

## Book reviews

### THE SPECIATION AND BIOGEOGRAPHY OF BIRDS

By Ian Newton

2003. Published by Elsevier Science. 668 pp., line drawings and tables. Hardback, \$A140, ISBN 0-12-517375-X.

This book puzzles me. Shrewdly, it tries to fill the vacant niche in ornithological texts of how population genetics and DNA sequences contribute to avian speciation and historical biogeography, (the study of how species evolved their present-day geographical distributions). Relevant sections in Parts 1 and 3 are eight chapters in 'Introduction', 'Evolution and Diversity of Birds' (Part 1), and 'Effects of Past Climate Change' (Part 3). The book also unites, I believe for the first time, topics in avian macroecology hitherto scattered in other texts. Relevant here are 10 chapters in the parts 'Major Distribution Patterns', 'Limitation of Species Distributions', and 'Bird Movements'. Topics treated include patchy distributions, migration biology and biogeography, latitudinal species diversity gradients, and ecological biogeography (the study of how ecological factors limit present distributions). Three of these chapters treat island birds and seabirds. There are conventional treatments of bird taxonomy in relation to major biogeographical regions and there are useful accounts of avifaunal divisions within continents. A 'Conclusions' chapter offers a synthesis and the author's own work is often cited throughout. Professor Newton is one of the world's finest avian population biologists and his book is a must for any student of avian macroecology and ecological biogeography. But for me, here's the rub. The book (or me?) has an identity crisis: if one's interests in speciation and biogeography are molecular, systematic or historical, Parts 1 and 3 are swamped by the weight of all the macroecology, even though this nonetheless legitimately falls under 'speciation and biogeography'.

I focus on Parts 1 and 3, which cover what is most new in ornithological texts and what I can most usefully review. They refreshingly describe the nature of current research in avian speciation and historical biogeography. Many southern hemisphere examples are cited here and throughout (pity about the cockatoo-like Budgerigars illustrated on p. 323, though). Expected topics are covered conventionally (species concepts, modes of speciation, subspecies, and vicariance v. dispersal) and there are full chapters on less familiar topics (effects on birds of glacial cycles in northern regions, Pleistocene climatic cycles in southern continents). Hall and Moreau's (1970) atlas of African bird speciation, Haffer's (1969) Amazonian refuge theory, and Keast's (1961) Australian speciation analyses, among others, are mainstays in treating the southern continents' birds. The fascinating complexity that DNA studies bring to these earlier foundations and to avian speciation generally is described but crammed into surprisingly few pages with few illustrations

of data. Given the current dominance of DNA studies in avian speciation and biogeography, their condensed treatment surprised me, their presence in the first place notwithstanding. Interestingly, theories of origins of south-western Australian endemics by invasions from eastern Australia are aired yet again. An opportunity is missed to show how phylogenetic thinking sets up ecologically plausible and testable alternatives (multiple invasions v. *in situ* diversification). Perhaps though, if the book can be so faulted, so too should we in the systematics and biogeography community for not having done the simple tests with which a courageous author such as Newton could work.

In Parts 1 and 3, the number of examples from recent molecular literature is impressive but some omissions were startling. Smith *et al.*'s (1997) landmark report on the role of ecological gradients, not historical allopatry, in diversification in the Little Greenbul, *Andorapadus virens*, was missed. Gibbs *et al.*'s (2000) demonstration with mitochondrial DNA (mtDNA) of sympatric host race differentiation in the European Cuckoo, *Cuculus canorus*, while not speciation, was missed. Avise and Walker's (1998) treatment of Pleistocene effects on avian phylogeography was oddly absent from the relevant discussion. Also omitted is any reference to exciting molecular detective work that has been accruing on differentiation by host switching in brood-parasitic indigobirds, *Vidua* spp. (e.g. Klein and Payne 1998; Payne *et al.* 2000, 2002; Sorenson *et al.* 2003). The book cites a number of 2002 papers, so I wonder how many omissions are a result of publication of examples after the book was written, an inevitable problem that the author acknowledges.

I have two main concerns that, although not strictly ornithological, are worth some detail. First is the dearth of discussion about phylogenetic trees and unrooted networks, which show, respectively, reconstructions of parts of the tree of life and how genetic diversity is distributed within a species. Second is the book's treatment of population genetics and molecular methods.

