed our data using methods in which vicariance was the null model, such as S-DIVA (Yu et al. 2010) and Bayesian binary MCMC (BBM) as implemented in program RASP version 2.1b (Yu et al. 2013), as well as using the dispersal-extinction-cladogenesis (DEC) model in program Lagrange (Ree and Smith 2008). All three analyses used the same geographic coding as described above in our parsimony reconstruction analysis. For the BBM model, we ran the MCMC for 5 million generations, sampling every 1,000 trees, and discarded the first 500 trees (10%) as burn-in.

RESULTS

Phylogenetic Analysis

The final program MUSCLE–generated alignment of the concatenated dataset was 4,018 characters, with a >95% complete matrix (only ~5% gaps or missing data). Many of the gaps came as a result of a large (665 base pairs) insertion or deletion (indel) in the FIB7 gene for both *Claravis pretiosa* specimens. Both the ML and Bayesian analyses generated similar trees (Figure 1), with support for the Bayesian analysis reaching stationarity, convergence based on the trace plots, and effective sample sizes >200 for all parameters. In addition, the ML mitochondrial tree generated in program GARLI did not have any major conflicting nodes (<75% bootstrap) with the fully concatenated tree. The concordant gene trees, mitochondrial and full trees, and ML and Bayesian trees support our decision to concatenate our data, and give credence to the robustness of subsequent results. The majority of in-group nodes (19/23) received high support (>90 bootstrap and >0.95 posterior probability) from both methods. There
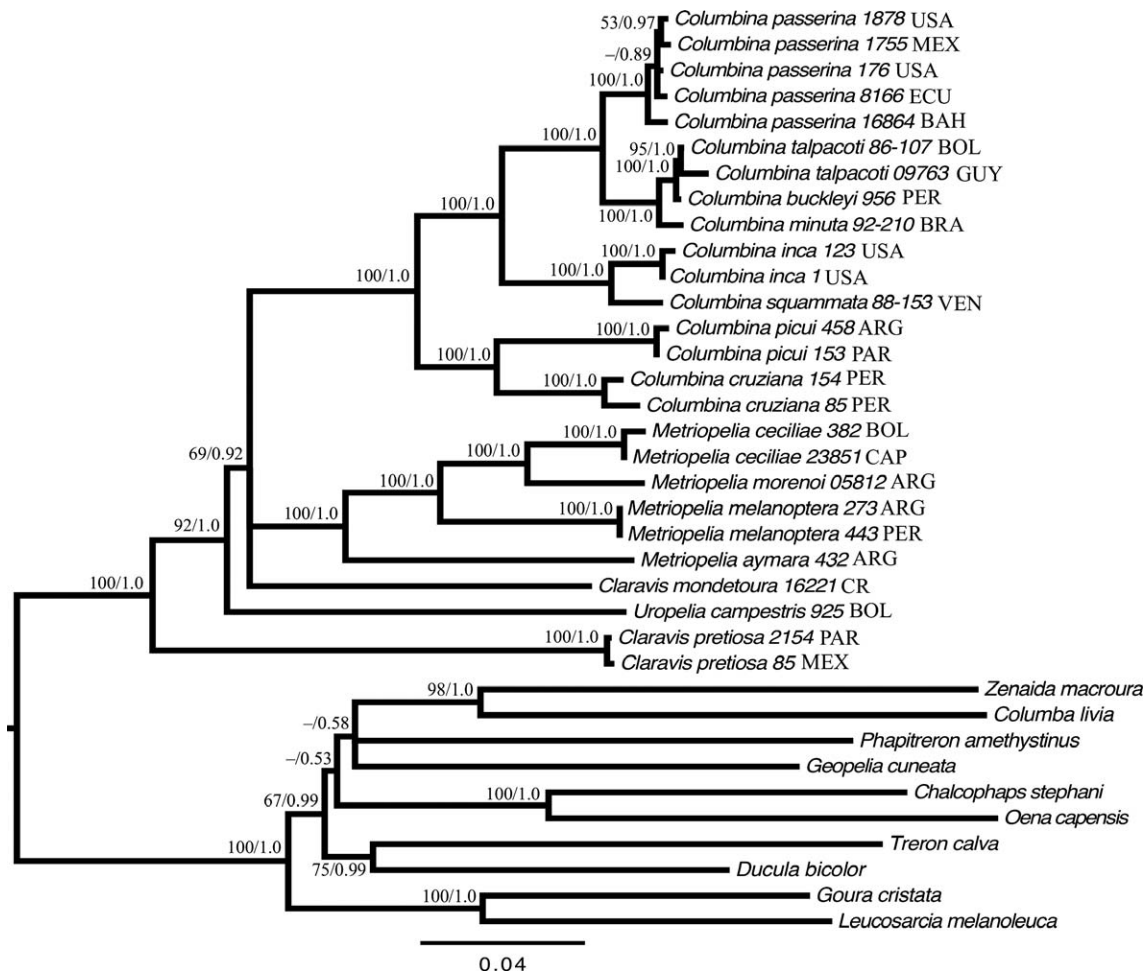
FIGURE 1. Maximum Likelihood and Bayesian tree of small New World ground doves. Support values are indicated at each node, with bootstrap values appearing first, followed by posterior probability values. Dashes indicate that the particular node was not recovered in the appropriate analysis. Scale bar indicates nucleotide substitutions per site. Numbers associated with each taxon name are museum voucher numbers, and are indicated in Table 1. The letter code at the end of each taxon name indicates the country of origin of the sample, as follows: ARG = Argentina, BAH = Bahamas, BOL = Bolivia, BRA = Brazil, CAP = captive, CR = Costa Rica, ECU = Ecuador, GUY = Guyana, MEX = Mexico, PAR = Paraguay, PER = Peru, USA = United States, and VEN = Venezuela.

