



The Birds of Northern Melanesia: Speciation, Ecology, and Biogeography

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The Birds of Northern Melanesia: Speciation, Ecology, and Biogeography. Ernst Mayr and Jared Diamond. 2001. Oxford University Press, Oxford, United Kingdom. 492 pp., 9 color plates. ISBN 0-19-

514170-9. Cloth, \$55.00.—In this tremendous book, we have two of biology's most well known and innovative practitioners combining forces to tackle their deep and common interest in one of the world's most incredible avifaunas, that of northern Melanesia. There is much to love here; Mayr and Diamond present a solid foundation for all future biogeographic studies of birds in that region. Their remarkably thorough analyses highlight how the interaction of geography, natural history, and evolution has shaped a diverse and fascinating assemblage of birds. At the same time, regardless of your theoretical predilections, it should surprise no one that there also is much fodder for complaint, whether in species concepts and limits, taxonomic definitions, island biogeography models, or interpretation of presence-absence data.

Northern Melanesia (the Bismarck Archipelago and the Solomon Islands) has two distinctive features that make it so compelling for the types of analyses that Mayr and Diamond present. First, all islands in northern Melanesia are of Eocene or later age; these islands have never been connected to remnants of Gondwanaland (in this case mainland New Guinea, Australia, or New Caledonia) nor to other archipelagos. Therefore, the entire avifauna is derived from over-water dispersal. That underpins how the northern Melanesian avifauna came into being and continues to diversify. Throughout their book, Mayr and Diamond correctly emphasize the importance of dispersal, which often has taken a back seat to vicariance in recent decades for explaining diversification. Second, compared to most other well-studied island avifaunas (e.g. the West Indies, Hawaii, or Madagascar), that of northern Melanesia is both young and geographically close to its potential sources of colonists. There have yet to be large radiations; in fact, aside from three genera endemic to the Solomon Islands—a pigeon (*Microgoura*), an owl (*Nesasio*), and a frogmouth (currently placed in *Podargus*, see below)—endemism in northern Melanesia has not advanced beyond the level of species. (Mayr and Diamond also recognize two honeyeater genera that are endemic to northern Melanesia, although they note that those are recognized more for their lack of resolution within Meliphagidae than for their distinctiveness.) As a result, we see an incredible array of bird taxa in the various phases of speciation (as defined by Mayr), from the first inkling of establishment of geographic variation (e.g. recently defaunated volcanic islands with all bird populations established within the last 300 years), through populations that were isolated at the end of the Pleistocene (10,000 years ago) as a result of rising sea levels, to populations long separated on pre-Pleistocene (>2 Ma old) islands that have never been connected to one another. Added to that is ongoing dispersal and colonization in many species, and the result is a highly complex island laboratory for looking at the

process of speciation. Mayr and Diamond tackle that complexity admirably.

The 36 chapters of this book are placed in eight sections. The first section (chapters 1–4) provides a general geographic perspective, covering important geological events, types of vegetation, and distributional patterns in taxa other than birds. Surprisingly they do not mention the geologic history of the neighboring archipelagos of the Santa Cruz Islands and Vanuatu ("New Hebrides" to Mayr and Diamond), important source areas for several taxa in the southern Solomon Islands.

The second section (chapters 5–7) covers human history and anthropogenic influences. Mayr and Diamond pay little more than lip service (pp. 40–41) to the effect that prehistoric anthropogenic extinctions have had on current bird distributions. Massive extinctions in Polynesia are well-documented (Steadman 1995), and the scant data so far from northern Melanesia, from New Ireland (Steadman et al. 1999), and Mussau (St. Matthias to Mayr and Diamond) (Steadman and Kirch 1998), also point to big-time losses of diversity, perhaps as much as 25% of the diversity before human contact. However, Mayr and Diamond diminish the significance of those losses by noting the proportionally larger losses (75%) further east in Polynesia. Then, for the rest of the book, Mayr and Diamond essentially ignore those documented extinctions, missing several opportunities to contemplate what effects that potential losses of rallids, columbids, and megapodes may have on their analyses. Mayr and Diamond do mention (p. 41) that New Ireland lost a cockatoo (almost certainly related to *Cacatua galerita ophthalmica*, now restricted to New Britain) and that Mussau lost this or a related species as well, but throughout their many analyses, they treat *C. g. ophthalmica* as a single island endemic. Even in their taxonomic and distributional appendix (Appendix 1) they do not mention the possibility of a wider native range than currently found. This important problem has cascading effects. In their analyses of vagility (Appendix 5), they rank *C. g. ophthalmica* as having the lowest vagility, on the basis in part of it inhabiting only one island.