The publication rate of avian phylogenetic trees and networks based on repeatable algorithms of phylogenetic inference, not just genetic distances between taxa (which are questionably phylogenetic), has been explosive for at least 10 years. The impact on speciation and historical biogeography has been huge. Incredibly, therefore, just three trees appear in this book (pp. 52, 75, 139). Readers learn little of how trees and networks are generated and of their use in portraying genetic changes accompanying speciation. Importantly, there is a sense of the difference between estimating phylogeny and having a species concept that can describe it, and of the decoupling of morphological and molecular evolution that phylogeny often reveals. Parsimony is mentioned (but not indexed) as a method of phylogenetic inference but little or nothing is said of how it works or its statistical basis. Readers do not learn that other forms of

phylogenetic inference exist and have become routine (maximum likelihood, Bayesian analysis). They won't really grasp how trees and networks precisely show evolutionary changes inferred to have occurred along each branch for the tree and data at hand. Nor will they appreciate the existence and importance of statistical tests such as bootstrapping. These tests show the statistical reliability of each grouping of taxa (clade) in a tree. They show the reliability of alternative hypotheses represented by different, alternative trees and so convey statistical reliability of different hypotheses of speciation and their biogeographical implications. 'Tree-thinking' underlies phylogeography, the bridge between population genetics and systematics, and its contribution to understanding speciation. Concepts in the book such as refugia and relevant examples do acknowledge this. But they are so sparingly described that one learns little of how the work is done and what the data offer. The map and graph about rates of evolution in Hawaiian honeycreepers (Fleischer *et al.* 1998) omit the phylogenetic tree and small error bars that accompanied the original.

Treatment of molecular methods emphasises genetic distance between taxa over phylogenetic inference based on DNA sequences within and between species. Description of DNA-DNA hybridisation, a coarse-grained distance-based technique, reflects this as much as the profound impact of Charles Sibley and Jon Ahlquist who worked with it. A minimal account of fine-grained DNA sequencing illustrates its higher analytical power. Page 38 notes that DNA differences bring explicit genealogical perspectives to complement genetic distances between taxa. The book never gets to the core of that genealogical (phylogenetic) perspective or its use in speciation and in estimating demographic parameters such as dispersal distances and instead concentrates on distances. 'Most cladistic methods assume a branching pattern of diversification, and make no allowance for reticulate evolution (hybridization)' (p. 44). Here 'cladistic methods' is vague and the statement misses the power of trees and networks to detect hybridization and reticulate evolution (example from *Zonotrichia* sparrows on p. 69; Australian examples in Degnan and Moritz 1992; Joseph and Moritz 1993a). Thus, the role of phylogenetic trees in speciation and biogeography is present but buried.

A golden opportunity is missed to show the diverse insights DNA-based trees bring to the history of ecological shifts accompanying speciation. A tree is a frame on which parsimony and maximum likelihood can reconstruct the evolutionary development of interesting biology (habitat specialisation, variation in body size and plumage patterns, diet, brood parasitism, migration) and the trail of speciation. Examples are links between speciation and host specificity in brood parasites (Lanyon 1992) and between habitat shifts and body-size changes accompanying speciation in insectivorous birds (Richman and Price 1992) (for Australian examples see Christidis *et al.* 1988; Joseph and Moritz

1993b). Similarly puzzling was that the phylogenetic thinking and methodologies of modern historical biogeography such as DIVA (dispersal-vicariance analysis), PAE (parsimony analysis of endemism) and Brooks parsimony analysis are not mentioned nor are relevant reviews, although papers are cited that used them. The methodology to generate robust phylogenetic trees has revolutionised historical biogeography but we get just a hint from one tree (p. 139).

