What's so special about New Guinea birds?1

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What's so special about New Guinea birds?[1]

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Summary.—I discuss why the tropical island of New Guinea has long been important in the development of our understanding of birds. There are two sets of reasons: New Guinea's birds, and its geography and peoples. New Guinea birds include: the famous birds of paradise, bowerbirds, and megapodes, which evolved in New Guinea (or New Guinea plus Australia) and are still concentrated there; pigeons, parrots, and kingfishers, which are especially species-rich and diverse in New Guinea and radiated there, whether or not they originally evolved there; and many groups that are morphologically and ecologically similar to European groups, such as 'wrens', 'creepers', and 'nuthatches', but that proved to be 'lookalikes' that evolved independently in New Guinea / Australia, just as numerous marsupial mammals and placental mammals converged on similar morphologies. Finally, the poisonous pitohuis and ifrit independently acquired the same neurotoxin as did South American poison-dart frogs; and a melampitta roosts and nests underground. The advantages offered by the island itself include: its equatorial location and its high mountains, so that New Guinea offers the entire range of habitats from coral reefs and rainforests through alpine grassland and glaciers on one short transect; the 'right size' (sufficient species to illuminate but not too many species so as to confuse); a simple geographic layout comprising a central mountain chain and its lowland ring; hundreds of islands of three types; virtually complete knowledge of the composition of its resident avifauna at the level of species; and the encyclopedic knowledge of birds among traditional New Guinea peoples. As examples of phenomena of general biological interest that New Guinea birds have illuminated, I discuss elevational sequences of congeners, culture in bowerbirds, evolution of 'aggressive mimicry' of larger bird species by smaller birds, brown-and-black mixed-species foraging flocks, and selection for and against overwater dispersal. These birds, landscapes, and topics are illustrated by photographs by K. David Bishop.

The tropical island of New Guinea has long played a pre-eminent role in ornithology, and in field biology in general (Wallace 1869, D'Albertis 1880, Mayr 1942, Diamond 1973, Beehler 2020). That pre-eminence caused New Guinea to be chosen as the site for the British Ornithologists' Union 1909 Jubilee Expedition (Wollaston 1912, Ogilvie-Grant 1915), and for the Archbold Expeditions of 1933–59 (e.g., Archbold & Rand 1940, Rand 1942). New Guinea's exploration was described by Wichmann (1909–12) and Souter (1964); its biological exploration by Frodin (2007); its ornithological exploration by Beehler & Mandeville (2017);

[1] This paper is an invited submission designed to partner a lecture that Prof. Diamond gave to the Club and the Linnean Society of London, originally planned to celebrate the occasion of the Club's 1,000th meeting since the inaugural assembly, held on 5 October 1892, and reported in the first issue of *Bull. Brit. Orn. Cl.* Unfortunately, this plan was one of the many casualties of the Covid-19 pandemic. Ultimately it was not possible for the presentation to go ahead until 6 October 2022, by which time it became the 1,005th meeting (see *Bull. Brit. Orn. Cl.* 142: 383–384). A recording of Prof. Diamond's address is available to view at https://www.youtube.com/watch?v=yJBGS7boZ6k.

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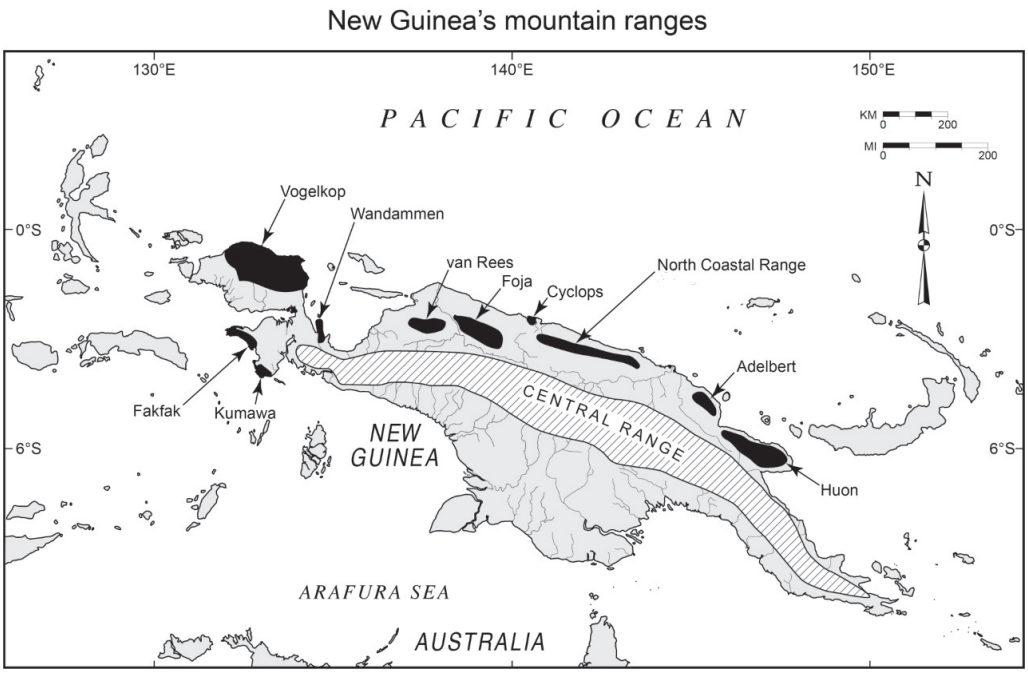

Map 1. New Guinea's mountain ranges: the Central Range running from west to east, and ten lower and much smaller outlying ranges along the north and north-west coasts.

and its ecology by Gressitt (1982) and Marshall & Beehler (2007). Illustrated guidebooks to its birds include Rand & Gilliard (1967), Coates (1985, 1990), Pratt & Beehler (2015) and Gregory (2017). Beehler & Pratt's (2016) book is a recent comprehensive systematic, taxonomic and distributional account to the level of subspecies.

In this paper I explain the two sets of factors that have made New Guinea a magnet for ornithologists: the island's remarkable groups of bird species; and advantages resulting from New Guinea's geography and peoples. I'll then present five examples to illustrate New Guinea's contributions to our understanding of biology.

My own first visit to New Guinea was in 1964. Since then, I have made a total of 31 expeditions, each lasting 1–5 months, to New Guinea and adjacent islands (e.g., Diamond 1969, 1972a, 1974, Diamond & Raga 1978). The 21 expeditions since 1986 have been conducted jointly with K. David Bishop, who has co-authored with me all of the publications resulting from those expeditions (e.g., Diamond & Bishop 1994, 1999, 2015, 2022) and who has provided all of the photographs for this article. These expeditions have been equally divided between the two halves into which New Guinea is divided politically: in the west, the Indonesian province of Indonesian New Guinea, alias Irian Jaya and now named Papua; and in the east, the independent nation of Papua New Guinea. Localities explored ornithologically during these expeditions have included a range of elevations from sea level to 4,000 m; both the northern and the southern watersheds; all main sections of the Central Range and the lowlands; and all ten of New Guinea's outlying mountain ranges (Map 1). Geographic highlights included the discovery and first ascents of the previously unidentified highest peaks of four of the outliers (e.g., Diamond 1969, Diamond & Bishop 2015). An ornithological highlight was the rediscovery, in Indonesian New Guinea's Foja Mts., of the long-lost Golden-fronted Bowerbird *Amblyornis flavifrons*, previously known only from four skins of uncertain

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provenance that appeared in a Paris hat shop in 1895 (Diamond 1982a). Some other results of these expeditions will be described below.