was modest support (67 bootstrap, 0.92 posterior probability) for the clade comprising *Claravis mondetoura*, *Metriopelia*, and *Columbina*. However, a clade comprising *Claravis mondetoura*, *Metriopelia*, *Columbina*, and *Uropelia*, to the exclusion of *Claravis pretiosa*, was highly supported (100 bootstrap, 1.00 posterior probability). The program BEAST–generated tree placed *Claravis mondetoura* as sister to *Metriopelia*, but with low posterior probability (<0.70). These results indicate that the genus *Claravis* is paraphyletic. All trees placed *Claravis pretiosa* as sister to all other small New World ground doves. The monotypic genus *Uropelia* also appeared to be highly divergent from other taxa, being placed as sister to the rest of the group excluding *Claravis pretiosa*. This placement of *Uropelia* and *Claravis pretiosa* is consistent with past phylogenies constructed with fewer species represented (Johnson and Clayton 2000, Pereira et al. 2007).

Divergence Time Estimation

Program BEAST produced a chronogram consistent with the program GARLI and MrBayes analyses, with support for convergence based on the trace files. The only major difference between the tree generated in program BEAST and the ML- and Bayesian-generated trees was the placement of *Claravis mondetoura* as sister to *Metriopelia* (Figure 2). Based on the 95% credibility intervals, the small New World ground dove clade diverged from other pigeons and doves ∼19–26 mya and began to radiate ∼13–18 mya. Some species have diverged from each other quite recently, e.g., *Columbina squammata* and *C. inca* (<2.5 mya), and *C. talpacoti*, *C. buckleyi*, and *C. minuta* (<2 mya). *Metriopelia* and *Columbina* diverged from each other ∼11–14 mya, with divergences within *Metriopelia* beginning ∼9 mya and within *Columbina* beginning ∼7.5 mya. The divergence dates that we estimated are
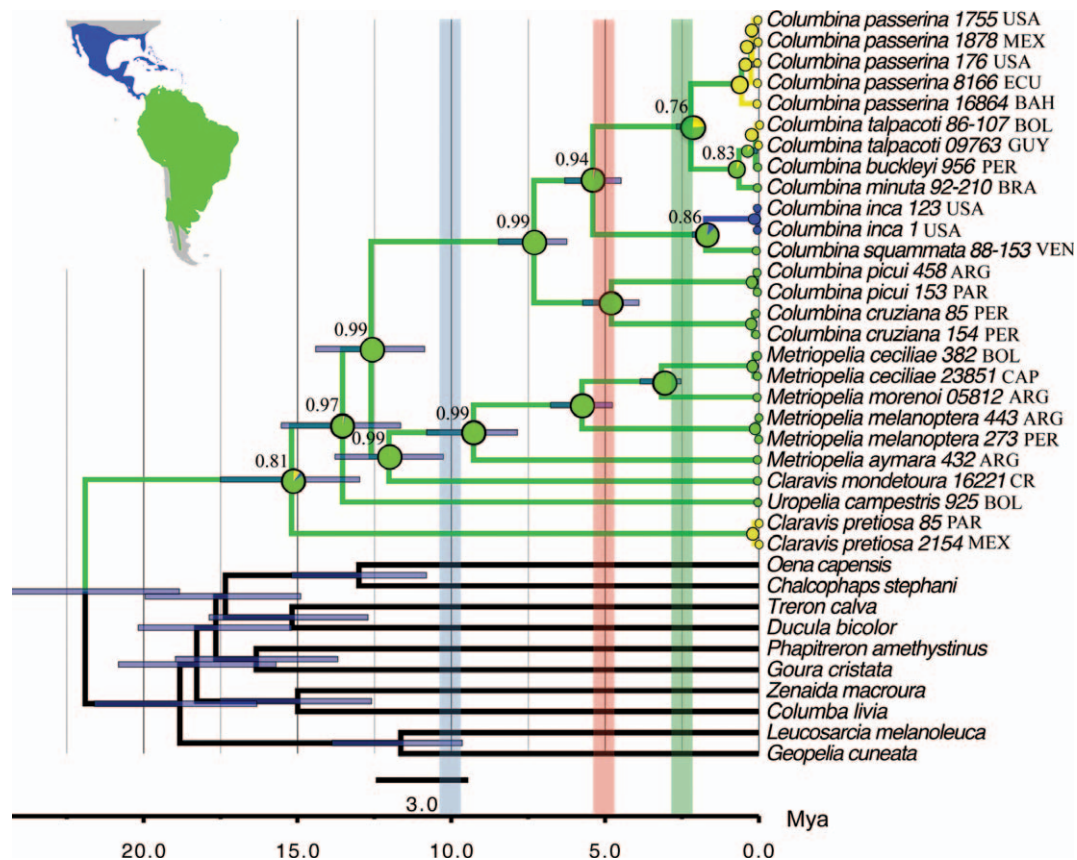
FIGURE 2. Chronogram generated by BEAST version 1.7.4 (Drummond et al. 2012) and biogeographic reconstruction of small New World ground doves. Time along the bottom axis is listed in millions of years before present, and blue error bars over each node indicate the 95% credibility intervals of the node age estimates. Colored branches of the in-group indicate results of the parsimony biogeographic reconstruction, and the pie charts over each node indicate the likelihood that a region is the ancestral area for that particular clade. Values to the upper-left of each pie chart are the proportional likelihoods for the most likely ancestral area at each