Introduction

The Grey Fantail complex consists of three species distributed across Australia, New Zealand, and Melanesia: Grey Fantail R. albiscapa (Australia and Melanesia), Mangrove Grey Fantail R. phasiana (Australia), and New Zealand Grey Fantail R. fuliginosa (New Zealand). A recent study of these and other fantail species, based mainly on single individuals per taxon, indicated that R. fuliginosa and Australian R. albiscapa were sister taxa, that R. phasiana was sister to these two, and that Melanesian R. albiscapa was sister to the rest of the Grey Fantail complex (Nyari et al. 2009). Thus, R. albiscapa was found to be polyphyletic.

Australian populations of the complex, all formerly considered conspecific, are now generally grouped into two species and six geographically isolated units: five subspecies of R. albiscapa (R. a. keasti, R. a. alisteri, R. a. preissi, R. a. albicauda, and R. a. albiscapa) and the monotypic R. phasiana (Fig. 1). The splitting of these two species (Foard 1981) was based largely on songs and habitat. Within R. albiscapa, the southern forms alisteri, preissi, and albicauda were proposed to be closely related based on tail coloration, song, habitat, and clutch size (Ford 1981). In this study, we assessed genetic variation in Australian populations of the Grey Fantail complex to address the following questions:

• Does the Grey Fantail Complex show genetic variation across its Australian range and, if so, is the variation geographically structured?
• Does genetic variation correspond to morphological, behavioral, and ecological variation in these taxa? Do R. albiscapa and R. phasiana form distinct clades, and do the southern subspecies alisteri, preissi, and albicauda form a clade?
• Alternatively, do R. albiscapa individuals from mainland Australia group into eastern and western Australian clades, as do some other Australian species?
• Does improved sampling within Australia change our ideas about relationships of the Australian forms to R. fuliginosa and Melanesian R. albiscapa?

Materials and Methods

Thirty-eight tissue samples, representing R. phasiana and all of the Australian subspecies of R. albiscapa, were obtained from museum collections (Fig. 2; see Acknowledgments). DNA was extracted, amplified, and Sanger sequenced using standard protocols. The mitochondrial genes ND2 and ND3 were sequenced for all individuals and the nuclear intron beta-fibrinogen intron 5 (Fib5) for selected individuals. Sequences were edited and aligned in Sequencer 5.2.4. Seven additional sequences for ingroups and outgroups were obtained from Nyari et al. (2009). Maximum parsimony and maximum likelihood analyses were performed using MP 

\[ 0.01 \times 10 \] and RAxML respectively. One thousand MP and 100 ML bootstrap replicates were conducted to assess node support for the resulting phylogenetic trees.

Results

• Complete ND2 and ND3 sequences were obtained for all 38 individuals and Fib5 sequences for 21 individuals.
• Trees based on mtDNA were well resolved; trees based on the combined data were similar, although resolution was slightly reduced (Fig. 2).
• R. phasiana and Australian populations of R. albiscapa were each found to be monophyletic, but were not sister taxa.
• Melanesian R. a. brenchleyi was not closely related to Australian populations of R. albiscapa, making R. albiscapa polyphyletic.
• Sequence variation within Australian R. albiscapa was low, with a maximum sequence divergence of 1.13% in mtDNA.
• With three exceptions, Australian R. albiscapa grouped into three taxonomically and geographically coherent clades: (1) albiscapa (Tasmania), (2) keasti and alisteri (eastern Australia), and (3) preissi and albicauda (western Australia).
• Two of the three easternmost preissi individuals grouped with keasti and alisteri, and one individual from the range of alisteri grouped with albicauda.
• An east-west genetic divide was observed near the Nullarbor Plain, a known geographic barrier, but was shifted slightly west of the Nullarbor.

Discussion

Our results support the evolutionary distinctiveness of R. phasiana relative to R. albiscapa (Foard 1981, Nyari et al. 2009) and the polyphyly of R. albiscapa when Melanesian subspecies R. a. brenchleyi is included (Nyari et al. 2009). Within R. albiscapa, the southern forms alisteri, preissi, and albicauda are not sister taxa (contra Ford 1981) but instead span the entire genetic diversity of Australian R. albiscapa. Thus, genetic variation is congruent with phenotypic variation in supporting species status of R. phasiana, but inconsistent with phenotypic variation in Australian populations of R. albiscapa.

The exceptions to the geographical patterns in R. albiscapa are likely due to different factors. An east-west genetic break near the Nullarbor Plain is roughly consistent with that in some other Australian species, such as Mulk Duck B. zebra batesi (Gray et al. 2010); however, the shift of the break slightly west of the Nullarbor may indicate dispersal across the Nullarbor, introgression of alisteri mtDNA into preissi, or lack of lineage sorting. In contrast, the individual from the range of alisteri that grouped with albicauda appears to be a wintertime migrant. This sample was collected in late August (winter) within the known wintering area of migrant albicauda and the skin has since been identified as albiscapa (R. Faucette, pers. comm.).

Acknowledgments

We thank the National Science Foundation (DEB-0846607) for funding this research and Elizabeth Gerald, Eugene Hunt, and Virginia Power of the Natural History Research Experience program. We thank Rob Fleischer, Jesus Maldonado, and Nancy McClennen for access and assistance in the genetic lab of the Center for Conservation and Evolutionary Genetics. We thank Marko Kantes, Sarah Rees-Davies, Simon Tye, Nancy McClennen, and Elizabeth Gerald for assistance in the field, and Elizabeth Gerald for assistance and permission to use images from the National Museum of Natural History and Culture, and the American Museum of Natural History for contributing images for this project.

Literature Cited


Figure 1. Geographic ranges and sampling localities for R. phasiana and subspecies of R. albiscapa. Some points represent more than one sample. Colors correspond to species and subspecies on tree. Four-point stars indicate samples that do not group with others in their geographic range. Map modified from Schodde and Mason (1999).

Figure 2. Single most parsimonious tree based on analyses of mtDNA. Numbers above branches indicate bootstrap support for mtDNA analyses (MP:ML); numbers below branches for combined analyses of nuclear and mitochondrial data (ML). Four-point stars correspond to samples specified in Fig. 1.

Patterns of genetic variation in the Australian Grey Fantail complex: Rhipidura albiscapa and Rhipidura phasiana

Shaina Lu1,2,3, Laura M. Bergner3, and R. Terry Chesser4

1 Swarthmore College, Swarthmore, PA; 2 Division of Birds, Department of Vertebrate Zoology, National Museum of Natural History, Washington, DC; 3 Center for Conservation and Evolutionary Genetics, Smithsonian Conservation Biology Institute, National Zoological Park, Washington, DC; 4 USGS Patuxent Wildlife Research Center, National Museum of Natural History, Washington, DC