



Genetic differentiation within a widespread “supertramp” taxon: Molecular phylogenetics of the Louisiade White-eye (*Zosterops griseotinctus*)[☆]



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ABSTRACT

“Supertramp” species are highly specialized overwater dispersers, and are useful taxa for investigating the influence of dispersal ability on speciation and diversification in island settings. The Louisiade White-eye (*Zosterops griseotinctus*) is a widespread avian supertramp endemic to Papua New Guinea’s off-shore islands. We used maximum likelihood and Bayesian inference to reconstruct phylogenetic relationships based on 2 mitochondrial and 1 nuclear loci (1813 bp total) from 88 individuals representing all 4 named subspecies and the full breadth of the species’ range. We found significant geographic and population genetic structure, and support for a major clade containing the coral islets of the central Louisiade Archipelago and outlying Nissan Island. We found evidence of metapopulation structure and gene flow within the Louisiade Archipelago clade, and relatively high genetic distinctiveness of outlying island populations, including the population on volcanically-defaunated Long Island. We reject a hypothesis of panmixia within the Louisiade White-eye despite their long-range dispersal ability, and find evidence of selection against dispersal ability in populations on high-elevation islands where disturbance is rare. Our study represents a rare intraspecies phylogeny of an avian supertramp, and sheds light on patterns of evolution in highly vagile island species.

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1. Introduction

Variation in dispersal ability across groups of organisms is a critical factor in the genesis of biological diversity and novel species (Diamond and Mayr, 2001). New species arise when barriers to gene flow emerge between taxa (Dobzhansky, 1937; Mayr, 1942). Barriers to gene flow can be geographic or behavioral, or arise through adaptive evolution in response to varied ecological conditions. Geographic barriers physically restrict the transfer of alleles among populations, as in vicariance and allopatric speciation (Wright, 1931; Mayr, 1942). In sympatric populations, reproductive isolation can arise through behavioral barriers such as species recognition (Shaw and Parsons, 2002; Seehausen et al., 2008; Uy et al., 2009), or from divergence driven by varied selec-

tive pressures across an environmental gradient, as in ecological speciation (Rundle and Nosil, 2005; Nosil, 2012). As dispersal ability influences relative rates of gene flow, it can determine whether these barriers and selective pressures are sufficiently strong to result in reproductive isolation.

Dispersal ability is particularly significant in island contexts, where the evolutionary trajectories of organisms are strongly influenced by their ability to cross open water. Highly sedentary species rarely reach other islands, and once there, in the absence of gene flow may rapidly diverge. Highly vagile species may frequently cross between islands, maintaining gene flow and precluding divergence. While groups of sedentary species in island contexts populate the literature as classic examples of adaptive radiations (Lovette et al., 2002; Baldwin and Robichaux, 1995; Grant, 1981), the evolutionary histories of highly vagile species remain poorly understood (but see Andersen et al., 2014).

One group of highly vagile species with shared ecological and distributional characteristics have been termed supertramps (*sensu* Diamond, 1974). Avian supertramps are prevalent in the island

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avifaunas of Melanesia in the southwest Pacific, and are characterized by their occurrence primarily on small islands with low alpha diversity (Diamond and Mayr, 2001; Andersen et al., 2014; Jönsson et al., 2008). Based on these characteristics and field observations, Diamond hypothesizes supertramps represent an extreme case of *r*-selection in birds: they are highly specialized for rapid breeding and overwater dispersal, but at the expense of competitive ability and refined local adaptation (Diamond, 1974). He posits that as a result, they are restricted in distribution to islets with relatively marginal habitat and few competitors, and to islands defaunated by volcanic eruptions with lower species numbers than equilibrium expectations (Diamond, 1974).

Clades that include both supertramps and less vagile species are useful taxa for investigating the influence of lineage-specific life-history traits on rates of speciation (Moyle et al., 2009). Further, they can help address a famous paradox: how can lineages show such high degrees of differentiation across oceanic islands when their necessarily excellent dispersal ability and resulting gene flow should limit divergence? Moyle et al. (2009) explored this question by studying the pattern and tempo of speciation in the Zosteropidae (White-eyes), a species-rich avian family with high rates of endemism and a concentration in the tropical Pacific and Indian Oceans. They reconstructed phylogenetic relationships in the *Zosterops* [*griseotinctus*] superspecies, a Melanesian species group containing multiple highly sedentary taxa and a single widespread supertramp. Concluding that a rapid shift in dispersal ability may have played a prominent role in the diversification of White-eyes, their study suggests that disparate populations within a supertramp species may represent incipient species. Their results highlight the potential for intraspecific studies of supertramps to shed light on the balance of natural processes underpinning speciation.