Section 3 (chapters 8–12) presents the avifauna of northern Melanesia, with descriptive analyses of family composition, species-area relationships, endemism, habitat preferences, abundances, and dispersal abilities. The last chapter in this section presents a short version of Diamond's incidence functions, including the complex figures to which his readers are accustomed (the legend for Figure 12.6 has 23 lines!).

Section 4 (chapters 13–15) is a straightforward but largely speculative summary of how these taxa came to northern Melanesia, considering three possible origins (New Guinea, Australia, and further out in Oceania). For three genera with one species in northern Melanesia and another further east in Oceania

(the rails *Nesoclopeus* and *Pareudiastes*, and white-eye *Woodfordia*), Mayr and Diamond presume an eastern proximate origin for the northern Melanesia taxa. These should have been left as origin undetermined, because it is just as parsimonious to invoke an origination in northern Melanesia and dispersal eastwards. In addition, the center of radiation for white-eyes in Oceania is Micronesia, and the two flightless rails are almost certainly remnants of once much larger radiations.

The seven chapters of Section 5 analyze the avifauna from a taxonomic perspective. Chapter 16 is a classic Mayr review of biological species, without elaboration on alternative species concepts. The next six chapters analyze geographic variation, dealing separately with increasing degrees of variation. Each chapter analyzes how the level of geographic variation (Chapter 18: species that lack geographic variation; Chapter 19: species with distinct subspecies; Chapter 20: species with distinct mega-subspecies, and so on) correlates with dispersal ability, abundance, habitat preference, and degree of endemism. Chapter 23 is a fascinating account of the many purported instances of hybridization in northern Melanesia, a particularly rich field for future analyses. Two of those instances are on Long Island, off New Britain, which was defaunated by a volcanic blast three centuries ago. Two populations there (of *Hirundo tahitica* and *Eudynamis scolopacea*) appear to involve introgression between colonists from two separate subspecies, one from New Britain (*H. t. ambiens* and *E. s. salvadori*) and the other from New Guinea (*H. t. frontalis* and *E. s. rufiventer*). It would be incredibly interesting to analyze those populations using modern methods of molecular genetics. Chapter 24 gives an in-depth look at northern Melanesia's most distinctive birds: the 35 endemic full species and the five or so endemic genera.

Definitions in this taxonomic section take on special importance because so many of their analyses are linked to what they are calling each taxonomic unit. Mayr and Diamond take great care to define mega-subspecies, allospecies, and superspecies. However, I would have liked to see a better definition of "subspecies," given the wide variation in how that term is applied to different taxa or in different areas. Mayr and Diamond frequently cite the 70% rule, but never, to my knowledge, state that they are using that criterion. In addition, their definition of "superspecies" makes exceptions for narrow sympatry, which obliterates the definition, because "allospecies" should form the components of a superspecies. If Mayr and Diamond consider a few instances of hybridization sufficient enough to say that reproductive isolation does not exist and thus two populations are only subspecies (e.g. *Megapodius freycineti* *eremita* and *M. f. affinis*), then why is one case of sympatry not enough to demonstrate that two taxa no

longer belong to the same superspecies (e.g. *Lorius lory*, which has two "allospecies" on New Ireland)?

Another concern in the taxonomic section is that Mayr and Diamond retain the status quo even when the evidence at hand indicates otherwise. For instance, it is hard for me to imagine that a female *Pachycephala "pectoralis" feminina* on Rennell Island in the Solomons, where both males and females are hen-plumaged (see plate 2), would "revert" to choose a normally male-plumaged whistler as a mate should that hybridization opportunity present itself. After all, the population had already lost the male plumage once before. Any such skewedness toward mate selection would lead to reproductive isolation and thus satisfy requirements of allospecies status for *P. feminina*.

Section 6 (chapters 25–33) provides equally in-depth analyses as the previous section, but this time from a geographical perspective. Using their taxonomy (presented in Appendix 1), Mayr and Diamond assess the geography of endemism (Chapter 25), present various sharing and nonsharing indices (chapters 26–27), and then, over the next six chapters, look at how various barriers have functioned between archipelagos, within archipelagos, or within island groups that were joined during lower sea-levels of the late Pleistocene.