Remarkable New Guinea birds

Three famous families.—If you ask any ornithologist or birdwatcher which birds first come to mind at the mention of New Guinea, the answer will surely be 'birds of paradise' (Paradisaeidae) (Gilliard 1969, Cooper & Forshaw 1977, Frith & Beehler 1998). They are widely regarded as the world's most beautiful birds, and as the most extreme avian examples of sexual selection and male ornamental plumage (Figs. 1–3). While one species in the family (Trumpet Manucode *Phonygammus keraudrenii*) and three riflebird allospecies (genus *Ptiloris*) extend to Australia's east coast, and two others are endemic to the Moluccas, this family of 22 species or superspecies is otherwise confined to New Guinea and its satellite islands, especially to the mountains of New Guinea. (Throughout, I take as my unit of analysis the isolated full species, or the superspecies consisting of two or more allopatric allospecies. More often in the recent ornithological literature, individual allospecies are treated as separate species. The

Figure 1. Wilson's Bird of Paradise *Cicinnurus respublica* (K. David Bishop)

Figure 2. King of Saxony Bird of Paradise *Pteridophora alberti* (K. David Bishop)

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latter definition recognises 39–45 rather than 22 species of Paradisaeidae; Rand & Gilliard 1967, Gilliard 1969, Cooper & Forshaw 1977, Frith & Beehler 1998, Gregory 2017.)

Male plumage decorations of birds of paradise include tail feathers up to 1 m long, feathers reduced to long wires protruding from the tail or the head, profuse soft plumes, and (in King of Saxony Bird of Paradise *Pteridophora alberti*) a pair of highly modified feathers consisting of erectile wires each supporting a row of several dozen hard blue squares resembling glued pieces of plastic (Fig. 2). The *Pteridophora* male decorations are so extraordinary and un-birdlike that, when they were first described in 1894 by A. B. Meyer, the bird of paradise monographer Bowdler Sharpe dismissed the report by saying that any fool could see that the specimen was a human artifact. Males of two genera of birds of paradise, *Parotia* and *Diphyllodes* = *Cicinnurus*, construct terrestrial display courts as do bowerbirds.

Figure 3. Blue Bird of Paradise *Paradisornis rudolphi* (K. David Bishop)

The bowerbirds (Ptilonorhynchidae), confined to New Guinea and Australia, are nearly as famous and distinctive among New Guinea birds as birds of paradise (Gilliard 1969, Cooper & Forshaw 1977, Frith & Frith 2004). The terrestrial display courts built and decorated by male bowerbirds are the most elaborate structures constructed by any animal: stick huts up to several metres in diameter, or stick towers up to a few metres tall, decorated with up to hundreds of fruits, flowers, mushrooms, snail shells, beetle elytrae, pandanus leaves, and (near human settlements) stolen car keys, ballpoint pens, and other shiny or colourful objects (Fig. 4). Gilliard (1969) recognised that, in the course of bowerbird evolution, females' attention has become transferred from male ornamental plumage to male bowers: the duller the male's ornamental plumage, the more elaborate the bower's structure and decorations. Female bowerbirds choose a male with which to mate on the basis of bower quality (Borgia 1985); hence males devote spare time to pilfering and wrecking bowers of rival males, to reduce rivals' sex appeal.

The remaining New Guinea-centred or New Guinea-plus-Australia-centred family that I will mention (extending to islands east and west of New Guinea) consists of the megapodes alias mound-builders or brush-turkeys (Megapodiidae). These are the world's only birds whose eggs are incubated by heat sources other than the parents' body heat: variously, fermentation heat of decaying vegetation scraped together into huge mounds (Fig. 5), volcanic heat, or sunbaked sand (Jones *et al*. 1995). On hatching, chicks dig their way up to the surface, never encounter their parents, forage and feed entirely precocially, and eventually may make overland or overwater dispersal flights.

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Figure 4. Bower of Vogelkop Bowerbird *Amblyornis inornata* in the Arfak Mts. (K. David Bishop)

Figure 5. Dusky Scrubfowl *Megapodius freycinet* and its egg incubator mound (K. David Bishop)

Three worldwide families that radiated.—Those three families for which New Guinea is famous are still confined to New Guinea plus Australia and (Megapodiidae) some other islands, and surely evolved there. We now turn to three families or orders with worldwide distributions but that are especially speciose and diverse in New Guinea and must have radiated there, whether or not their distant origins were in New Guinea: pigeons (Columbidae), parrots (Psittaciformes) and kingfishers (Halcyonidae and Alcedinidae) (Beehler & Pratt 2016).

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Figure 6 (left). Victoria Crowned Pigeon *Goura victoria* (K. David Bishop)
Figure 7 (right). Red-breasted Pygmy Parrot *Micropsitta bruijnii* (K. David Bishop)

With 41 New Guinea species or superspecies (50 if allospecies are counted separately), pigeons reach their greatest morphological and ecological diversity in New Guinea. The region's pigeons range from the world's largest extant species (the crowned pigeon *Goura* superspecies: Fig. 6) to one of the world's smallest (Dwarf Fruit Dove *Ptilinopus nainus*). Distinctive groups of New Guinea pigeons besides *Goura* include fruit doves and fruit pigeons (*Ptilinopus* and *Ducula*), cuckoo-doves (*Macropygia* and *Reinwardtoena*), the extreme supertramp Nicobar Pigeon (*Caloenas nicobarica*) nesting colonially on small or remote islands, and 12 ground pigeons including the distinctive monotypic genera *Trugon* and *Otidiphaps* as well as *Goura* and *Caloenas*.

With 37 New Guinea species or superspecies (47 if allospecies are counted separately), parrots also reach, even more conspicuously, their greatest morphological, ecological and taxonomic diversity in New Guinea plus Australia (Forshaw & Cooper 1973). Again, New Guinea parrots range from one of the world's largest (Palm Cockatoo *Probosciger aterrimus*) to the world's smallest (*Micropsitta* pygmy parrots, barely *c*.8 cm long: Fig 7). Parrot groups or families confined to or centred on New Guinea and Australia, besides the pygmy parrots, are the cockatoos and the lories (the latter with brush tongues as specialisations for feeding on nectar and pollen) (Joseph *et al*. 2012, 2020).

Finally, New Guinea's 19 kingfishers (or 27 including allospecies) are also diverse in morphology, ecology and taxonomy (Forshaw 1987). They include river and lake kingfishers, a saltwater species (Beach Kingfisher *Todiramphus saurophagus*), and a large majority of woodland species; one of the world's largest kingfishers (Blue-winged Kookaburra *Dacelo leachii*, mass 350 g), as well as one of the smallest (Little Kingfisher *Ceyx pusillus*, 14 g); one of the world's few nocturnal kingfishers (Hook-billed Kingfisher *Melidora macrorrhina*); the bizarre Shovel-billed Kingfisher *Clytoceyx rex*, which excavates prey from the ground

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Figure 8 (left). Brown-headed Paradise Kingfisher *Tanysiptera danae* (K. David Bishop)
Figure 9 (right). Papuan Treecreeper *Cormobates placens* (K. David Bishop)

with its enormous bill; and the five species or superspecies (*c*.9 allospecies) of paradise kingfishers *Tanysiptera* (Fig. 8), with greatly elongated central tail feathers like those of male *Astrapia* and *Epimachus* birds of paradise, suggesting a role in sexual selection—but the long tail feathers of *Tanysiptera* are shared by both sexes, so their function remains unknown.

