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Short Communication

The flight of the Passenger Pigeon: Phylogenetics and biogeographic history of an extinct species

Kevin P. Johnson [a,*], Dale H. Clayton [b], John P. Dumbacher [c,d], Robert C. Fleischer [d]

[a] Illinois Natural History Survey, University of Illinois, Champaign, IL 61820, USA
[b] Department of Biology, University of Utah, Salt Lake City, UT 84112, USA
[c] California Academy of Sciences, San Francisco, CA 94103, USA
[d] Center for Conservation and Evolutionary Genetics, Smithsonian Conservation Biology Institute, National Zoological Park, Washington, DC 20008, USA

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ABSTRACT

The human-caused extinction of the Passenger Pigeon (*Ectopistes migratorius*) is one of the best known and documented of any bird. This event was particularly alarming because the Passenger Pigeon went from being one of the most numerous avian species in the world to extinct in a period of decades, when the last individual died in captivity in a Cincinnati Zoo in 1914. While a great deal of information exists on the likely direct and indirect causes of its demise, as well as information on life-history, the phylogenetic relationships of this species have been subject to considerable speculation. Here we use DNA sequences obtained from museum specimens to resolve the phylogenetic position of this species with respect to other pigeons and doves (Columbiformes). We show that the Passenger Pigeon is not related to the New World mourning doves (*Zenaida*) as many authors have suggested, but is the sister taxon of all other New World pigeons (*Patagioenas*). Biogeographic analysis suggests the Passenger Pigeon lineage may have colonized North America from Asia, and subsequently dispersed into South America, leading to a more extensive radiation of New World pigeons.

1. Introduction

The Passenger Pigeon (*Ectopistes migratorius*) was once the most numerous species of bird in North America but, due to human over-exploitation combined with other factors, became extinct in a matter of decades. This dramatic decline is perhaps one of the best known and documented extinctions for any species, and has served as a poignant reminder of the impact humans can have on nature. Unlike many cases, where uncertainty exists regarding the exact timing of extinction, considerable documentation of the demise of the Passenger Pigeon exists (Schorger, 1955; Blockstein, 2002); the last bird died in captivity in a Cincinnati Zoo in 1914. Information on the natural history of the Passenger Pigeon has also been relatively well documented (Blockstein, 2002). However, the evolutionary relationships of the Passenger Pigeon have been the subject of speculation, with little or no rigorous phylogenetic testing.

The phylogenetic relationships of the Passenger Pigeon are generally unclear, and it has typically been placed in the monotypic genus *Ectopistes*. Most authors suggest that the Passenger Pigeon is closely related to the New World mourning doves (*Zenaida*), which include representatives in North and South America (Goodwin, 1983; Gibbs et al., 2001; Blockstein, 2002). Although the Passenger Pigeon shares a few superficially similar plumage patterns and a long tail with some members of *Zenaida* (Goodwin, 1983), it differs by its considerably larger size, sexual plumage dimorphism, and lack of a facial stripe. Because extant pigeons and doves (Columbiformes) in the New World have undergone three distinct radiations (Johnson and Clayton, 2000; Pereira et al., 2007), understanding the phylogenetic position of the Passenger Pigeon is important to more fully understand the origin of these radiations. Prior studies with limited taxon and gene sampling (Shapiro et al., 2002; Pereira et al., 2007) indicate that the Passenger Pigeon may not be closely related to *Zenaida*, as previously hypothesized. The goals of our study were to use additional DNA sequences obtained from museum specimens of the Passenger Pigeon and denser taxon sampling to identify its phylogenetic position within Columbiformes. We used this information to reconstruct biogeographic patterns in New World pigeons and doves.

2. Materials and methods

Sequences of the mitochondrial cytochrome *b* and ATPase8, as well as the nuclear beta-fibrinogen intron 7 (totaling 2401 aligned base pairs), are available for 78 species of pigeons and doves from

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* Corresponding author. Address: Illinois Natural History Survey, 1816 South Oak Street, Champaign, IL 61820, USA. Fax: +1 217 244 0729.
E-mail address: kjohnson@inhs.uiuc.edu (K.P. Johnson).