respective node. Likelihoods of >0.99 for a particular area at a node are not indicated. Color indication for each region is as follows: green = South America, blue = North America, yellow = widespread on both continents. The map indicates the overall distribution of the small New World ground dove clade in relation to the geographic regions under consideration. Columns indicate the approximate estimated timing for three major geologic events. The blue column indicates the approximate timing of the rapid elevation increase in the central Andean plateau, the red column indicates the approximate rapid elevation increase in the Northern Andes, and the green column indicates the approximate estimate for the Panamanian Land Bridge formation. Scale bar indicates nucleotide substitutions per site. Country codes are as in Figure 1.

considerably more recent than the estimates of Pereira et al. (2007), who reported a divergence time of >50 mya for the small New World ground dove clade, with divergences within the clade beginning >30 mya. However, Pereira et al. (2007) used several external calibrations on deep and highly divergent nodes and an internal minimum age constraint based on the oldest Columbiformes fossil for divergence estimates. Using solely external calibrations on such deep nodes can be misleading (Ho et al. 2008).

Biogeographic Analysis
Both parsimony and likelihood reconstructions of historical biogeographic regions indicated an ancestral origin in South America for the small New World ground dove clade, with multiple colonization events of North America

(Figure 2). All of these colonization events were inferred to have occurred after ~2 mya. As expected, the ancestral area reconstructions implemented in programs S-DIVA and Lagrange seemed to be biased toward vicariance events, and produced results that are unlikely. For example, while both analyses estimated a South American origin for the clade, both estimated the ancestor of *Columbina inca* and *C. squammata* as being widespread in both North and South America, and indicated a subsequent separation by vicariance. This is in contrast to the parsimony and likelihood character reconstructions, which estimated the ancestor of *C. inca* and *C. squammata* as present in South America, with subsequent dispersal into North America. The BBM model estimated an identical scenario, as the results from the MCMC chain

produced posterior probabilities nearly identical to the likelihood values at each node over the entire tree (likelihood values recorded as pie charts over each node in Figure 2).