Convergent lookalikes.—In apparent contrast to the obviously distinctive groups of New Guinea bird species, many other New Guinea (and Australian) bird species are morphologically and ecologically similar to European groups already familiar to Australia's first British colonists and scientists: warblers, wrens, creepers, nuthatches, sallying flycatchers, robins, and nightjars (Figs. 9–10). Among New Guinea's and Australia's mammals as well, along with unequivocal members of European rat and bat families are many other mammals morphologically and ecologically similar to other European mammals such as cats, moles, wolves and flying squirrels. However, it was immediately obvious that the New Guinea and Australian mammalian lookalikes were not members of European mammal families because they all gave birth to undeveloped offspring in a pouch. That identified them as a very distinct mammalian branch (marsupials), whereas all European mammals are placental mammals giving birth to more developed young. But New Guinea and Australian lookalike bird species do not share any distinctive morphological feature like a pouch. It remained for late 20th-century DNA studies to prove that apparently familiar groups of New Guinea and Australian birds are not closely related to their European lookalikes (Sibley & Ahlquist 1990). Instead, like marsupials, they

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Figure 10. Emperor Fairywren *Malurus cyanocephalus* (K. David Bishop)

represent independent radiations superficially very similar in morphology and behaviour to European bird groups. New Guinea and Australian 'wrens' (Fig. 10), 'warblers' and 'creepers' (Fig. 9), etc. are now recognised as belonging to separate bird families confined to New Guinea and Australia, plus in some cases neighbouring islands. The superficial resemblance between the New Guinea / Australian and European bird families exemplifies the phenomenon of convergent evolution: 'The repeated evolution of similar phenotypes in response to similar environmental conditions…is referred to…as convergent evolution when similar phenotypes evolve in distantly related forms' (Losos *et al*. 2014: 455). A familiar obvious example of this phenomenon is the evolution of superficially similar large swift marine carnivores among mammals, cartilaginous fishes, teleost fishes and reptiles to give rise to dolphins, sharks, tuna and the extinct ichthyosaurs, respectively.

Two surprises.—Finally, among remarkable birds that make New Guinea special, I will mention two species or groups of species that had been described already in the 19th century, and are common or locally common, but whose unexpected properties or behaviours were recognised only recently. One of the two surprises is that in 1990 Dumbacher *et al*. (1992) discovered that Hooded Pitohui *Pitohui dichrous* (Fig. 11) and some other common New Guinea species contain the neurotoxin homobatrachotoxin, previously known only in South American poison-dart frogs. Although such chemical defence agents are widespread among other vertebrate classes and insects, this was one of the first cases documented among birds. Several of the toxic New Guinea species are so similar to each other in their orange-brown and / or black plumage that they were considered congeneric with *P. dichrous*, but they proved to be only pseudo-pitohuis not closely related to *P. dichrous* (Dumbacher *et al*. 2008, Jønsson *et al*. 2008, Dumbacher 2014). Hence, they are convergent in plumage, as well as in their independent evolution of toxicity. (The toxin is probably acquired from beetles consumed in the diet, rather than synthesised by the birds themselves: Dumbacher *et al*. 2004.) As I shall discuss below, most toxic New Guinea bird species associate in mixed-

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Figure 11. Hooded Pitohui *Pitohui dichrous* (K. David Bishop)

species flocks of deceptively similar brown and / or black species of which some are toxic and others not, and which may thus constitute examples of Müllerian mimicry and Batesian mimicry.

My other example of a surprising discovery in a species described a century ago involves Greater Melampitta *Megalampitta gigantea*, a large black bird previously known only from six specimens collected without any field observations. Puzzling peculiarities of the specimens were their stiffened and spiny but heavily worn tail and wing feathers; an exposed bony spur at the wing bend; and egg cases of feather mites covering the head. In 1981 I discovered in New Guinea's Fakfak Mts. (Diamond 1983), and confirmed at other New Guinea locations in subsequent years, that this melampitta is a locally common specialist of limestone karst terrain with abundant deep narrow vertical sinkholes. According to my New Guinea field companions, the melampitta roosts and nests underground in the sinkholes, which are too deep and narrow for a short-winged bird like the melampitta to exit just by flying vertically upwards. Instead, the bird may scurry up a sinkhole's rock face by propping itself with its stiffened wings and tail, whose feathers thereby become abraded. The function of the wing's bony spur remains unknown, as does the reason for infestation with feather mites.

Advantages of New Guinea itself

Those are some of the advantages offered to ornithologists by New Guinea's remarkable birds. Let us now consider six advantages offered by New Guinea's geography and peoples.

Equatorial location and elevation.—New Guinea lies on the equator, but its mountains rise to nearly 5,000 m. As a result, New Guinea is one of only three places in the world where there is permanent snow on the equator, because New Guinea has equatorial mountains high enough to support glaciers. (The other two are the Andes of South America, and Mt.

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Kilimanjaro and a few other mountains of East Africa.) New Guinea's glaciated highest peaks lie just 100 km from the coast. Already when the Dutch explorer Jan Carstenz sailed past New Guinea in 1623, he could see white in the sky that he correctly inferred meant high snow-capped mountains. (The only other place in the world with equatorial glaciers sufficiently near the coast that one can stand on a coral reef and see snow is Colombia's Sierra Nevada de Santa Marta.) However, the difficulties of overland travel in New Guinea are so great that it was not until 1909 that a Dutch military expedition reached the snowline, and only in 1962 did a team led by the Austrian mountaineer Heinrich Harrer (famed for his first ascent of the notoriously difficult Eiger North Face in the Swiss Alps) succeed in climbing New Guinea's highest peak (Wichmann 1909–12, Souter 1964).

The height of those snow-capped equatorial mountains means that in New Guinea, within a distance of 100 km as the crow flies, one traverses a range of habitats similar to the range encountered at sea level as one proceeds 7,500 km from the equator to the Arctic Circle. The succession of habitats encountered in New Guinea, proceeding inland from the coast, is: coral reefs, sand beaches, mangrove and swamp forests, lowland rainforest, hill forest dominated by *Castanopsis* and *Lithocarpus* oaks, montane forest dominated by southern beech (*Nothofagus*), subalpine forest with conifers, alpine grassland with cycads and tree ferns, alpine rock fields, and finally the snow (Figs. 12–18). That range of habitats contributes to New Guinea's biological richness: each elevational band has its own distinct species. New Guinea even has a small endemic alpine avifauna. The New Guinea bird species with the highest elevational range is Snow Mountain Robin *Petroica archboldi*, discovered only in 1938, with an elevational floor of 3,850 m (Rand 1942). While the climax vegetation of most of New Guinea below the treeline is various types of forest, there are also extensive swamps, lakes and (in dry areas of the southern lowlands) savanna. The only major habitat type lacking in New Guinea is desert.

The right size.—New Guinea is often described as the world's largest tropical island. With approximately 515 breeding species or superspecies on its mainland (621 if allospecies are counted separately), New Guinea is rich: the size of its resident avifauna is comparable to those of North America, Europe or Australia (Salvadori 1880–82, Mayr 1941, Rand & Gilliard 1967, Coates 1985, 1990, Pratt & Beehler 2015, Beehler & Pratt 2016).

Of course, South America is much larger and much richer. I recall a conversation soon after my first visit to New Guinea, when I chatted with a well-known ornithologist specialising in South American birds. After I had given him a brief summary of the New Guinea avifauna, he commented, "Didn't you feel that New Guinea is impoverished, depauperate?" No, I don't, and here's why.

It's a misnomer for an ornithologist to call New Guinea the largest tropical island. Instead, New Guinea rates as the smallest continent. If one's distinction between an 'island' and a 'continent' is based solely on landmass area, such a distinction would be completely arbitrary. But to a biologist, there is a non-arbitrary distinction: a continent is a landmass large enough for many of its species to have been generated by speciation and radiation within the landmass, rather than by colonisation one species at a time from other landmasses. By that criterion, New Guinea clearly is for birds a continent: its avifauna includes many radiations of endemic subgenera (e.g., groups of *Rhipidura* fantails), genera (*Melanocharis* berrypeckers) and families (e.g., Cnemophilidae satinbirds). Its 515 species or superspecies constitute a database large enough to test major questions of biology, but small enough that in a decade or two an ornithologist can observe most of New Guinea's species and learn the distributions of all of them. While South America of course offers a far larger database of about 3,000 species, that includes so many species with highly local or poorly known distributions that no ornithologist can observe or understand all of them in a lifetime

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Figure 12. Coastal forest (K. David Bishop)

Figure 13. Lowland rainforest (K. David Bishop)

Figure 14. David Bishop and Jared Diamond at a native-built vine suspension bridge over the upper Digul River, 215 m elevation (K. David Bishop)

Figure 15. Small aircraft dropping down to land at a one-way bush airstrip, Yolban, 1,250 m (K. David Bishop)

Figure 16. Moss forest, Arfak Mts. (K. David Bishop)

Figure 17. Alpine grassland with cycads, Mt. Doma (K. David Bishop)

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of study. That's why I say that New Guinea is just the right size for an ornithologist: big and rich enough, but not too big or too rich.