Inadequacies of molecular clocks, which use genetic distances between two taxa to estimate time since they diverged from their common ancestor, are repeatedly mentioned. If so unreliable, why does Newton quote so many examples? I note that maximum likelihood's toolbox offers log-likelihood ratio tests, which are routinely used to test the applicability of molecular clocks to DNA data. True, few molecular clocks have been externally calibrated in birds. True, few are likely to be, so let's reverse the issue and ask whether a rate calibrated in one or more groups of birds generates biologically and geologically plausible hypotheses when applied to yet another group. Lovette's (2004) review of molecular clocks is good reading for ornithologists. The issue of selective neutrality of DNA sequences recurs. Consider p. 33: 'The idea of neutrality in much of the DNA is based largely on assumption rather than on critical evidence. The evidence known to me provides consistency with the idea rather than testing of it (which would anyway be difficult).' Ouch! Readers get a hint of that debate's complexity and learn nothing of the statistical tests of neutrality so often applied to avian molecular datasets. The tests are described in the population genetics and molecular evolution texts that are not cited. If neutrality cannot be rejected, application of a standard molecular clock is at least not being done uncritically. Random genetic drift, a most important concept in molecular phylogeography and systematics, is defined rather unhelpfully and, I submit, even misleadingly on pages 56–57 as the incidental effects of selection on characteristics other than those that the selection is directly targetting. This is not a good definition of drift, of how it is studied in natural populations and of what it means to speciation and biogeography.

This is a refreshing book and a tasty entrée into ornithology's role in the current revolution in evolution and phylogeny. As an entrée balances with a meal's later courses, so too the ornithology, macroecology, ecological and historical biogeography, and molecular systematics and phylogeography here could be better balanced. The diversity and excitement of speciation and historical biogeography studies of ever more birds are either not conveyed or are swamped by legitimately included but extensive macroecology. The book will serve those with dominant interests in population biology and macroecology. Those with dominant interests in systematics, speciation, phylogeny and historical biogeography will find a useful compendium of examples but will look for the next edition. All should remember that focusing on one interest more than another is at one's own intellectual peril.

- Avise, J. C., and Walker, D. (1998). Pleistocene phylogeographic effects on avian populations and the speciation process. *Proceedings of the Royal Society of London B* **265**, 457–463.
- Christidis, L., Schodde, R., and Baverstock, P. R. (1988). Genetic and morphological differentiation and phylogeny in the Australo-Papuan scrubwrens *Sericornis* (Acanthizidae). *Auk* **105**, 616–629.
- Degnan S., and Moritz, C. (1992). Phylogeography of mitochondrial DNA in two species of white-eyes in Australia. *Auk* **109**, 800–811.
- Fleischer, R., McIntosh, C. E., and Tarr, C. L. (1998). Evolution on a volcanic conveyor belt: using phylogeographic reconstructions and K-Ar-based ages of the Hawaiian Islands to estimate molecular evolutionary rates. *Molecular Ecology* **7**, 533–545.
- Gibbs, H. L., Sorenson, M. D. Marchetti, K., de L. Brooke, M., Davies, N. B., and Nakamura, H. (2000). Genetic evidence for female host-specific races of the common cuckoo. *Nature* **407**, 183–186.
- Haffer, J. (1969). Speciation in Amazon forest birds. *Science* **165**, 131–137.
- Hall, B. P., and Moreau, R. E. (1970). 'An Atlas of Speciation in African Passerine Birds.' (British Museum (Natural History): London.)
- Joseph, L., and Moritz, C. (1993a). Hybridization between the Atherton and White-browed Scrubwrens: detection with mitochondrial DNA. *Emu* **93**, 93–99.
- Joseph, L., and Moritz, C. (1993b). Phylogeny and historical ecology of eastern Australian scrubwrens: evidence from mitochondrial DNA. *Molecular Ecology* **2**, 161–170.
- Keast, J. A. (1961). Bird speciation on the Australian continent. *Bulletin of the Museum of Comparative Zoology* **123**, 305–495.
- Klein, N. K., and Payne, R. B. (1998). Evolutionary associations of brood parasitic finches (*Vidua*) and their host species: analyses of mitochondrial restriction sites. *Evolution* **52**, 299–315.
- Lanyon, S. M. (1992). Interspecific brood parasitism in blackbirds (Icterinae): a phylogenetic perspective. *Science* **255**, 77–79.
- Lovette, I. (2004). Mitochondrial dating and mixed support for the '2% rule' in birds. *Auk* **121**, 1–6.
- Payne, R. B., Hustler, K., Stjernstedt, R., Sefc, K. M., and Sorenson, M. D. (2002). Behavioural and genetic evidence of a recent population switch to a novel host species in brood-parasitic indigobirds *Vidua chalybeata*. *Ibis* **144**, 373–383.
- Payne, R. B., Payne, L., Woods, J. L., and Sorenson, M. (2000). Imprinting and the origin of parasite–host species associations in brood-parasitic indigobirds, *Vidua chalybeata*. *Animal Behaviour* **59**, 69–81.
- Richman, A. D., and Price, T. (1992). Evolution of ecological differences in the old world leaf warblers. *Nature* **355**, 817–821.
- Smith, T. B., Wayne, R. K., Girman, D. J., and Bruford, M. W. (1997). A role for ecotones in generating rainforest biodiversity. *Science* **276**, 1855–1857.
- Sorenson, M. D., Sefc, K. M., and Payne, R. B. (2003). Speciation by host switch in brood parasitic indigobirds. *Nature* **424**, 928–931.

