

## 4.9. Birds of Papua

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APPROXIMATELY 831 bird species have been recorded from the New Guinea region, including Papua and Papua New Guinea (Beehler et al. 1986; Coates 1985, 1990; Rand and Gilliard 1967; Sibley and Monroe 1990). This represents approximately 8.6% of the extant global avian alpha diversity (Table 4.9.1) and is roughly equivalent to the number of species recorded on the continent of Australia. Approximately 657 species are recorded from Papua (Appendix 8.2). This list is tentative because a full systematic review of the literature, existing collections, and sight records has not yet been completed.

Although most species are shared with Papua New Guinea, 67 species recorded from Papua have not been recorded in PNG (Appendix 8.2). Of these 38 are also unknown from surrounding Indonesia, Australia, or Melanesia and can be considered endemic to Papua. Of the nonendemic taxa, 285 occur only in PNG and Melanesia (thus comprising endemics to the New Guinea/Melanesia region), 141 species are fairly widespread globally, 110 are shared with Australia, and the remaining 83 have distributions overlapping with Australia or the remainder of Indonesia. Seventy-six species on the list can be classified as migrants, with at least some of the population moving in and out of Papua, either to Australia or Asia; 21 can be considered vagrants; one species is introduced; and approximately 558 are presumably breeding permanent residents (Appendix 8.2).

Table 4.9.1. Distribution of bird species of Papua and neighboring regions

Distribution	No. of species	Percent of avifauna
World	9,702	100*
New Guinea Region	831	8.6*
Papua	657	6.8*
Land and freshwater species breeding in Papua	552	5.7*
Endemic to Papua	38	5.8•
Shared with PNG and Melanesia	285	43.4•
Shared with Australia	110	16.7•
Shared with eastern Indonesia and Australia	83	12.6•
Widespread	141	21.5•

Note: \* indicates percent of the world's avifauna (bird species), • indicates percent of Papua's avifauna.  
 Source: Classification follows Sibley and Monroe (1990). Distribution data compiled from various sources, including Beehler et al. 1986; Beehler and Finch 1985; Coates 1985, 1990; Mayr 1941; Rand and Gilliard 1967; Sibley and Monroe 1990.

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Several bird families have important radiations in Papua. One of the most notable avian groups is the birds of paradise (Paradisaeidae) with 24 species in Papua, excluding the Cnemophilines and *Macgregoria* (Cracraft and Feinstein 2000). Birds of paradise have been the focus of more research than any other avian family in New Guinea because of their unusual mating systems, behaviors, and plumage (Frith and Beehler 1998). However, other families are comparably diverse and dominant in the New Guinea avifauna, such as honeyeaters (Meliphagidae) and bowerbirds (Ptilonorhynchidae). Twelve species of berrypeckers are placed in two families, Melanocharitidae and Paramythiidae (Sibley and Monroe 1990). These are the only widely recognized bird families endemic to New Guinea. No berrypeckers have been studied in the field, so our knowledge of this unique radiation is limited to what can be gleaned from museum data and a few published observations. Twenty-three species of kingfisher occur in Papua (four species of Alcedinidae and 19 species of Dacelonidae), more than four times the number of kingfisher species found in North and South America combined. Other notably species-rich families include Columbidae (42 species of about 300 species worldwide), Meliphagidae (55 species of about 178 species worldwide), Megapodiidae (9 of the world's 19 species), Acanthizidae (20 of the world's 65 species), and Psittacidae (46 species of about 340 worldwide).

### *History of Ornithological Exploration*

Since humans first arrived in Papua, they have studied and used birds. The first humans arrived in New Guinea sometime between 26,000 and 50,000 years ago (Bulmer 1982). Traditional societies of New Guinea have used birds for food, clothing, decoration, rituals, clan totems, and as wealth to be traded both within New Guinea and to outside countries (Bulmer 1982; Majnep and Bulmer 1977). Over thousands of years, native New Guineans have accumulated great stores of taxonomic (Diamond 1966) and natural history information about birds (e.g., Feld 1990; Kocher-Schmid 1991, 1993; Majnep and Bulmer 1977). While most of this anthropological information remains unrecorded, some groups of anthropologists and ethnographers (especially Bulmer, Diamond, and others) have gone to great lengths to record and preserve this information. Much work remains to be done in this field.