Simple geographic layout.—The mountains of New Guinea comprise a single central chain running west to east, on which differentiation has created west / east chains of subspecies or allospecies, plus ten outlying mountains along the north and north-west coasts, with endemic subspecies and allospecies but only two endemic species (Diamond 1985: see Maps 1–2). The lowlands of New Guinea consist of a ring enclosing that central chain—a ring around which differentiation has created three main lowland regions (northern, southern, and far western), each with endemic subspecies or allospecies, or chains of them (see Map 3). That is a much simpler geography than South America offers for reconstructing evolutionary history.

Figure 18. Alpine pools at 4,000 m below the summit of Mt. Mandala (K. David Bishop)

Hundreds of islands of three types.—Much of New Guinea's underwater shallow continental shelf was dry land at Pleistocene times of low sea level. Rising sea level at the end of the Pleistocene, and repeatedly during the Pleistocene, submerged lower parts of the shelf and isolated the higher parts as land-bridge islands of various elevations and areas, which were formerly part of Pleistocene Greater New Guinea (Diamond 1972b, Diamond & Bishop 2020: see Map 4). When those land bridges to modern New Guinea were intact during the Pleistocene, the islands could be reached not only by flightless mammals, but also by New Guinea's several hundred bird species unable or unwilling to colonise over water (Diamond 1972b). With the severing of the land bridges at the end of the Pleistocene, populations of non-water-crossing species on the islands became isolated and subject to the risk of extinction without the possibility of recolonisation. They thus constitute a convenient test system for understanding species differences in risk of extinction as isolated populations (Diamond 1972b).

Hundreds of other 'oceanic' islands lying beyond New Guinea's continental shelf could be colonised only by species capable of crossing water barriers (e.g., Mayr & Diamond 2001). Some of those oceanic islands lie on volcanic arcs at tectonic plate boundaries and have periodically been defaunated by volcanic eruptions. That has led to the evolution of a group of *c*.20 species without parallel in the Caribbean or elsewhere in the world: so-called supertramps with high dispersal ability, specialised for colonising small or remote or recently defaunated islands, and absent from large, central, species-rich islands (Diamond 1974, 1975).

Completeness of species-level cataloguing.—Knowledge of the composition of New Guinea's resident endemic avifauna can be considered near-complete at the level of species/superspecies. The next-to-most-recent discoveries were of one monotypic

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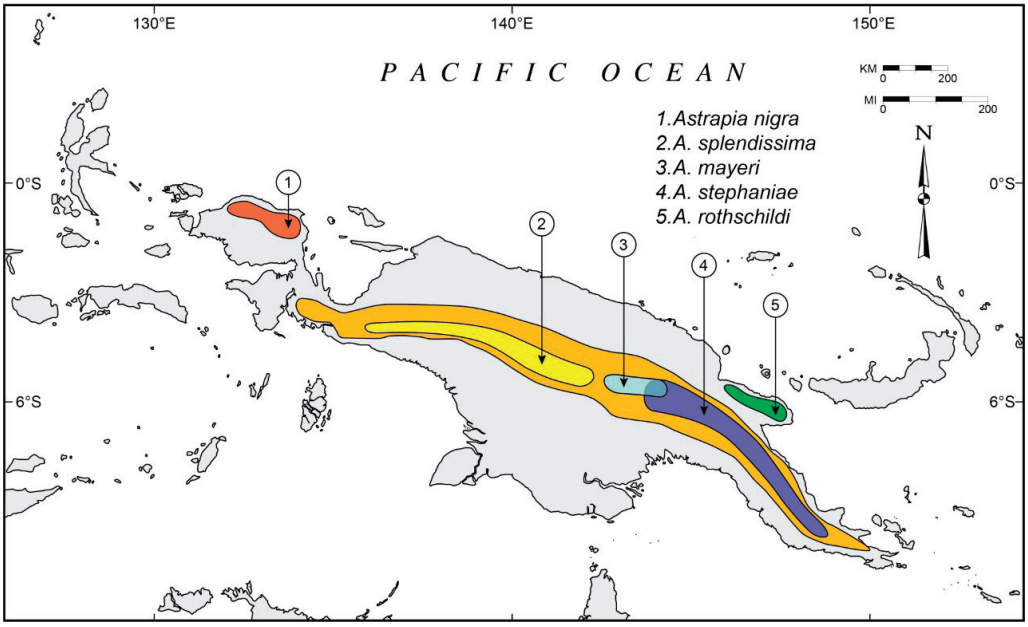
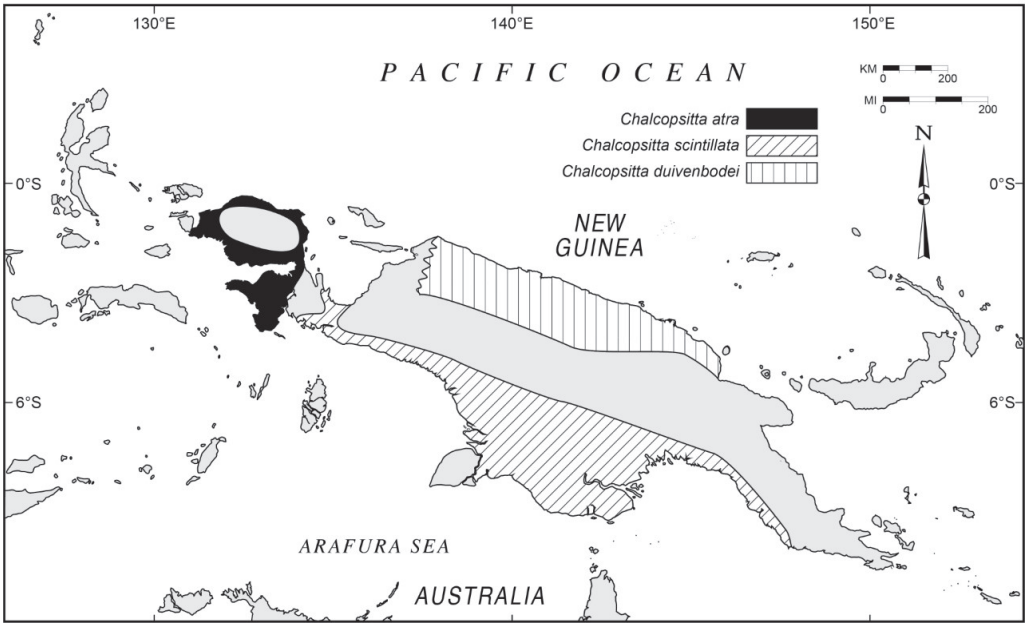


Map 2. Speciation in *Astrapia* birds of paradise. The five allospecies of the *Astrapia* superspecies have differentiated from west to east along the Central Range, plus one each on the two highest outlying ranges (*A. nigra* on the Vogelkop, and *A. rothschildi* on Huon). All five allospecies are allopatric, except that the easternmost population of *A. mayeri* and the westernmost of *A. stephaniae* overlap, with elevational exclusion in the zone of sympatry.