DISCUSSION

Phylogenetic Relationships of Small New World Ground Doves

Phylogenetic relationships among small New World ground doves based on nuclear and mitochondrial gene regions, with comprehensive species-level sampling, are generally well-resolved and well-supported. This tree is broadly in agreement with previous, less exhaustive phylogenetic analyses that included some members of this clade (Johnson et al. 2001, Shapiro et al. 2002, Pereira et al. 2007); however, some important novel results emerged from our comprehensive analysis. Similarly to prior results, we estimated *Claravis pretiosa* as sister to the rest of the clade, with *Uropelia* estimated as sister to *Metriopelia* plus *Columbina* (Table 1). Both *Metriopelia* and *Columbina* were estimated as monophyletic with high support (100 bootstrap, 1.0 posterior probability). The molecular tree also placed *Columbina inca* and *C. squammata* within *Columbina*. These two species are often placed in a separate genus (Goodwin 1983, del Hoyo et al. 1997, Gibbs et al. 2001), *Scardafella*, but the American Ornithologists' Union recognizes them as members of *Columbina* (Lack 2003, American Ornithologists' Union 1998). Since the clade is nested within *Columbina* based on comprehensive sampling, this provides further support for the inclusion of this clade within the genus. Recognizing these species as a separate genus (*Scardafella*) would render *Columbina* paraphyletic.

We also found that some species very recently diverged from each other. The divergence among *Columbina talpacoti*, *C. buckleyi*, and *C. minuta* was relatively recent (1–2 mya). Although the ranges of *C. buckleyi* and *C. minuta* overlap to some degree, the ranges of *C. buckleyi* and *C. talpacoti* do not tend to overlap. *C. buckleyi* has a limited range along coastal Ecuador and Peru, while *C. talpacoti* has a more widespread range, but is found east of the Andes and in Central America (IUCN 2014). While the estimation of *C. buckleyi* and *C. talpacoti* as allopatric sister species is consistent with previous work (Gibbs et al. 2001), this very recent divergence seems inconsistent with theories on separation by the Andean uplift (see discussion below), and indicates a more recent separation event.

Finally, and perhaps most surprisingly, our phylogeny indicated that the genus *Claravis* is paraphyletic. While the placement of *Claravis pretiosa* is consistent with previous work (as sister to the rest of the clade), *C. mondetoura* was estimated together in a clade with *Uropelia*, *Metriopelia*, and *Columbina*. While the exact placement of *C. mondetoura* within this clade is uncertain, the exclusion of *Claravis pretiosa*, and thus the paraphyly of the genus *Claravis*, is very highly supported (100 bootstrap, 1.0 posterior probability). Members of the genus *Claravis* are unique among small New World ground doves in that males have mostly blue-gray plumage coloration. Females, however, are brownish, similar to most other small New World ground doves. It may be that having blue-colored males was the ancestral condition in this clade and that this trait was later lost in other lineages, with males evolving a more similar plumage coloration to females. Another genus of New World dove, *Geotrygon*, has also been shown to be paraphyletic, despite strong morphological similarities (Johnson and Weckstein 2011, Banks et al. 2013). Therefore, such a finding is not unprecedented among pigeons and doves.

Divergence Time Estimation with Respect to Major Geologic Events

Andean uplift. Since the small New World ground dove clade is widespread throughout South America, the effect of Andean uplift on the radiation of this group is expected to have been pronounced. There are three clades that are of particular interest: the genus *Metriopelia*, the *Columbina cruziana–C. picui* clade, and the *Columbina talpacoti–C. buckleyi* clade. Species in *Metriopelia* are found in the Puna grasslands of the high Andes. *Columbina cruziana* is found on the coasts of western Peru and Ecuador, while *C. picui* is primarily found in the lowland semiarid scrub and grasslands east of the Andes, though it does also occur in the lowlands of southern Chile. *Columbina buckleyi* and *C. talpacoti* show a similar geographic structure, with *C. buckleyi* found exclusively on the Ecuadorian and northern Peruvian coasts west of the Andes, and *C. talpacoti* found throughout the Amazonian lowlands and Central America.