Birds have been important for New Guinea's trade and exploration for millennia. Birds and bird of paradise plumes were traded with Asia as long as 5,000 years ago (Frith 1971; Swadling 1995), and birds, as well as other aspects of New Guinea's unique biota, attracted European naturalists such as Alfred Russel Wallace to spend months or years exploring mainland New Guinea.

The birds of New Guinea and the ornithologists who studied them have played pivotal roles in broader arenas of science, exploration, and modern biological thought. A. R. Wallace's treatise on the Malay Archipelago (Wallace 1869) has become important reading for any student of biogeography. His time in Papua helped him to postulate independently that natural selection is the process that

explains much of evolution (a proposal that greatly affected the entire world when Charles Darwin published *The Origin of Species*.) And New Guinea's birds motivated many of the early expeditions into the rugged interior of Papua (e.g., Ogilvie-Grant 1915). New Guinea's birds also affected Ernst Mayr, who later formulated ideas about evolution and speciation that form the foundation of modern evolutionary biology.

The history of academic ornithological studies date back to the early and mid-1800s when a number of seaboard naturalists surveyed natural resources on Pacific islands (e.g., Lesson on the *Coquille*, Quoy and Gaimard on the *Astrolabe*, and other ships including the *Triton*, *Basilisk*, and *Rattlesnake*). These early collectors were followed by explorer-naturalists who probed deeper into the hostile terrain of New Guinea in the mid- and late 1800s. Odoardo Beccari explored the Arfak Mountains of the Vogelkop region; Wallace explored the Raja Ampat Islands of western Papua and the Aru Islands; Luigi D'Albertis sailed up the Fly River on three different expeditions; Carl Hunstein explored the Sepik; William Macgregor penetrated the mountains of southeast Papua New Guinea, and numerous government patrols explored Dutch New Guinea.

The first significant synthesis of Papuan birds was Count Tommaso Salvadori's *Ornitologia della Papuasias e delle Molucche* that appeared in 1880–1882 in three volumes. Following Salvadori, ornithological exploration flowered, and several private collectors funded expeditions to document avian species and collect bird specimens. These include Lord Walter Rothschild of England who sponsored collectors and volumes of ornithological studies based upon the collections. Much of this work was published in Rothschild's own journal, *Novitates Zoologicae*, by Ernst Hartert, Erwin Stresemann, William Ogilvie-Grant, Ernst Mayr, and others in the late 1890s through the early 1900s. The work of professional, independent collectors (e.g., A. S. Meek, A. E. Pratt and sons, Andrew Goldie, and others) came to be overshadowed by the large expeditions, such as the Dutch expedition led by Hendrik A. Lorentz in 1909, the British Ornithologists' Union expedition led by Goodfellow in 1909–1910, and a second BOU expedition led by Wollaston in 1912 (Ogilvie-Grant 1915; Wollaston 1912). After a lull in exploration during World War I (1914–1918), ornithological work resumed in the 1920s, notably by Ernst Mayr, the Pratts, Shaw Mayer, and Stein.

Building on the growing museum collections, a major jump forward began with Richard Archbold's three New Guinea Expeditions between 1933 and 1939. These expeditions brought intensive, multi-taxa collections out of key areas across the island of New Guinea, using amphibious aircraft for support. Perhaps most notable was the Archbold Snow Mountains Expedition of 1938–1939, which procured nearly 4,000 specimens of birds from Papua. Other similar museum expeditions included the Dennison-Crockett and Whitney South Seas expeditions that collected widely across the region. The Archbold Expeditions continued with a brief respite during the Second World War, ending with the seventh in 1964. Biological study matured in New Guinea during the mid-20th century, with numerous publications in the American Museum of Natural History's *Bulletin* and *Novitates*. A

journal *Novae Guinea* appeared and carried many important scientific papers about the region, including on ornithology.