Map 3. Speciation in New Guinea's lowlands, as illustrated by the three allospecies of the parrot superspecies *Chalcopsitta*. Speciation in the lowlands consists of differentiation in the lowland ring around the Central Range, usually with one or more isolates each in the northern, southern and western lowlands.

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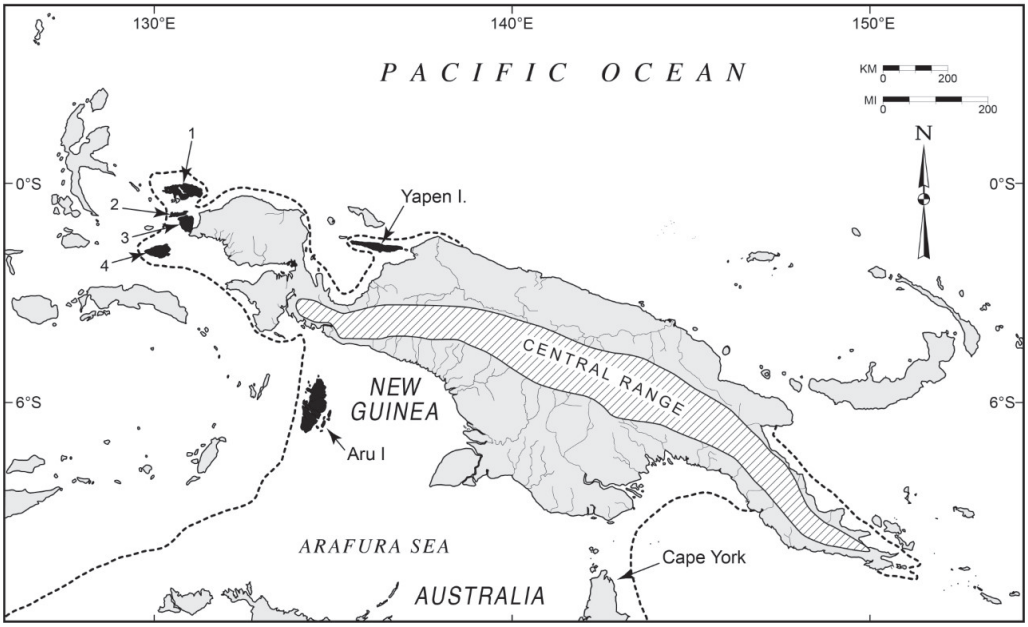

Map 4. New Guinea's six largest land-bridge islands. The dashed line around New Guinea and northern Australia marks the edge of New Guinea's continental shelf, corresponding to the 200-m depth contour in the ocean today. When sea level dropped by nearly 200 m at Pleistocene times of low sea level, the Arafura Sea became dry land, New Guinea and Australia were joined in a single landmass, and Greater New Guinea extended to the edge of the continental shelf. At the end of the Pleistocene, as glaciers melted around the world, rising sea level flooded the continental shelf and converted the six highest portions of the shelf into land-bridge islands: Yapen, Aru, 1 = Waigeo, 2 = Batanta, 3 = Salawati, 4 = Misool. Many of those modern-day islands' bird populations arrived overland during the Pleistocene. Islands lying beyond the edge of the continental shelf are oceanic islands, which lacked a recent land connection to New Guinea and have derived their birds entirely by overwater colonisation.

genus (Archbold's Bowerbird *Archboldia papuensis*) and four species unrelated to known superspecies (Brass's Friarbird *Philemon brassi*, *Petroica archboldi*, Black-breasted Mannikin *Lonchura teerinki*, and possibly Archbold's Owlet-nightjar *Aegotheles archboldi* whose status is still debated), discovered in 1938–39 by the Third Archbold Expedition in a biologically unexplored large area of western New Guinea: Rand 1942). The most recent discovery was of Satin Berrypecker *Melanocharis citreola* in the outlying Kumawa Mts. (Mila *et al*. 2021). Two other recently discovered taxa have been described as endemic allospecies rather than as subspecies: Long-bearded Honeyeater *Melionyx princeps* (Mayr & Gilliard 1951) and Wattled Smoky Honeyeater *Melipotes carolae* (Beehler *et al*. 2007). Some other allopatric populations discovered since 1939 may also prove to be allospecies rather than subspecies, and numerous previously known allopatric populations are regarded as allospecies, rather than subspecies, by recent authors (e.g., Beehler & Pratt 2016).

Of course, there have been, and will continue to be, innumerable discoveries about distributions and biology. However, it seems that our knowledge of New Guinea's resident endemic avifauna at the level of the species or superspecies is much more complete than is true of South America, where distinct new species continue to be discovered annually, and occasionally even new genera.

New Guinea peoples.—Traditionally, New Guinea peoples were either (a minority) hunter / gatherers or (a majority) subsistence farmers with protein-poor crops and few domestic animals, hence dependent on hunting and gathering for much of their dietary

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Figure 19. Dugout canoe on the Elevala tributary of the Fly River (K. David Bishop)

Figure 20. Huli man (K. David Bishop)

Figure 21. Man wearing phallocarp at Yolban, 1,250 m (K. David Bishop)

Figure 22. Traditional highland sweet potato farm (K. David Bishop)

protein (Figs. 19–23). As a result, traditional New Guineans are walking encyclopedias of information about local birds, with up to 200 local-language names for local bird species or groups of species (Majnep & Bulmer 1977, Diamond & Bishop 1999). Routinely, whenever I arrive at a New Guinea village to study birds, I devote much time to learning names of bird species in the local language, of which New Guinea has about 1,000, because it is essential for tapping into New Guineans' encyclopedic knowledge of local bird species, and to find species of particular interest. That requires knowledge of local-language names. Questions about '*Phonygammus keraudrenii*' or 'Bicoloured Mouse-Warbler' will produce no response; one must instead ask about the '*isawanotaba*' or the '*kri-kro*', having first figured out those names' English or Latin equivalents.

As examples: when Jack Dumbacher discovered by accident (as a result of his reaction to being scratched) that *Pitohui dichrous* (Fig. 11) is poisonous, and he reported his 'discovery' to local New Guineans, after their initial response (in effect, 'Of course, are you Europeans

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Figure 23. Children at Yolban, 1,250 m (K. David Bishop)

so stupid that you don't even know *that*?') they proceeded to tell Dumbacher about other bird species known to them, but not to Europeans, to be poisonous. My local guide Robert Uropka in New Guinea's Star Mts. described to me, along with 165 other bird species, a bird he called the *densiki* in his Ketengban language, and which he said is rare and very similar to but smaller and greyer and with a more cocked tail than the abundant *sewi*, which I had already identified as Grey-streaked Honeyeater *Ptiloprora perstriata*. Robert twice succeeded in finding for me a *densiki*, which proved to be the rare and little-known Leaden Honeyeater *P. plumbea*, a sibling species of *P. perstriata*. Those are the only two occasions in my life that I have seen *P. plumbea*.

Those six advantages—equatorial location and elevation, the right size, simple geographic layout, hundreds of islands of three types, completeness of species-level cataloguing, and New Guinea peoples—have made New Guinea ideal terrain for studying evolution, speciation, community ecology, behaviour, sexual selection, and other fields and topics of biology.

What have we learned?

We've now discussed some of New Guinea's remarkable bird species, and some of New Guinea's advantages for bird studies. What have those birds and those advantages taught us? I'll give five examples of conclusions of general biological interest.

Elevational sequences.—One of the ecological segregating mechanisms by which related or congeneric species co-exist on New Guinea's mountains depends on elevation. The New Guinea montane avifauna includes dozens of pairs, a dozen triplets, several quartets, and one quintet of taxonomically related and ecologically otherwise similar species that co-exist by inhabiting different elevations, often occupying mutually exclusive elevational ranges (Diamond 1972a, 1973, Freeman & Freeman 2014). For instance, Mt.