Metriopelia is estimated to have diverged from its ground-dove ancestor ~11–14 mya. This estimate is somewhat consistent with the timing of the uplift of the Central Andes—the current range of species within the genus—reaching >50% of current elevation (Gregory-Wodzicki 2000). This divergence time estimation could also coincide with the ecological and geographical isolation of the Puna grasslands—the primary habitat for birds in this genus—due to geographic and climatic changes. Vandervoort et al. (1995) and Gregory-Wodziki (2000) present data indicating that internal draining for the region was established ~15 mya, indicating isolation from the surrounding lowlands. There is also indication of a climatic shift to a much drier environment. Most of the speciation events within *Metriopelia* do not appear to occur until much later, however. This diversification coincides with the traditional estimate of the timing of rapid elevation increase in the Altiplano plateau and Eastern Cordillera

within the last 10 myr. Garzione et al. (2008) estimated that the central Andean plateau rose from ∼2,000 m to the current ∼4,000 m between 6.5 and 10.0 mya. Alternatively, the patterns seen in *Metriopelia* could be consistent with more recent estimates of rapid elevational uplift in the Puna–Altiplano region (Garzione et al. 2014). In this scenario, the initial divergence of the group was perhaps initiated by a rapid uplift of ∼1,900 km and subsequent climatic changes between 13 and 16 mya, rather than as a result of climatic changes over a more gradual uplift period. Similarly, the later increase in speciation events within the genus could be related to the second rapid uplift event of ∼700 m between 9 and 13 mya. While it is difficult to form strong conclusions about the effect of Andean uplift on this genus—primarily because both the group's diversification and the uplift events occurred over a long period of time—there are nonetheless indications that diversification in the genus coincided with a rapid increase (or increases) in Andean elevation. A similar pattern of increased diversification associated with rapid elevation increase has been documented in tanagers endemic to the Northern Andes (Sedano and Burns 2010).

Columbina cruziana and *C. picui* were estimated as sister species, but their geographic ranges are separated by the Andes. Thus, it might be expected for these species to have diverged around the time of Andean uplift; however, divergence time estimation indicated that these taxa diverged 3–7 mya, which is significantly more recent than the divergence time estimate of *Metriopelia* and therefore the southern–central Andean uplift. In this case, however, *C. cruziana* and *C. picui* are separated by the northern range of the Andes, which is estimated to have formed 2.5–10.0 mya. By 2.5–7.0 mya, coastal Peru would have been cut off from the Amazonian lowlands to the east by the rise of the Eastern Cordillera of Colombia. This event coincides with the divergence time estimate for *C. cruziana* and *C. picui*, and strongly suggests northern Andean uplift as the cause of vicariance and subsequent divergence. The geographic range of *C. picui* does extend to the western side of the Andes in central Chile, but does not extend farther north than the Atacama Desert. A large body of research indicates that the Atacama underwent a rapid increase in aridity ∼6 mya, and subsequently developed toward its current extreme conditions (Hartley and Chong 2002). The timing of this environmental change coincides with the development of the Northern Andes and rapid elevation increase in the Central Andes, probably due to the climatic changes associated with western South America being closed off to the rest of the continent by the entirety of the Andes mountain range (Hartley 2003). The timing also coincides with the estimated *C. cruziana*–*C. picui* divergence time. This could indicate that the speciation event was the direct result of a north–south divergence due to the formation of the Atacama, an east–west divergence due to the rapid elevation increase in the Northern Andes, or a combination of both geologic events. In other words, *C. cruziana* could have been isolated by both the Andes to the east and the Atacama Desert to the south. Other research has indicated that the Atacama formed much earlier, reaching a point of extreme aridity ∼14 mya (Houston and Hartley 2003, Dunai et al. 2005). If this were the case, the *C. cruziana–C. picui* ancestor would have already been hindered from spreading north along the Chilean Pacific Coast by ∼14 mya, and the subsequent speciation event would be more directly attributable to the rise of the Northern Andes.