After the Dutch departed Papua, ornithological exploration diminished. In the second half of the 20th century most work has been done on short visits by a small number of individuals and survey teams (e.g., Beehler et al. 1995; Diamond 1982b, 1987; Mack and Alonso 2000; Mees 1980, 1982).

The need for continued exploration in Papua is greater than ever. Because of its rugged terrain and poor infrastructure, many parts are still relatively unexplored and others have not been visited by ornithologists in more than half a century. Given the growing threats to Papua's forests from mining, logging, and human expansion (Chapter 7.1), it is important that exploration improve (see Supriatna 1999) and that basic surveys be conducted and specimens collected. Moreover, virtually no long-term studies of Papua's birds have been undertaken. Our knowledge of the ecology and behavior of Papuan birds is almost entirely derived from field studies in neighboring Papua New Guinea, which has more active and developed research programs.

Historical collections are very important for understanding the ornithology of Papua, and the work of these earlier ornithologists has left a legacy of avian taxonomy and systematics that far exceeds that of any other vertebrate or invertebrate group.

### *Biogeography of New Guinea Birds*

Biogeography is a science that focuses primarily on understanding and explaining the geographical distribution of organisms. Especially in places as geologically complex as Papua, biogeographical distributions may help explain the origin of bird families, understand the processes of evolution and speciation, and it may help with practical problems such as identifying priority areas for nature conservation. For Papua, we will split the biogeography section into two major sections: the first involves understanding the composition of Papuan bird fauna and its origin in the South Pacific, and the second involves understanding the distribution and ranges of bird species within the island of New Guinea.

#### ORIGIN AND COMPOSITION OF PAPUAN AVIFAUNA

Understanding the Papuan avifauna and its origin has been informed by several recent developments. With recent advancements in geology such as plate tectonics, island-arc dynamics, and sophisticated GIS and dating techniques, we now understand that New Guinea is a composite landmass consisting of the northern margin of the Australian continental plate and at least 32 distinct tectonostratigraphic terranes (Chapter 2.1; Davies et al. 1996; Pigram and Davies 1987; Polhemus 1996). At the risk of repeating concepts treated in greater detail elsewhere in this volume, we shall summarize some geological events and their effects on the current Papuan avifauna.

The Australian continent broke away from Antarctica roughly 50 million years

ago (mya) and has been drifting northward to its present position. Because New Guinea is located at the northern fringe of the Australian continent, the avifauna of Papua is inextricably tied to that of Australia. Thus, Australia and New Guinea's combined avifauna has been relatively isolated from other continents for the last 50 million years or more. Approximately 92% of New Guinea's bird families are shared with Australia (numbers cited are based on Beehler et al. 1986 and Pratt 1982, with modifications from more recent molecular phylogenetics findings). Prior to the Miocene, much of what is now New Guinea may have been underwater or have formed island archipelagos (Dow 1977; Dow and Sukamto 1984); geologists disagree about how much land was present and how continuous it was with other nearby islands and the continent. Regardless of the details, the Australian continent was certainly the primary source of the present avifauna at least of southern Papua, which is part of the Australian plate.

The northern basins of Papua, the Vogelkop peninsula, and the far eastern portion of Papua New Guinea are composed of terranes (tectonic plates) that originated or wandered elsewhere before colliding with New Guinea over the last 25 million years (Pigram and Davies 1987; Pigram and Symonds 1991). Tremendous advances in theory and empirical measurement (through GIS, magnetic positioning, and radio-isotope dating) have allowed geologists to reconstruct the historical movements of many of these terranes (Hall 2001, 2002). It now appears that many of these terranes originated or traveled far out in the Pacific Ocean, and may have had very distinct avifaunas. If a bird family originated in New Guinea or on an oceanic plate, then one would expect that it would have a center of distribution in New Guinea and would be poorly represented elsewhere. Several endemic or near-endemic families show a distribution that suggests that they evolved primarily in New Guinea or Pacific Islands rather than primarily on the Australian mainland. These families include owlet-nightjars (Aegothelidae), birds of paradise (Paradisaeidae), cnemophilines (Cnemophilinae), and berrypeckers (Melanocharitidae and Paramythiidae).