Leo Joseph

Academy of Natural Sciences, Philadelphia

## THE BOWERBIRDS: PTILONORHYNCHIDAE

By Clifford B. Frith and Dawn W. Frith

2004. Bird Families of the World Series, Oxford University Press, Oxford, UK. 508 pp., 8 colour plates, many black and white photographs, line drawings and maps. Hardcover, \$A250, ISBN 0-19-854844-3.

'Of all living creatures... short of man himself, bowerbirds are the most bizarre' E. T. Gilliard (1969)

*The Bowerbirds* is the tenth (and, alas, one of the last) volume to be produced in Oxford University Press (OUP)'s Bird Families of the World series. It is also one of the most impressive of what is widely regarded as the foremost scholarly ornithological series ever produced, most of which have come to be regarded as the authoritative reference for the family featured. For Clifford Frith, this volume is his second major compilation for the Bird Families series of what is very much his life's work: field studies of the birds of paradise (*The Birds of Paradise* was published in 1998 as the sixth volume) and the bowerbirds. In this latest book, Clifford Frith is joined by Dawn, his partner and long-term collaborator in all of his many studies in remote locations throughout Australia, New Guinea and elsewhere.

Despite being both pioneers and significant contributors to contemporary knowledge of this extraordinary family, the Friths consistently acknowledge the various major figures who have added important observations – and above all, ideas – to attempts at understanding the many bizarre and unique features of these birds. Indeed, an important feature of this book is a distinct sense of history and the development of hypotheses and explanations. Much is made of the way that the birds have fascinated a range of formidable ornithologists (including Ernst Mayr, 'Jock' Marshall, Tom Gilliard and Jared Diamond) and excellent use is made of many appropriate – and sometimes provocative – quotations. From someone other than Gilliard, a towering figure in the ornithology of the New Guinea area, the quote reproduced above would simply sound like hyperbole; in its proper context it is just one reaction to what is a truly bewildering and almost unbelievable array of features.

The Ptilonorhynchidae consists of 20 species within nine genera, although many subspecies are sufficiently well known now for the book to treat these in detail. The authors usefully categorise the species using general plumage (silky, satin and grey) and bower architecture (gardeners, maypole and avenue builders) as key criteria, with the non-bower-constructing catbirds a distinct group. Following the standard structure of the other volumes in the series, each of the species has its own detailed account. As is the norm with these authors, the level of detail provided for even the least known of these species is extraordinary and is yet further testament to the 'no-stone-unturned' approach the authors apply to all their work.

Mention must be made of the artwork provided by Eustace Barnes. It is perhaps inevitable that anyone venturing into the depiction of bowerbirds cannot escape some level of comparison with the legendary work of William T. Cooper, who also provided the plates for OUP's *Birds of Paradise*. To our considerable pleasure and relief, Barnes' six paintings are superb: clear, exceptionally life-like and include the level of detail necessarily required of the subjects. Particularly pleasing is the unusual inclusion of wonderful depictions of fledglings for many of the species,

and an example of a motley subadult male for both the Satin and Regent Bowerbirds. And OUP, here at least, is to be congratulated on the printing process used, which has retained the vibrancy of the birds themselves.