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around the world (Johnson, 2004). For the present study we also extracted DNA from the extinct Passenger Pigeon (*E. migratorius*) from museum skins. Because DNA from museum skin material is highly fragmented, only short sequences of the mitochondrial cytochrome *b* (130 bp) and ATPase8 (169 bp) genes could be obtained for the Passenger Pigeon, and both genes could only be sequenced from a single specimen USNM293588 (GenBank Accession Nos. HM195099–HM195100). Sequences from other individuals for one gene or the other were identical or differed by only one or two base pairs from these sequences. These sequences were obtained using methods described elsewhere (Sorenson et al., 1999; Dumbacher and Fleischer, 2001). We also compared our sequences of the cytochrome *b* gene to that of Shapiro et al. (2002), and only one substitution difference was detected. Thus, we used the longer 1044 bp cytochrome *b* sequence from this previous study in our analyses. As in previous studies (Johnson and Clayton, 2000; Johnson, 2004) the tree was rooted on a swiftlet.

First we used parsimony analyses to reconstruct a tree from all genes combined, with the Passenger Pigeon coded as missing data for the beta-fibrinogen intron 7 gene (10 random addition replicates). However, the phylogenetic placement of a taxon for which a large number of base pairs are missing (1188 of 2401 bp missing, i.e., the nuclear beta-fibrinogen intron 7) may be subject to bias. To account for this we also constructed a parsimony tree for only the 78 taxa for which we had complete sequences. This tree was then used as a constraint tree to evaluate the phylogenetic position of the Passenger Pigeon. We used this constraint in a second parsimony analysis where we analyzed only the two mitochondrial genes that were available for the Passenger Pigeon. This technique should lead to an unbiased placement of the Passenger Pigeon within the broader tree of pigeons and doves, while at the same time allowing the overall tree structure to be determined by the maximum number of available sequences.

For the purposes of comparison, we also conducted a Bayesian analysis using MrBayes (Huelsenbeck, 2001), with the GTR + I + G model. Posterior probabilities were calculated by sampling trees every 1000 generations from a 10 million generation chain. Inspection of likelihood scores indicated that they stabilized by 100,000 generations, so the first 100 trees were discarded as burn-in. This analysis was conducted with all sequences simultaneously and the Passenger Pigeon was coded with missing data for the beta-fibrinogen intron 7 gene.

Much of the radiation of pigeons and doves appears to have been the result of dispersal and this occurred after the breakup of Gondwana (Pereira et al., 2007). Thus, historical changes in biogeographic distribution between continental regions are likely due to dispersal. Brooks (1990) parsimony method is the most appropriate method for biogeographic reconstruction where changes are the result of dispersal (Johnson and Sorenson, 1999; DaCosta and Klicka, 2008). Because we were most interested in broad scale changes between major regions, with particular focus in the New World, we coded biogeographic areas as New World and Old World (including the Australasian region). No species has a native distribution in both the New and Old World so this coding is appropriate for examining major changes in distribution.

3. Results

Trees from both parsimony and Bayesian analyses were generally well resolved and in broad agreement about phylogenetic relationships among pigeons and doves (Fig. 1). Phylogenetic analyses suggest that the Passenger Pigeon is closely related to the clade containing a western North American pigeon, the Band-tailed Pigeon (*Patagioenas fasciata*), and other large-bodied New World pigeons (*Patagioenas*, Fig. 1). The Passenger Pigeon was distributed throughout eastern North America, and was likely the eastern counterpart of the western Band-tailed Pigeon.

Based on Brooks (1990) method of biogeographic reconstruction, pigeons and doves invaded the New World three times from the Old World (Fig. 1). The large-bodied New World pigeon clade, including the Passenger Pigeon, is embedded within a clade of Old World Columbiformes; within this clade, they are sister to a clade of cuckoo-doves (*Macropygia* and *Reinwardtoena*) from south-east Asia.