The sister species *Columbina talpacoti* and *C. buckleyi* show a similar distributional pattern to *C. cruziana* and *C. picui*, but are estimated to have diverged more recently (<1 mya, and probably <50 kya); this divergence does not coincide with major Andean uplift events. The mitochondrial uncorrected pairwise distance between the two species is also relatively small (0.3–0.8%), consistent with a very recent speciation event. This pattern of closely related species on either side of the Andes has been documented in several other cases of birds (Brumfield and Capparella 1996, Miller et al. 2008, Weir and Price 2011, Lougheed et al. 2013). Some of these instances were shown to be the probable result of trans-Andean gene flow (Miller et al. 2008), but this seems unlikely with ground doves given their poor long-distance flight ability. Dispersal of the ancestors of this group over the Andes seems unlikely. Another possibility is that the ancestor of *C. talpacoti* and *C. buckleyi* was distributed across the Northern Andes throughout forested glacial refugia (Haffer 1969). These corridors would have provided suitable habitat for dispersing around the Northern Andes, thereby allowing for a continuous distribution on both sides of the Andes. It seems plausible that, when these corridors disappeared with the glacial retreat of the Pleistocene, patches of habitat (and presumably representatives of the *C. talpoacoti–C. buckleyi* ancestor) remained isolated on either side of the range, leading to a speciation event.

Panamanian land bridge formation. In many cases, the focus of biogeographic studies is on vicariance events, the separation of two previously connected areas (Bauzà-Ribot et al. 2012, Maderspacher 2012, Phillips et al. 2013). However, North and South America represent a case of two continents connecting after millennia of separation. We therefore modeled our biogeographic comparison under the assumption of dispersal (Christenhusz and Chase 2013), and estimated the origin and direction of dispersal of small New World ground doves, which now occur on both continents. Our results indicated several dispersal events into North America from South America, and the timing of the colonization events appeared to coincide with the Panamanian land bridge formation

(Figure 2). Both the parsimony and the maximum likelihood biogeographic reconstructions estimated only South to North America dispersal events. Likewise, the posterior probabilities at this node from the MCMC chain of the BBM model were very similar to the likelihood values from the ML character reconstruction. The BBM results indicated that the ML results were robust to our use of a third character state (present in both North and South America) rather than use of a polymorphic character state (present in North America and present in South America). Using a third character state instead of a polymorphic state is not ideal, but is required in current implementations of likelihood ancestral character reconstructions. Nevertheless, our BBM results—an ancestral area reconstruction model that allowed polymorphic states—indicated that our ML analysis produced consistent results.

Based on all three analyses, all South to North American dispersal events occurred after the formation of the land bridge. The lack of dispersal prior to land bridge existence is not surprising given the strong support for a South American origin of the small New World ground doves and the unlikely possibility of these ground doves flying across a significantly large water barrier. It is possible that the doves could have dispersed into North America by "island hopping" on small land masses thought to have existed between the two continents (Stehli and Webb 1985, DaCosta and Klicka 2008), as *C. passerina* seems to have done in colonizing Caribbean islands, but our results strongly suggest otherwise. Of particular significance are the sister taxa *Columbina squammata* and *C. inca*. Although the geographic reconstruction estimates their ancestor as a South American species, the current range of *C. inca* is exclusively in North America, while *C. squammata* is a South American species. Their estimated divergence time is ~2.0–2.5 mya, which indicates a dispersal and speciation event shortly after the land bridge formed. Species that currently are distributed across both continents are reconstructed as having originated in South America, with recent range expansion into North America. This pattern is interesting in that it is a reversal of the general trend in other systems (Smith and Klicka 2010), where lineages with a South American origin tend not to disperse into North America.

Conclusion

Through sampling representatives of each extant species of small New World ground dove, we were able to reconstruct a fairly well-resolved and well-supported phylogeny of this group. More importantly, we were able to use a dated phylogeny to understand the timing of diversification in this group as it relates to historic biogeographic events. Due to their ranges throughout the New World, we were able to test hypotheses regarding the effects of Andean uplift and formation of the Panamanian land bridge. If neither Andean uplift nor land bridge formation had had a major effect on New World ground dove speciation patterns, we would have expected the estimated divergence times and ancestral area reconstructions among relevant species to not coincide with either of these geologic events. In particular, we would not have expected the divergence time estimates of relevant clades (e.g., sister taxa separated by the Andes) to coincide with Andean uplift events. Furthermore, we would not have expected the timing of dispersal events between North and South America to coincide with the land bridge closure. However, our results in this study support several divergence time estimates that are consistent with Andean uplift events, as well as biogeographic reconstructions consistent with dispersal events from South to North America occurring near or after Panamanian land bridge formation. These results suggest that Andean uplift and the formation of the Panamanian land bridge were important events in the evolutionary history of small New World ground doves, and provide further insight into how these events contributed to the diversification of New World birds.

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