The nominate race of the *Zosterops* [*griseotinctus*] group, the Louisiade White-eye, *Z. griseotinctus*, is a supertramp species inhabiting islands in the Louisiade, Bismarck, and Admiralty archi-

pelagos of Papua New Guinea. Current taxonomy recognizes four named subspecies spread across the species' 800 linear mile range, distinguished by their disjunct ranges and by minor differences in bill length (van Balen, 2008; Pratt and Beehler, 2014). These are: *Z. g. griseotinctus* in the western Louisiades, *Z. g. longirostris* in the eastern Louisiades, *Z. g. pallidipes* on Rossel Island, and *Z. g. eichhorni* on the islands of the Vitiaz Strait, Nissan Island, and Admiralty Archipelago (Fig. 1; van Balen, 2008). Additional available names include Admiralty group populations as *Z. g. ottomeyeri* and Misima Island population as *Z. g. aignani* (van Balen, 2008; ITIS, 2014). For consistency, we follow van Balen (2008) in synonymizing *Z. g. ottomeyeri* with *Z. g. eichhorni*, and *Z. g. aignani* with the nominate subspecies.

Similar to other Melanesian supertramps, *Z. griseotinctus* is primarily restricted in distribution to small coral islets, such as those comprising the central Louisiade Archipelago. However, *Z. griseotinctus* is also found on several relatively large, mountainous (hereafter "high") islands across its range, where it occurs in both typical littoral habitat as well as primary lowland and montane moist forest: Rossel, Long, Crown, and Tolokiwa Islands. The latter three islands are particularly interesting in having suffered volcanic defaunation during Long Island's most recent violent eruption in the late 1600s, and are held as evidence of the species' dispersal ability and limited tolerance for interspecies competition (Diamond, 1974). Despite the geographic and ecological breadth of its distribution, no field or molecular studies to date have investigated levels of gene flow among populations of *Z. griseotinctus*.

Here, we present a phylogenetic hypothesis for the Louisiade White-eye, *Zosterops griseotinctus*. We sample three loci (two mitochondrial and one nuclear) from 88 individuals representing all four named subspecies across the species' range, and reconstruct phylogenetic relationships using Bayesian inference. We test for a genetic signal consistent with the supertramp hypothesis, with an expectation of genetic homogeneity. We also use phylogeographic patterns among sampled populations to investigate two

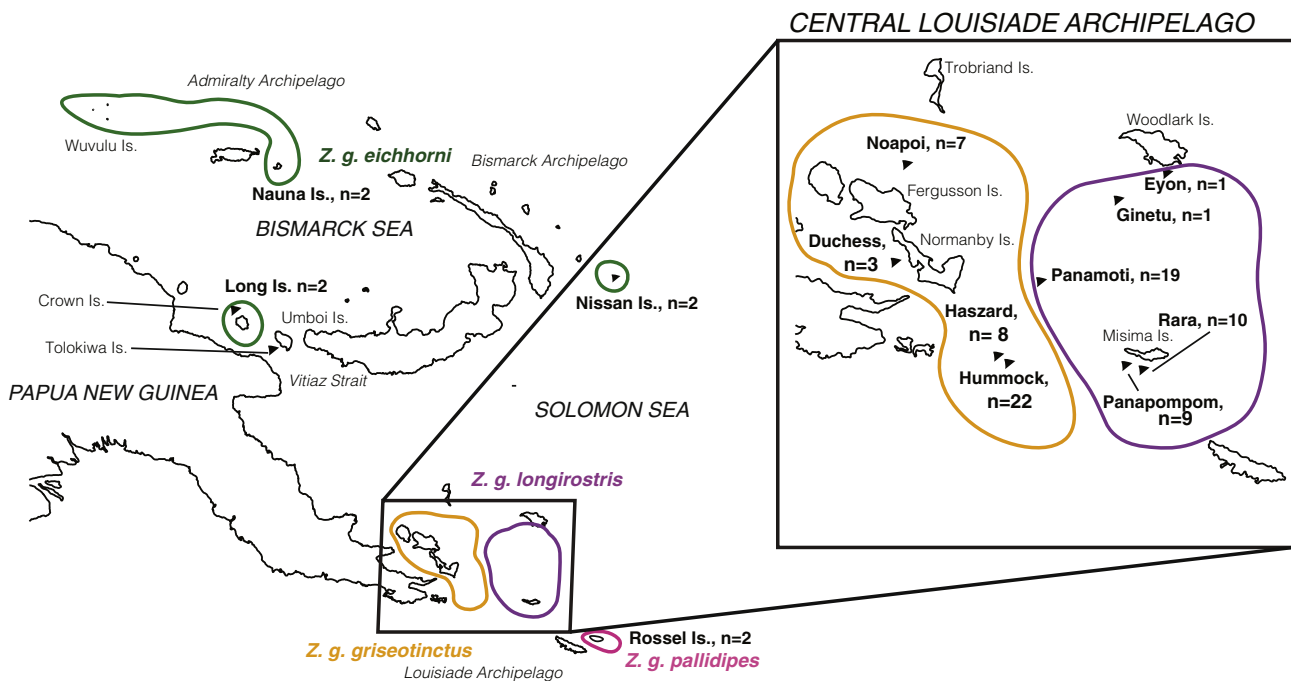


Fig. 1. Sampling locations for *Z. griseotinctus*. Boldface island names denote sampling localities, and are annotated with sample size. Known unsampled populations are marked by plain text island names within illustrated range limits. Subspecies ranges are color coded, with green indicating *Z. g. eichhorni*, pink indicating *Z. g. pallidipes*, orange indicating *Z. g. griseotinctus*, and purple indicating *Z. g. longirostris*. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

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