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Karimui's north-west ridge in 1965 supported two abundant and territorial warbler species of the genus *Crateroscelis*, with no elevational overlap at all: *C. murina* from the lowlands to 1,643 m and *C. robusta* from 1,646 m to 2,320 m. Such sequences are also frequent among Andean birds (Terborgh 1971).

The distributions of many pairs of populations have been interpreted as constituting 'snapshots' of successive intermediate stages in speciation (Diamond 1972a, 1973). They suggest that these elevational sequences arise via allopatric speciation of eastern and western populations along New Guinea's Central Range (Map 2), rather than through sympatric speciation along an elevational gradient. Map 5 depicts seven stages in that suggested allopatric evolution of one species into a sympatric species pair co-existing by elevational segregation. This hypothesis, based on distributional evidence, remains to be tested by molecular phylogenetic approaches. The seven distributional stages are as follows.

In the presumed first stage, one species without close relatives is distributed continuously from the western to the eastern end of the Central Range, with no consistent variation in elevational range (e.g., Blue-capped Ifrit *Ifrita kowaldi*).

In the presumed second stage, a species' western and eastern populations become separated by a large distributional gap, due perhaps either to local extinctions or to a distributional barrier across the Central Range such as the Strickland Gorge (e.g., Papuan Treecreeper *Cormobates placens*; Fig. 9).

In the presumed third stage, the western and eastern populations are still separated by a distributional gap, but have now evolved slightly different elevational ranges and sufficient morphological and genetic differences to be classified as distinct allospecies of a superspecies, rather than as subspecies of an allospecies or species (e.g., Short-bearded Honeyeater *Melionyx nouhuysi* in the west, Long-bearded Honeyeater *M. princeps* in the east).

In the presumed fourth stage, the western and / or eastern population expand eastwards and/or westwards, respectively, to approach each other's ranges without yet having achieved sympatry (e.g., Western *Paramythia olivacea* and Eastern Crested Berrypeckers *P. montium*).

In the presumed fifth stage, geographic expansion has proceeded further, to the point where western and eastern forms have achieved partial sympatry, with truncated and mutually exclusive elevational ranges in the zone of sympatry, but with each species occupying a broader elevational range in its own zone of allopatry (e.g., Green-backed *Pachycephalopsis hattamensis* and White-eyed Robins *P. poliosoma*).

In the presumed sixth stage, one taxon has completely overrun the geographic range of the second, with the two species still co-existing by elevational segregation, but the first taxon still maintains a zone of allopatry where it occupies a wider elevational range.

In the presumed seventh stage, the two taxa are now geographically fully sympatric as an elevationally segregating species pair, with neither species existing in allopatry, and both species widely distributed geographically from west to east over the Central Range. This whole process may then repeat itself to generate an elevationally segregated species trio (stage eight), quartet, or quintet.

Culture in bowerbirds.—Culture may be defined as the set of behaviours that characterise a local population of a species, and which are transmitted not genetically but instead by learning and copying among individuals. Culture was previously considered unique to humans. When Jane Goodall and other field biologists studying chimpanzees, gorillas and other animal species observed differences in behaviour between conspecific but geographically separated populations (such as in tool use by chimpanzee populations), their interpretation of the differences as cultural was initially dismissed by other biologists.

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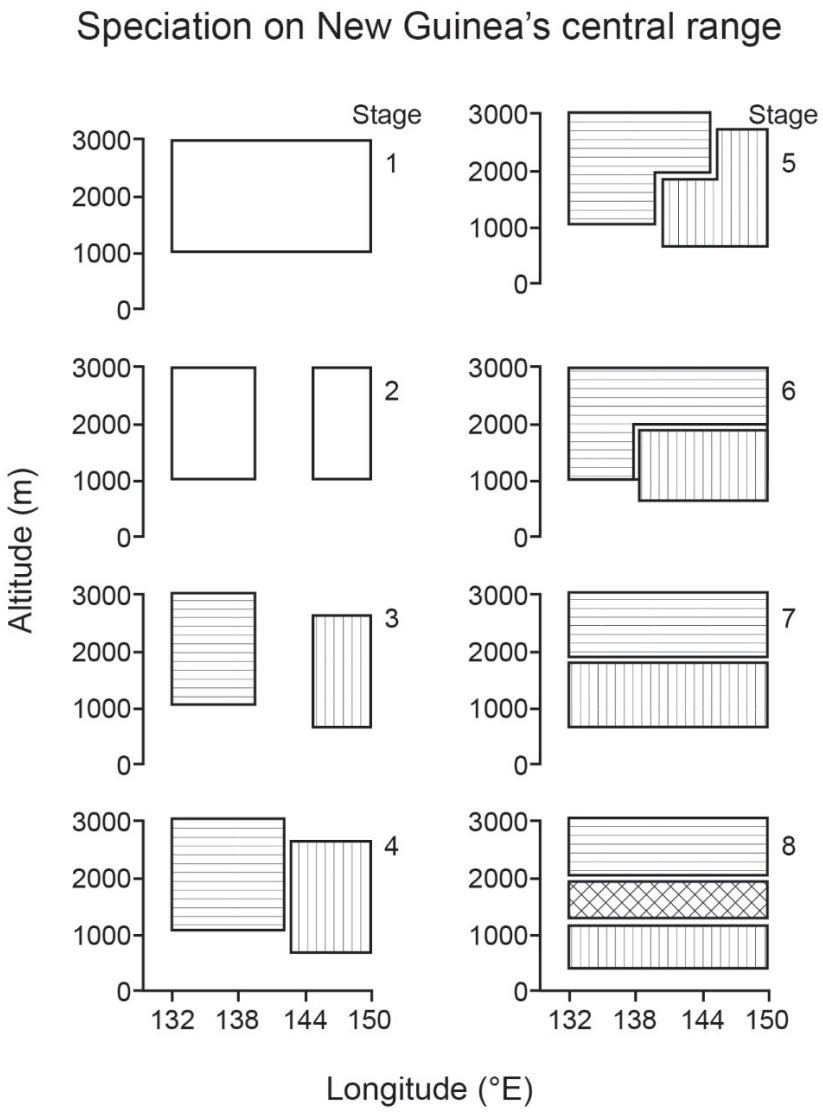

Map 5. Speciation on New Guinea's Central Range. This figure depicts eight postulated stages in the evolutionary transformation of one species, initially distributed from the west to east end of the Central Range, into two (stage seven) or even three (stage eight) fully sympatric species co-existing with elevational segregation. Each of the eight subfigures depicts the actual elevational and longitudinal distribution of one taxon, or of a pair or a triplet of closely related taxa (distinguished by horizontal, vertical, or cross-hatching), on the Central Range. Each subfigure is interpreted as constituting a 'snapshot' of one stage in speciation. In each subfigure, longitudinal distribution is shown along the horizontal axis, and elevational distribution along the vertical axis. For example, stage four depicts two taxa with allopatric but abutting geographic distributions and slightly different elevational ranges; stage five depicts two taxa each with largely allopatric geographic distributions and mutually exclusive elevational ranges in the zone of sympatry; and stage seven shows two fully sympatric taxa both distributed from the west to the east end of the Central Range, with mutually exclusive elevational ranges everywhere. See text for discussion.

Gradually, though, it has become accepted that behavioural differences between conspecific animal populations may indeed be cultural.