In Section 7, Mayr and Diamond provide conclusions about speciation (chapter 34) and biogeography (chapter 35) of the northern Melanesian avifauna. The final chapter (36) outlines their opinions on promising directions for future research. They correctly place heavy priority on accumulating molecular and fossil evidence for northern Melanesian birds, but their recommendations for further ornithological exploration is notably underdeveloped. The underlying cause of that problem, I presume, stems from their erroneous assumption that the natural history and taxonomy of northern Melanesian birds is already well-established (e.g. see p. xiii in the introduction). This is way off target. In two short field seasons on one island (Isabel) in the Solomon Islands, my colleagues and I collected a wealth of new natural history data relevant to Mayr and Diamond's analyses, including evidence that published distributional data on *Accipiter imitator* and *A. albogularis* are probably incorrect (LeCroy et al. 2001), several montane species regularly or at least occasionally use lowland forests on Isabel (Kratter et al. 2001a, b), and that geographic variation in *Nesoclopeus woodfordi* is far from being resolved (Kratter et al. 2001a, A. W. Kratter unpubl. data). In addition, N. Cleere recently discovered that *Podargus ocellatus inexpectatus*, considered by Mayr and Diamond to be conspecific with *P. ocellatus* of New Guinea and northern Australia, may not even belong in *Podargus* (N. Cleere et al. unpubl. data). If so much new information can be gathered from two short field seasons of general collecting and observation on one Solo-

mon island, the amount to be learned across the two archipelagos must be staggering.

One needs only to look at the current revolution in defining species limits in Neotropical birds to see the benefits of combining traditional characters from museum skins with new characters derived from molecular biology and from field work on voice, behavior, and habitat selection. The resulting new taxonomy is full of reorganizations at the generic level, splitting at the species level, and identification of new cryptic species. I am confident that such a revolution awaits the avifauna of northern Melanesia, even without blind adherence to the phylogenetic species concept.

In suggesting fertile grounds for new research, Mayr and Diamond had the opportunity to emphasize collecting new natural history data and specimens. Not only is that needed for ornithological reasons (see above), but the future stewards of this avian paradise—indeed the next generation of Mayrs and Diamonds, as well as managers and land-owners living in Melanesia—could have used this inspiration. Most of those students will have little access to the avenues Mayr and Diamond emphasize (molecular and fossil work). Instead, with incentive and a little funding they could take to the bush to study species whose natural history (habitat selection, food habits, voice, breeding biology) remain poorly known. They could also learn from their elders, who already possess a vast yet largely untapped knowledge of northern Melanesia's birds. Mayr and Diamond's insistence that the natural history of these birds is already well known will shut doors to those students.

The 52 maps (one per page) are meant to illustrate the vast diversity of distributional patterns shown by northern Melanesian birds, not to be exhaustive for all species. The maps include informative legends, giving all taxonomic units. I think it should be standard for such regional volumes to have a map and legend of the study area on the inside covers of the book. The complexity of this region's geography makes it extremely important for the reader to have ready access to the maps, instead of thumbing through the introductory pages.

The real meat of the book is the seven data-rich appendices. The first appendix is the foundation of the entire book, presenting a full taxonomic account of the resident avifauna in northern Melanesia. The basic units are the 191 zoogeographic species (=super-species). For each, Mayr and Diamond list the allo-species and then the subspecies. Included in this appendix are citations (author, date) of all taxonomic units in northern Melanesia and detailed north Melanesian distributions of all taxa. Distinctive groups of subspecies, termed "megaspecies," follow. Notes on taxonomy follow, although those do not include recent treatments by other authorities. For example, ignored here are the six published volumes of *Hand-*

book of the Birds of the World (del Hoyo et al. 1992–2001), most recent family-level treatises (e.g. Cleere 1998, Juniper and Parr 1998, Taylor 1998, Gibbs et al. 2001, etc.), and even the otherwise widely cited Sibley and Monroe (1990).

Mayr and Diamond's reluctance to appreciate the importance of fossil evidence is evident in their taxonomy. For instance, they list as allospecies several populations in the *Ducula aurorae* superspecies that now occur allopatrically. However, as they mention in Appendix 1, prehistoric bones on many Pacific islands have shown that two allospecies within the superspecies once were sympatric. Although Mayr and Diamond stretch the definition of superspecies to allow one or two doublets (instances of sympatry limited to only one or a few islands) within a superspecies, the paleontological evidence far surpasses this.

The six other appendices are nonbreeding visitors (Appendix 2); a thankfully unimportant account of introduced species (Appendix 3); a thorough and most welcome chronology of ornithological exploration (Appendix 4); ecological and biogeographical attributes of each species (endemism, habitat, dispersal ability, abundance, number of allospecies and subspecies, number of islands occupied, and a ratio of the latter two) that form the basis of many analyses (Appendix 5); evidence of over-water dispersal (Appendix 6), and biogeographic attributes with general distributions within the Bismarck and Solomon islands and in New Guinea, Australia, and eastward in Oceania (Appendix 7).

