



Integrating phylogeography and morphometrics to assess conservation merits and inform conservation strategies for an endangered subspecies of a common bird species



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ABSTRACT

Understanding the evolutionary history of threatened populations can improve their conservation management. Re-establishment of past but recent gene flow could re-invigorate threatened populations and replenish genetic diversity, necessary for population persistence. One of the four nominal subspecies of the common yellow-tufted honeyeater, *Lichenostomus melanops cassidix*, is critically endangered despite substantial conservation efforts over 55 years. Using a combination of morphometric, genetic and modeling approaches we tested for its evolutionary distinctiveness and conservation merit. We confirmed that *cassidix* has at least one morphometric distinction. It also differs genetically from the other subspecies in allele frequencies but not phylogenetically, implying that its evolution was recent. Modeling historical distribution supported a lack of vicariance and suggested possible gene flow among subspecies at least since the late Pleistocene. Multi-locus coalescent analyses indicated that *cassidix* diverged from its common ancestor with neighboring subspecies *gippslandicus* sometime from the mid-Pleistocene to the Holocene, and that it has the smallest historical effective population size of all subspecies. It appears that *cassidix* diverged from its ancestor with *gippslandicus* through a combination of drift and local selection. From patterns of genetic subdivision on two spatial scales and morphological variation we concluded that *cassidix*, *gippslandicus* and (*melanops* + *meltoni*) are diagnosable as subspecies. Low genetic diversity and effective population size of *cassidix* may translate to low genetic fitness and evolutionary potential, accordingly we recommend managed gene flow from *gippslandicus* (with which it can be inferred to have recently experienced natural gene flow) to favor recovery of *cassidix*.

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1. Introduction

As resources allocated to conservation are limited, identification of management units to maximize persistence of diversity is critical. Best conservation outcomes are achieved when ecological and evolutionary processes are conserved, rather than specific phenotypic variants, which are the products of those processes. This is

because evolution can recreate or replace adaptive phenotypes if demographic processes and mutation continue (Frankel, 1974; Moritz, 1999, 2002). Gene flow is a major process maintaining genetic diversity across populations and species. It increases standing genetic variation and can lower frequencies of deleterious alleles in small populations (Frankham et al., 2011). Adaptive introgression can also introduce novel adaptive genetic variation (Hedrick, 2013). Management units (sensu Moritz, 1994) differing in allele frequencies might best be managed using occasional gene flow among them (Frankham et al., 2011; Moritz, 1999). Immigration of genetically divergent individuals can reduce fitness through outbreeding depression but this is unlikely between conspecific, karyotypically compatible populations in similar habitats and

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isolated for <500 years (Frankham et al., 2011). Integration of genetic, distributional and morphological data can reveal insights into population evolutionary history, divergence, demography, and the interplay between gene flow and local selection, to guide optimal management.

The yellow-tufted honeyeater *Lichenostomus melanops* (Aves: Passeriformes: Meliphagidae) is a common bird endemic to eastern and south-eastern Australia (Schodde and Mason, 1999). Four subspecies (hereafter *melanops*, *meltoni*, *gippslandicus* and *cassidix*) have been diagnosed based on plumage and morphometrics (Appendix A) (Crome, 1973; Wakefield, 1958; but see Schodde and Mason, 1999). One of these, *cassidix*, is the focus of this paper. Known as the helmeted honeyeater for its distinctive ‘helmet’ of long, erected crown feathers, it is critically endangered under IUCN criteria (Garnett et al., 2011a) and is restricted to a single natural population (~65 adult individuals augmented with captive-bred birds; Menkhorst, 2008) confined to an area of less than 5 km² in the Yellingbo Nature Conservation Reserve (Fig. 1). This population is clearly at risk of extinction from environmental and demographic stochasticity (McCarthy, 1996). Efforts to prevent its extinction began in 1965 (Menkhorst, 2008; Menkhorst and Middleton, 1991). The population remains small and new management strategies are needed.

Schodde and Mason (1999) challenged the diagnosability of *cassidix* and thus the necessity of efforts to preserve it. They argued that its diagnostic morphometric characters (Appendix D; Crome, 1973; Wakefield, 1958) represent the end of a cline along coastal populations, and that the range recognized by Crome (1973) as *gippslandicus* represents intergradation between south-western *cassi-*

dix and eastern *melanops* (Fig. 1A and B). Offering no formal supporting analysis, Schodde and Mason (1999) encouraged genetic testing of this hypothesis. There is no evidence of immigration or emigration in the natural Yellingbo population in recent decades (Smales et al., 2010), but pairing and hybridisation between *cassidix* and *gippslandicus* was recorded recently at a *cassidix* reintroduction site in Bunyip State Park close to the western limits of *gippslandicus* (Quin and Campbell, unpublished data). A better understanding of the evolutionary history of *L. melanops* is needed.