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Amblyornis bowerbirds provide a good example. Bowers of Vogelkop Bowerbird *A. inornata* differ drastically between mountains (Diamond 1986a). In the Arfak, Tamrau and Wandammen Mts. bowers are stick 'huts' up to 2 m in diameter, decorated with many coloured objects (red, pink, orange, yellow, green, blue and purple fruits, flowers, mushrooms and butterfly wings, as well as black, brown, grey and white objects) (Fig. 4). Bowers of the same species in the Kumawa and Fakfak Mts. are instead stick towers up to 2.4 m tall, usually decorated only with black, white, grey and brown objects. Those differences led Gibbs (1994) to conclude that the former populations could not be conspecific with the latter. But the two sets of populations are nearly identical morphologically, and they are similar genetically too (Kusmierski *et al*. 1997). Furthermore, there are differences in bower style even between three sites less than 10 km apart in the Kumawa Mts.: bowers in one area were decorated with fruits and flowers of four colours, in another with black, grey and white objects plus propped-up pandanus leaves, and in still another area with neat rectangular rows of pieces of buff-coloured clay. These differences are not due to differences in local availability of those objects: coloured fruits and flowers, and uncoloured stones and snail shells, are widely available; and when bowerbirds of a population decorating only with uncoloured natural objects were offered coloured poker chips, they discarded the chips, but coloured chips were promptly incorporated into the bowers of a population using coloured natural objects (Diamond & Bishop 2015).

Local bower style appears to be learned and transmitted by observation in both male and female bowerbirds (Diamond 1986b). Young males build crude bowers with locally inappropriate decorations and form, take up to seven years to develop the locally appropriate bower style, resemble females in plumage, and exploit that resemblance to enter bowers of adult males and elicit the adult male's display, thereby giving young males the opportunity to learn by closely observing mature bower design and display. Females sometimes form groups to visit bowers, thereby giving young females the opportunity to learn taste in bowers from older females.

'*Aggressive mimicry*'.—Over a century and a half ago, the great Alfred Russel Wallace (1869), co-discoverer of evolution and natural selection with Darwin, described a striking case of apparent visual mimicry between species of two different bird families: honeyeaters (Meliphagidae) and orioles (Oriolidae). Wallace attributed the apparent mimicry to the putative advantage that 'weak' orioles gained in deterring attack by aggressive crows and hawks, as a result of resembling the 'strong' pugnacious honeyeaters. But Wallace's interpretation was dismissed by Stresemann (1914) and forgotten. In recent years, however, interest in 'aggressive mimicry' has exploded, stimulated by discoveries of cases involving not only species that are taxonomically remote and obviously unrelated, but also between confamilial species that had previously been considered closely related. Especially shocking to European and North American ornithologists has been genetic evidence demonstrating that three pairs of confamilial species so similar that they had always been considered closest relatives—Middle Spotted *Dendrocopos medius* and Lesser Spotted Woodpeckers *D. minor*, Hairy *Picoides villosus* and Downy Woodpeckers *P. pubescens*, and Greater *Tringa melanoleuca* and Lesser Yellowlegs *T. flavipes*—are not close relatives but instead mimics or convergent (Weibel & Moore 2002, 2005, Gibson & Baker 2012, Prum 2014).

I re-appraised Wallace's classic example and concluded that Wallace was half-right (Diamond 1982b). Orioles (genus *Oriolus*) are predominantly yellow-and-black Afro-Eurasian species that, on invading the Indonesian archipelago and New Guinea, encountered a superspecies of big brown honeyeaters known as friarbirds (genus *Philemon*). The Indonesian and New Guinea orioles differ drastically in plumage from extralimital orioles, in being brown like friarbirds. Among Indonesian islands and New Guinea, both

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orioles and friarbirds exhibit marked geographic variation in plumage, but variation is parallel, such that on each island the oriole and the friarbird resemble each other. For example, geographic differences in patches of bare black facial skin in friarbirds are paralleled by corresponding patches of black feathers in orioles. While on each island the friarbird is larger than the oriole, paradoxically the more *dissimilar* the friarbird and oriole are in size (i.e., the larger the local friarbird relative to the oriole), the more *perfect* is the local plumage resemblance. David Bishop and I have often been confused in the field by species pairs that are merely 'quite similar' in plumage, as on New Guinea. On islands such as Seram and Buru, where the species pairs are virtually identical in plumage, they are very difficult to distinguish not only in the field, but even as specimens in museum trays: indeed, some museum specimens proved to be misidentified. Further complicating the picture is that the New Guinea oriole, which is 'quite similar' to the larger New Guinea friarbird, shares New Guinea with the smaller Streak-headed Honeyeater *Pycnopygius stictocephalus*, whose plumage is even more similar to the New Guinea oriole's than the New Guinea oriole's plumage is to the New Guinea friarbird's! All of these resemblances are even more confusing in the field than in museums, because of vocal mimicry and similarity in posture, movements and flight.

Hence, I agree that Wallace was partially correct: Indonesian and New Guinea orioles do mimic friarbirds. We can confidently refer to mimicry of friarbirds by orioles, rather than mutual convergence between friarbirds and orioles, because the friarbirds are typical honeyeaters in their brown plumage and bare facial skin, whereas Indonesian and New Guinea orioles are unique within the family Oriolidae in plumage and in their black facial patches resembling the friarbirds' black facial skin areas. The evidence for mimicry is now much stronger than that available to Wallace, who encountered only two pairs of island populations (on Seram and Buru), whereas we now know seven pairs. Especially convincing is the study of Jønsson *et al*. (2016), who obtained molecular data for all *Philemon* species and all brown *Oriolus* species, constructed molecular phylogenies, measured plumage reflectance, and calculated durations of co-existence.

What advantage do orioles gain by mimicking friarbirds? And why is plumage mimicry more perfect, the more dissimilar the model (i.e., the friarbird) is to the mimic (i.e., the oriole) in size? Here, like Stresemann (1914), I disagree with Wallace: crows and bird-hunting hawks are much too rare in habitats used by orioles and friarbirds to be a significant selective factor. Instead, I believe that selection involves attacks among friarbirds, orioles and Streak-headed Honeyeaters themselves, and the many other bird species congregating at fruiting and flowering trees where they feed on fruit and nectar. These feeding assemblages are 'veritable riots of interindividual aggression', to quote Beehler (1980: 516). Larger birds devote much time and energy to driving off smaller birds that overlap in diet and that can be safely attacked. Smaller birds that resemble larger birds would be less likely to be attacked by larger birds, and in turn would be more intimidating to even smaller species. That would explain why plumage mimicry of friarbirds by orioles is more perfect, the relatively larger is the friarbird: larger size makes the friarbird more dangerous to the smaller oriole, and in turn makes a friarbird-mimicking oriole more intimidating to even smaller birds.

These expectations are supported by my field observations in New Guinea. The New Guinea friarbird, oriole and Streak-headed Honeyeater all drive off smaller species overlapping in diet, but do not waste time and energy attacking species with quite different diets. However, it is striking that in 500 hours of observation at fruiting and flowering trees in many different areas of New Guinea, I have never seen the New Guinea friarbird attack the smaller New Guinea oriole, nor the oriole attack the smaller Streak-headed Honeyeater.

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Mimicry serves the function of deception. A pervasive question in mimicry studies is: who is intended to be the deceived victim? In studies of poisonous butterfly species and their non-poisonous mimics, the answer is clear: the deceit is aimed at predators of butterflies. The poisonous New Guinea pitohuis that I discussed earlier are unpalatable to humans and ectoparasites, and presumably also to snakes, hawks and other predators on bird nests and adult birds (Dumbacher *et al*. 2008). There are now dozens of cases of apparent mimicry of larger birds by smaller birds (Prum 2014), discussed under the title 'interspecific social dominance mimicry' = ISDM. Is the intended victim of deceit the larger model species itself, or other potential competitors of the mimic? This question of the relative importance of different potential victims of deceit remains to be established not only for New Guinea friarbirds, orioles and honeyeaters, but also for all putative cases of ISDM (Prum 2014).