4. Discussion

Previous authors have suggested that the extinct Passenger Pigeon is a close relative of the New World genus *Zenaida* (Goodwin, 1983; Blockstein, 2002). However, phylogenetic analysis of DNA sequences reveals that the Passenger Pigeon (*E. migratorius*) is closely related to other New World pigeons in the genus *Patagioenas* (Fig. 1). This group falls in a larger clade containing Old World pigeons (*Columba*), turtle-doves (*Streptopelia*), and cuckoo-doves (*Macropygia* and *Reinwardtoena*). This large clade has 97% bootstrap support and 100% Bayesian posterior probability, a result that is consistent with previous limited molecular systematic studies of Columbiformes (Shapiro et al., 2002; Pereira et al., 2007). There is one inferred colonization event of the New World in this clade, possibly from south-east Asia (the distribution of cuckoo-doves). Both cuckoo-doves and the Passenger Pigeon have long tails, and the juvenile Passenger Pigeon is superficially similar to some cuckoo-doves, with scaling on the neck and ruddy coloration in the wings. Furthermore, cuckoo-doves and the Passenger Pigeon both lack facial stripes, unlike *Zenaida*, which possess them. Many species of cuckoo-doves also exhibit sexual dimorphism, with males having iridescent plumage in the neck region, similar to the Passenger Pigeon, while species of *Zenaida* are sexually monomorphic.

Evidence from the distribution and phylogeny of ectoparasitic lice also supports these relationships for the Passenger Pigeon. A species of louse, *Columbicola extinctus*, has been described from the Passenger Pigeon (Malcomson, 1937). Lice are generally quite host-specific, so this louse was thought to be extinct along with the Passenger Pigeon (Stork and Lyal, 1993). However, recent revisions of the lice of pigeons and doves (Clayton and Price, 1999; Bush et al., 2009) have revealed that *C. extinctus* is also found on the Band-tailed Pigeon (*P. fasciata*), here shown to be a close relative of the Passenger Pigeon. The *extinctus* group of lice is closely related to the *Columbicola angustus* species group (Johnson et al., 2007), found mainly on cuckoo-doves (*Macropygia* and *Reinwardtoena*) of south-east Asia, which also appear to be the closest relatives of the New World pigeons (Fig. 1). Thus, the host distribution of these groups of lice broadly mirrors the host phylogeny.

If indeed North American pigeons were derived by colonization of a lineage from south-east Asia, this would be one of the few such long-distance dispersal events known for birds. A few other lineages of New World birds are believed to have their closest relatives in south-east Asia. These include the Wrentit (*Chamaea fasciata*) from the west coast of North America, believed to be closely related to babblers (Timaliidae) from south-east Asia (Barhoum and Burns, 2002) and New World vireos (Vireonidae), which are closely related to *Erpornis* from south-east Asia (Barker et al., 2004). It may also be possible that, prior to the Pleistocene, ancestors of these lineages lived further north than their current distributions, and the Beringian region served as a dispersal corridor between the Old and New World during the Miocene (Barker et al., 2004). Many species of large-bodied pigeons are exceptionally strong fliers and have colonized islands across much of the