The major handicap I found to using this volume is that Mayr and Diamond do not provide an appendix that cross-references each species by island. Thus, when I wanted to run through the birds of Santa Ysabel ("Isabel" in most recent literature), the island I know best in northern Melanesia, I had to go through each species account in Appendix 1. There you can find island distributions, although individual islands may not be listed—instead many accounts say something like "virtually every island in the Solomons." In this exercise, I found two species listed for Santa Ysabel for which I could not find previous citation (*Tyto alba* and *Acrocephalus stentotorus*) and two species whose occurrence has not been established (*Reinwardtoena crassirostris* and *Accipiter albobularis*; see Kratter et al. 2001a, LeCroy et al. 2001). I would expect that lists for other islands suffer from similar errors, which could have been remedied by an appendix consisting of two species \times island matrices, one each for the Bismarck and Solomon islands. These mistakes are compounded in Mayr and Diamond's analyses, as, for example, in their examination of the barrier between Isabel and Malaita on p. 247. They state that Isabel lacks *Ixobrychus flavicollis*, but it is listed in the appendix (presumably from the recent record in Kratter et al. 2001a, b, which they cited incorrectly) and *Tyto alba* (also listed for Isabel in Appendix 1, see above). Lacking such species \times

island matrices, any attempt to recreate the basis of their numbers for the species richness of islands (which are used repeatedly in their analyses) becomes a Herculean task.

I cannot help thinking that today's reader, perhaps a young graduate student intent on untangling the many evolutionary and ecological mysteries of this region's avifauna, will be disappointed and even confused by the consistently conservative approach taken by Mayr and Diamond. First, the species-level taxonomy will not be familiar to those who are learning ornithology from modern literature sources. Although Mayr and Diamond have thankfully avoided specific English names, their nomenclatural conservatism is evident in their use of English group names. For example, they repeatedly use the confusing group name "flycatcher" for various monarchs (e.g. *Monarcha*) and even for fantails (*Rhipidura*). Secondly, as mentioned above, most modern literature references are missing. Finally, Mayr and Diamond use out-of-date names for many islands and even archipelagos. Consulting a modern world atlas, one will not find many of the names that Mayr and Diamond use, such as New Hebrides (=Vanuatu), St. Matthias (=Mussau), New Hanover (=Lavongai), and San Cristobal (=Makira). Readers from northern Melanesia, to whom this book is dedicated, may be especially offended that Mayr and Diamond have reverted to using the old colonial names, which now have been out of use for decades.

One of the big bonuses of owning this book is the inclusion of nine beautiful color plates by Doug Pratt. The poses are generally natural and animated, the colors are well-produced, and the legends are informative. Many of the taxa represented have not been illustrated elsewhere, particularly those from the Bismarck Islands. My major criticism is that there are not more of these plates. Missing in particular is one that would illustrate some of northern Melanesia's most distinctive species-level taxa, those endemic to the islands that composed the Pleistocene island of Greater Bukida, such as *Accipiter imitator*, *Nesocolopeus woodfordi*, "*Podargus ocellatus*" *inexpectatus*, *Halcyon leucopygia*, and *Pitta anerythra*. A few minor complaints include two species endemic to Rennell Island, *Clytorhynchus hamlini* and *Woodfordia superciliosa*. In the former, the bill is too deep, and the illustrated bird lacks the often visible white tuft at the bend of the wing. In *W. superciliosa*, the bird has too deep a bill, the overall tone is too dark (especially the crown and tail, which should be concolor with the back), and the bare facial skin does not really look bare and is too dark. One important taxon is missing: *Monarcha verticalis ateralbus*, a "megasub-species" endemic to the small island of Dyaul off New Ireland, is mentioned in the text (p. 150), but not included on plate 3, which details the superspecies. In fact, I know of no illustration or description of this

distinctive taxon, aside from the original description in an obscure Danish journal (Salomonsen 1964).

In spite of my many criticisms, Mayr and Diamond have written a very important book. If you are interested in the mechanisms of how diversity arises, then this book is for you. All avifaunas should get this sort of in-depth treatment of taxonomy and biogeography. Though limited by a lack of molecular and fossil studies from the region (and further hampered by their own conservatism in taxonomy), Mayr and Diamond have laid out a foundation for future studies. The ornithology of northern Melanesia is not a closed book but a work in progress, with *The Birds of Northern Melanesia* as an impressive and very large first chapter. I thank D. W. Steadman and J. J. Kirchner for comments on this review.—ANDREW W. KRATTER, *Florida Museum of Natural History, PO Box 117800, University of Florida, Gainesville, Florida 32611-7800, USA. E-mail: kratter@flmnh.ufl.edu*

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