The intent of the book as outlined in the 'Plan of the Book' is to focus on the birds and their biology and to only provide a brief review and synthesis of theoretical research (sexual selection) on members of the family. The book is indeed the finest and most detailed almanac of bowerbird natural history to date. Yet, although the authors suggested that it was not their primary focus, the book is an excellent and comprehensive summary of all current theoretical research that used bowerbirds as models to investigate central themes within behavioural ecology and evolutionary biology. By contacting fellow workers within the bowerbird research community to gain access to draft manuscripts and unpublished data the Frith's ensured that their book was future proofed and contained the most up-to-date theoretical advances. This is a significant achievement given the recent strong growth in the numbers of bowerbird publications.

Information on bowerbirds from the behavioural ecology and evolutionary biology literature is presented in both Part I (General Chapters) and Part II (Species Accounts) of the book. If the reader is seeking to stay abreast of the latest theoretical bowerbird research they should focus their reading on Chapters 4, 5 and 7. However this signposting is not to imply that the other chapters do not review and present the current theoretical bowerbird literature. Indeed the authors excel in reviewing all relevant literature with each topic they discuss.

Chapters 4 and 5 discuss bower architecture, decoration use, bower painting, bower ownership, attendance and activities at bowers, bower destruction, decoration theft, vocalisations, vocal mimicry and courtship dance (posture and movement). Quantifying these aspects of the male's display is central to theoretical investigations of bowerbird biology and, indeed, much of the current bowerbird literature has focused on some of these components of male display. Importantly the authors note that this emphasis on male display has meant that female breeding biology and parental care are relatively unexplored (Chapter 6).

Chapter 7 focuses on bowerbirds as models for the investigation of major questions in evolutionary biology and behavioural ecology. Bowerbirds possess international fame as models for the investigation of sexual selection theory and the authors present an excellent 'all you need to know' summary of sexual theory. This information is important as it assists readers who are not normally fluent in sexual selection theory to critically interpret and appreciate the chapter's discussions. The chapter begins with mating systems and uses the bowerbird family's socially monogamous catbirds versus polygynous bowerbirds dichotomy to explore the evolution of monogamous and non-resource

based polygynous mating systems. It then proceeds to discuss the origins of bowers, their decoration and painting; the authors are correct to state that this is a topic about which much is written, but consensus is little closer today than it was when the debate began. Indeed, in the final sections of the chapter, the authors bravely discuss some of the most hotly debated hypotheses in the bowerbird research community: the protection hypothesis (bowers primarily function to protect females from predators), the rape hypothesis (bower building is best explained as a trait that attracts females because of the protection it provides them from forced copulations by bower owners), the threat reduction hypothesis (bowers shield females from intense male displays) and the 'hide the female' hypothesis (bowers prevent rival males from determining if females are present when the owner is displaying). Prior to entering into these more controversial hypotheses, the chapter presents a review of how sexual selection theory has been used to explore and possibly explain bower building. The sexual selection review includes discussion of Gilliard's famous transferral effect, male-male interactions (intra-sexual selection) and female choice (including good genes/indirect benefit versus direct benefit models of sexual selection). This section of the chapter also includes a succinct review of Al Uy's recent work on the mate searching tactics of female Satin Bowerbirds. Current theoretical bowerbird research has tended to explain skewed male mating success (that is, sexual selection) by focusing on the female's preferences for well-constructed bowers and numbers of particular decorations, yet many other components of the male's display remain relatively unexplored. Although it is most appropriate that the chapter presents these findings, it could have more critically appraised the current work and placed more emphasis on the potential of a multiple-signal sexual selection approach to further explain the phenomenon of bowerbirds' extravagant displays.

*The Bowerbirds* is a major work of immense and critical international significance. It appears at a time when interest in the family appears to be increasing rather than waning. We warmly recommend it to a wide audience though many are likely to baulk at the price (allowance for exchange rates and freight would suggest that c. \$A210 would better reflect the UK price of £85).

Gilliard, E. T. (1969). *Birds of Paradise and Bowerbirds.* (Weidenfeld and Nicolson: London, UK.)

Tim Robson  
Gold Coast City Council

Darryl Jones  
Griffith University

## BIRDS OF THE CHATHAM ISLANDS

By Hilary Aikman and Colin Miskelly

2004. Published by the Department of Conservation, Wellington Conservancy, NZ. 116 pp., numerous colour photographs and distribution maps. Paperback, \$NZ25, ISBN 0-478-22565-2.