We used morphometric, distributional and multilocus genetic data to explore the evolutionary history of *L. melanops* and test for distinctiveness of four nominal subspecies (*sensu* Crome, 1973). Our objectives were to (1) assess the taxonomic validity of the subspecies; (2) identify potential forces that have led to their divergence; (3) estimate divergence time among recognizable subspecies; and (4) informed by these results, assess whether gene flow between *cassidix* and the population most genetically similar to it would be advisable in management. To achieve these objectives, we tested morphological distinctiveness of *cassidix* by morphometric comparison with its most phenotypically similar subspecies, *gippslandicus* (Wakefield, 1958). Second, we used species distribution modeling to test whether climatic cooling during the Last Glacial Maximum could have resulted in vicariant divergence of ancestral *L. melanops*. Third, we used multi-locus population genetic and phylogenetic analyses (13 microsatellites, one mitochondrial gene, 14 nuclear introns and a nuclear coding gene) to estimate levels of genetic diversity within, and divergence among, populations representing nominal *L. melanops* subspecies.

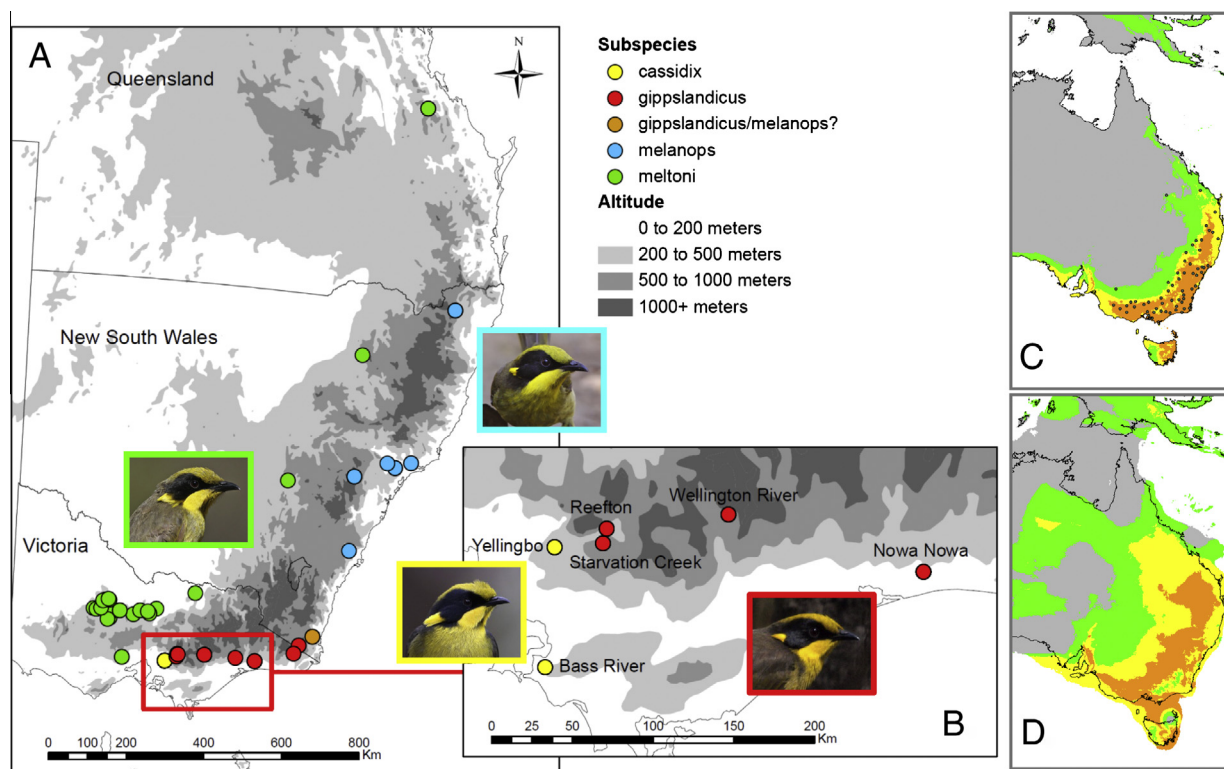


Fig. 1. A and B: Geographic distribution of *Lichenostomus melanops* samples used for genetic (A) and morphological (B) analyses; colors indicate subspecies *sensu* Crome (1973): blue – *melanops*, green – *meltoni*, yellow – *cassidix*, red – *gippslandicus*, orange – unknown subspecies. The Great Dividing Range is indicated by gray shading. Distribution of seven historical DNA samples (Appendix C) is not shown. Currently restricted to Yellingbo, the former distribution of *cassidix* comprised middle-reaches and tributaries of the Yarra River and Western Port drainages of south-central Victoria (Cooper, 1967a,b), with type specimens collected from Bass River in 1867 (now extinct). C and D: Species distribution models for *Lichenostomus melanops* for the present (C), and the Last Glacial Maximum (D). The colors indicate the logistic probability of suitable habitat (gray: <0.065; green: 0.065–0.25; yellow: 0.25–0.5; orange: 0.5–0.75, white is ocean), points indicate presence localities used to train and test the models. The current coastline is outlined in black on the LGM map.

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