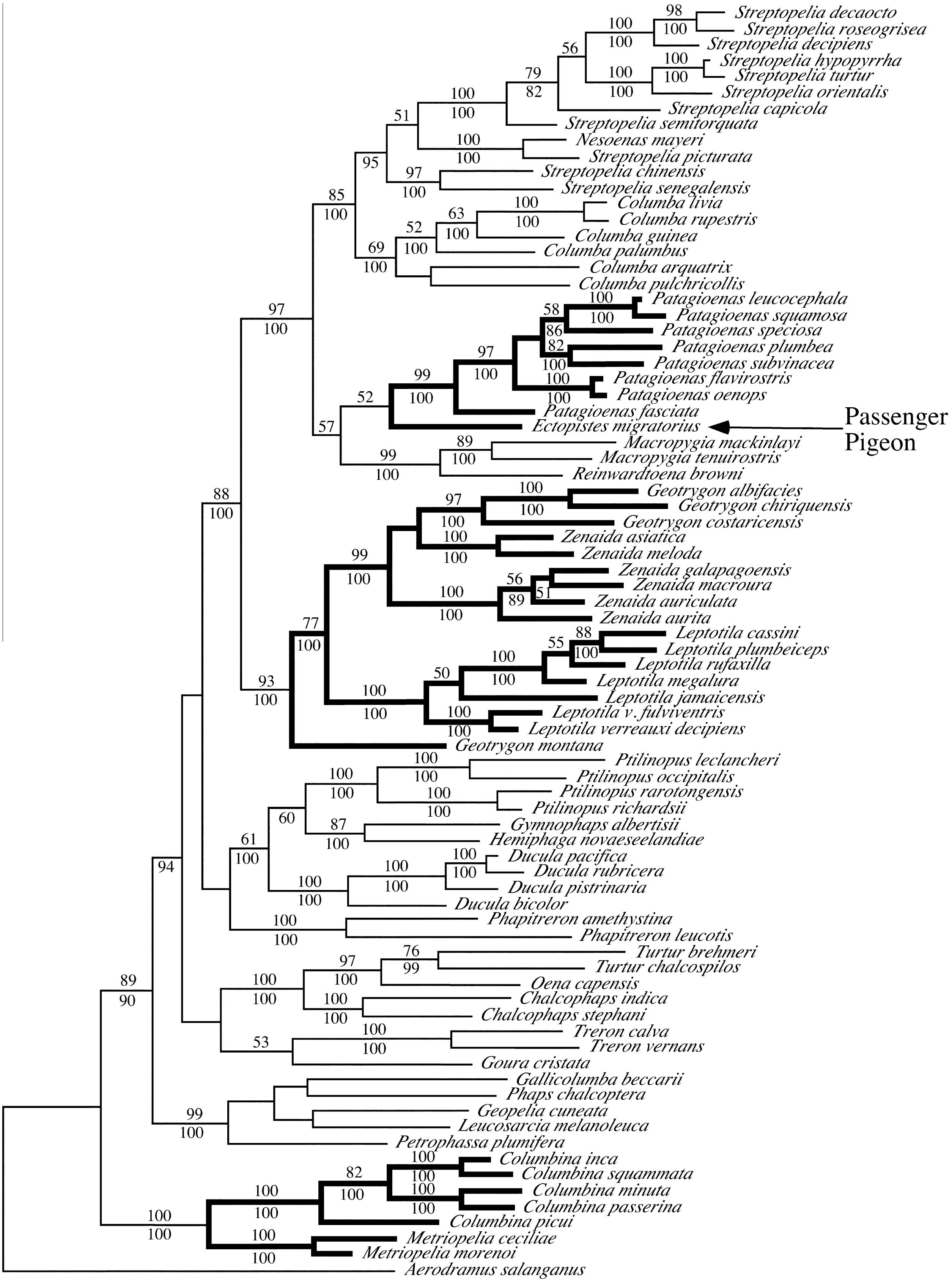

Fig. 1. Phylogeny for 79 taxa of pigeons and doves (Columbidae) reconstructed using parsimony analysis of nuclear (1188 aligned bp of beta-fibrinogen intron 7) and mitochondrial (1044 bp cytochrome *b*, 169 bp ATPase 8) sequences. GenBank Accession Nos. AF182648–AF182713. An identical placement of the Passenger Pigeon resulted from parsimony analyses that first excluded the Passenger Pigeon and then used this tree as a constraint in searches including only the mitochondrial genes with the Passenger Pigeon included. Numbers above branches are support from 1000 parsimony bootstrap replicates, and numbers below branches are posterior probabilities from Bayesian MCMC analysis. Bold branches are lineages that occur in the New World, while thin branches are Old World taxa (Eurasia, Africa, and Australasia).

south Pacific Ocean. The Passenger Pigeon was one of the fastest flying pigeons (ca. 100 km/h, Schorger, 1955), undergoing rapid long distance movements in large flocks. Thus, the ancestors of the Passenger Pigeon may have engaged in such an extraordinary flight.

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