The Chathams (44°S, 176°W) of New Zealand represent a demonstrably significant island group to ornithology within the Australasian region. They are about 450 km east of Christchurch, South Island, comprise some 96 500 ha and are home to approximately 600 people. Ornithologists, internationally, know the Chathams as home to a relatively large number of bird taxa that breed nowhere else, including the endemic Black Robin, *Petroica traversi*, that was saved from the brink of extinction by the impressively systematic revival of a population of less than half a dozen to more than 200 individuals. In addition, the gadfly petrel previously known as the Magenta Petrel, *Pterodroma magentae*, and now called Chatham Island Taiko was rediscovered there, having eluded detection for 110 years, in 1978. Some readers may be surprised to see text and photographs included in this book for a handsome but as yet undescribed albatross named therein the Pacific Mollymawk *Thalassarche* sp. (previously known as the Northern Buller's Mollymawk, *Diomedea bulleri platei*).

This delightful little volume provides full coverage and photographs of all surviving 18 endemic taxa plus three additional species all-but confined to the islands, and less detailed information/illustrations for another 47 breeding species (of which 16 are introduced) plus four non-breeding regular migrants. The species are dealt with within sections based upon the broad habitat types of oceanic, coastal, freshwater, open country, and forest. One appendix comprehensively lists 179 bird species known from the islands, including 21 locally or globally extinct taxa, with notes of their status. A second lists the 11 plants mentioned in the text. A good full-page map of the islands is provided.

A 12-page Introduction provides an interesting account of the islands (apparently submerged beneath the sea until as recently as 1–2 million years ago), their human inhabitants and culture, and of those residents and visiting ornithologists of significance to conservation and who have contributed to our knowledge of the avifauna. A selected bibliography lists less than 20 publications not by author but, oddly, by their titles in alphabetical order.

Although this is certainly largely a mostly admirable contribution it does, for me, fall down in just a couple of areas. Although not stated in the 'Scope and format of this book' (that occupies but half of an otherwise blank page that

could have therefore easily contained more information), the book is clearly aimed at a popular readership. I think it is therefore unfortunate, given that they feature so conspicuously throughout the book, that subspecies are not fully explained at length at the outset (notwithstanding a brief explanation within the Glossary). All the more so because many subspecies are afforded a common name of their own. The systematic order of birds within each habitat section appears to be that of the *Checklist of the Birds of New Zealand* (Ornithological Society of New Zealand (OSNZ), 1990) and this might have been pointed out. Given that family name subheadings do not subdivide the species accounts, these should surely have appeared within the comprehensive checklist of Appendix 1.

Given the popular nature of the book, I do think that a page or so of text might have been dedicated to explaining to lay readers the background to and reasons for the extensive recent changes in taxonomy, at the genus, species and subspecies levels (and also in common names) apparent in it (e.g. between seabirds herein and those in the OSNZ *Checklist*, the *Field Guide to the Birds of New Zealand* (B. Heather and H. Robertson, Viking, 1996 and subsequent editions) and the *Handbook of Australian, New Zealand and Antarctic Birds (HANZAB)* (Oxford University Press, 1990–)). Although the most pertinent synonym is blandly given in parentheses within species accounts where necessary, this has little meaning and value to non-ornithologists. The authors do not, regrettably in my view, follow the OSNZ *Checklist* and *HANZAB* policy of capitalising the common names of birds. Unfortunately, the book lacks an index. There are nearly 150 colour photographs and, although not as well reproduced as they could have been, they are both attractive and informative.

The above few criticisms aside, this is otherwise a well-contrived, useful and highly attractive book that is a fine addition to the popular ornithological literature. It is a sensible size for field use and the price is reasonable. I found it a delight to read and use. Every person living on or visiting the Chatham Islands should own a copy, as should anyone interested in the avifauna of New Zealand, southern seabirds and/or island-isolated avifaunas. I would urge those with the slightest interest in bird conservation to consider purchasing a copy not only for its inherent pleasures and information but also in order to assist and encourage the authors and the Department of Conservation, Wellington Conservancy, in their fine work. Copies are available from the Department of Conservation, P.O. Box 5086, Wellington, NZ.

Clifford B. Frith

Malanda and the Queensland Museum, Brisbane