Brown-and-black flocks.—Itinerant mixed-species foraging flocks are known from many parts of the world: throughout the year in the tropics, and in the winter in temperate zones. They consist especially of small (<40 g) midstorey insectivores, often sharing a single predominant colour or colour-mixture. New Guinea also possesses such small insectivore flocks, especially of flycatchers and warblers.

But, in addition, New Guinea has another type of flock, consisting of medium-sized or large (40–220 g) species, most feeding on both fruit and arthropods, and at any moment concentrated at a given height anywhere from the understorey to the lower canopy. All constituent species are passerines; all are forest species; and most are strictly endemic to New Guinea and its large land-bridge islands, hence the flocks are absent from New Guinea-region oceanic islands, Australia, and all other sites outside the New Guinea region. Notably, flock members are either brown or black in both sexes (ranging to grey in cuckooshrike member species), or black in the male and brown in the female. Brown-and-black flocks have been studied especially by the late Harry Bell (1982, 1983) and by me (Diamond 1987). In New Guinea, brown-and-black flocks occur everywhere in lowland forests, up to elevations only occasionally above 1,200 m in the mountains.

Flock leaders are drawn from six species: Papuan Babbler *Garritornis isidorei* and five species of pitohuis or pseudo-pitohuis. Those are the sole flock species that regularly forage in intraspecific groups of five or more and maintain a constant stream of contact calls. Among the babblers, Harry Bell identified a leader individual with a distinctive leader call. These leader species constitute a hierarchy: the babbler is the leader species whenever it is present in the flock; if the babbler is absent, then the 'second-choice' leader is the pseudo-pitohui Rusty Shrikethrush *Pseudorectes ferrugineus*, which would otherwise follow the babbler; if both of those species are absent, the 'third-choice leader' becomes Variable Pitohui *Pitohui kirhocephalus*/*P. uropygialis*; and if all three of those species are absent, then the leader is *P. dichrous* (Fig. 11) or two pseudo-pitohui species. This means that at least some flock members are known to be poisonous.

Another regular flock member is New Guinea's lowland Spangled Drongo *Dicrurus bracteatus* or (above the lowlands) Drongo Fantail *Chaetorhynchus papuensis* (now revealed by molecular studies to be related to fantails [Irestedt *et al*. 2008], but formerly believed to be a drongo because of its similarity to drongos in behaviour). Drongos are notorious elsewhere in the world for following mixed flocks of birds, large mammals or people. (I was once momentarily frightened, while walking alone in a remote New Guinea forest, to sense something black following me; it proved to be *Chaetorhynchus*!) Still other regular flock members are one or more of at least 16 bird of paradise species, and one or more of all seven New Guinea forest species of cuckooshrikes (genera *Coracina* and *Edolisoma*).

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As for the function of joining brown-and-black flocks, the observable or suggested benefits include the usual ones suggested for mixed-species flocking elsewhere in the world: flushing prey, kleptoparasitism, benefitting from other species as sentinels, confusing predators, improved foraging efficiency, and acting as a 'gang' to overwhelm the defences of solitary territorial species.

Neotropical mixed flocks converge on a single colour or colour mix, perhaps to promote flock cohesion and predator confusion (Moynihan 1968). Why do New Guinea brown-and-black flocks instead converge on two alternative colours? One speculation is that the answer may involve the flock's long co-evolutionary history with birds of paradise, of which females are often brown (to aid crypsis at the nest?) and males are often glossy black (display plumage for sexual selection?). While some bird of paradise species have brightly coloured males, individuals that join flocks are mainly females and female-plumaged immature males.

Obviously, we still have much to learn about brown-and-black flocks, especially about their poisons, the functions of their two colours, and the roles and histories of their birds of paradise.

Selection for and against overwater dispersal.—Except for four flightless species—the three species of cassowaries, and New Guinea Flightless Rail *Megacrex inepta*—all New Guinea bird species are capable of flight, and many are outstandingly strong fliers. Nevertheless, New Guinea bird species differ enormously in their ability to colonise distant islands overwater.

At one extreme are the already mentioned so-called supertramps that specialise in living on oceanic islands requiring overwater colonisation to found populations. They dominate the avifaunas of Krakatoa-like recently defaunated volcanic islands, of which there are many in the New Guinea region along the Bismarck Volcanic Arc (fig. 1.2 of Mayr & Diamond 2001). For example, Long Island, defaunated by a volcanic eruption in the late 1600s, now has an avifauna dominated by ten supertramp species (Diamond 1974). Another set of islands dominated by supertramps are small islands where population extinctions are frequent, and where frequent recolonisations are necessary to maintain populations. Supertramps also occupy remote islands difficult for other species to reach. They have evolved high dispersal ability, and probably large reproductive outputs, at the expense of competitive ability. This may explain why they are absent on species-rich New Guinea itself, and on large and / or nearby islands in the same region. A human equivalent of avian supertramps is the Polynesians, who colonised every island of the tropical Pacific Ocean, no matter how remote, but who are confined to outlying islands on archipelagos closer to New Guinea, such as Rennell, Bellona and Sikaiana of the Solomons, whose central islands are all occupied by Melanesians.

At the same extreme of high overwater dispersal ability are species whose geographic ranges encompass islands scattered over thousands of kilometers of ocean, such as Buff-banded Rail *Hypotaenidia philippensis*, the *Megapodius* [*reinwardt*] superspecies, and Pacific Imperial Pigeon *Ducula pacifica*. On many remote islands that they have colonised, these species have evolved local endemic allospecies, many of which in the cases of *Hypotaenidia* and *Megapodius* went on to evolve flightlessness (Steadman 2006).

At the opposite extreme are several hundred New Guinea species absent from every oceanic island in the region (i.e., islands lacking a land connection to New Guinea at Pleistocene times of low sea level) (Diamond 1972b). The only islands of the New Guinea region, other than New Guinea itself, on which these species may occur are the larger so-called land-bridge islands, i.e., islands on New Guinea's shallow continental shelf, which were part of New Guinea at Pleistocene times of low sea level (Map 4). These 'land-bridge

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relict species' reached the islands overland when they were part of Pleistocene Greater New Guinea. Their island populations have subsequently been subject to differential extinction: more extinctions on smaller land-bridge islands with smaller populations, and extinction even on large islands for species with small populations due to low population density (e.g., New Guinea Harpy Eagle *Harpyopsis novaeguineae*, now absent even on the largest islands, and confined to New Guinea itself).

An initially surprising feature of the land-bridge relict fauna is that it includes many notably strong fliers, whose ecology on New Guinea involves daily long overland flights of dozens of kilometres and many hours. These surprising species include nomadic fruit pigeons, parrots and other species that fly long distances in search of fruiting and flowering trees, and three species of swifts whose foraging is entirely aerial. Yet these species are never seen flying overwater. The land-bridge relict species are entirely absent, even as visitors, from all oceanic islands more than 10 km from the New Guinea mainland—a distance that they could cover in a flight of ten minutes. Hence their absence from those islands is not because they are incapable of reaching them: it is because they *choose* not to fly overwater.

These facts illustrate that overwater dispersal is subject to natural selection, which variously either favours or opposes overwater dispersal depending on the species. The land-bridge relict fauna consists mainly of New Guinea forest species, although swifts are an exception. Their selection against dispersal may arise in part because their low reproductive potential makes them poor colonists even if they did reach islands. Hence any individuals inclined to disperse overwater would be selected out of the mainland population, and would also fail to found offshore island populations.

Disadvantage of New Guinea bird studies

I have discussed the advantages that New Guinea's remarkable birds, its geography, and its peoples offer to visiting ornithologists. I have provided examples of the questions of broad interest that New Guinea birds lend themselves to exploring. But I will conclude by acknowledging a disadvantage of field work in New Guinea. After one has come to know New Guinea, the rest of the world seems boring by comparison.

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