An alternative hypothesis would explain the same observed distribution. Because these families are rainforest-adapted birds, they may have evolved in Australian humid tropical forests that were absent or uncommon in other parts of the continent. As the Australian climate became hotter and more arid, forest bird species would have retreated north and east, where rainforest remnants still occur. Because rainforest is now rare in Australia, many of these bird families would now have species or family distributions that are centered on New Guinea.

Finally, although Papua is currently located at the eastern end of the Malay Archipelago, Papuan avifauna only weakly reflects its proximity to other Indonesian provinces and to Asian avifauna. Several Asian or Indonesian bird families are noticeably absent from Papua, including woodpeckers (Picidae), babblers (Timaliidae), broadbills (Eurylaimidae), bulbuls (Pycnonotidae), and several other smaller groups. Likewise, many Papuan or Australian groups do not extend into Asia or Borneo, including the birds of paradise (Paradisaeidae), bowerbirds (Ptilonorhynchidae), cassowaries (Casuariidae), owlet-nightjars (Aegothelidae), honey-

eaters (Meliphagidae), jewel-babblers (Cinclosomatidae), and others. Furthermore, many of the Asian avian families that do appear in Papua are only sparsely represented, such as thrushes (Turdidae), shrikes (Laniidae), and hornbills (Bucerotidae). Similarly, many primarily Australian lineages are poorly represented in Borneo or Southeast Asia. Alfred Russel Wallace was the first naturalist to understand and appreciate that New Guinea's avifauna was more allied with that of Australia than with that of most other Indonesian provinces. He identified a line, now known as Wallace's Line, which demarcates the boundary between primarily Asian fauna and the primarily Australian fauna. The line falls just east of Java and Borneo, and west of the Moluccas, and the line is known to coincide with stretches of deep water ocean that have persisted for millions of years (Wallace 1869, 1876). These oceanic stretches have hindered dispersal of mammals and birds, and thus the two avifaunas (Asian and Australasian) have only weakly mixed.

#### DISTRIBUTION OF THE AVIFAUNA WITHIN NEW GUINEA

The island of New Guinea is rugged, so populations of bird species can be isolated by a number of geographic barriers. For montane species, mountaintops may be separated by deep valleys or uninhabitable expanses of lowland forest. Lowland populations may be separated by wide rivers, high mountain ranges, or even inland ocean bays. Consequently, populations are often broken into multiple avian subspecies or even separate species, and many species have broken "checkerboard" distributions, separated by regions where the species is absent. The following sections describe biogeographic regions that are important for understanding bird distributions.

#### Montane Regions

Many bird species are limited to high montane regions, and several mountain ranges have endemic species or subspecies. Mountains have long been considered by biologists to be "islands in the sky" separated from other mountains by "seas" of unsuitable lowland habitat. Thus when a bird population on one mountain can be morphologically distinguished from bird populations on other mountains, the populations are often described as distinct species. If variation is weak or poorly understood, then the populations are usually at least given the designation of subspecies.

In Papua montane habitats are found in several regions: the Raja Ampat Island highlands (Batanta, Salawati, and Waigeo islands), the Vogelkop Mountains (Tamarau and Arfak), the Bomberai highlands (Fakfak and Kumawa mountains), the Wandammen Range, the Van Rees Mountains, the Foja Mountains, the Cyclops Mountains, the mountains of Yapen Island, and the mountains of the Central Range (Diamond 1985).

Although the Papuan land west of Cenderawasih Bay is mostly composed of Gondwanan continental terranes, these plates probably did not arrive in their present position until about 10 mya (Pigram and Davies 1987; Pigram and Symonds 1991). These terranes likely each had a different history, and are home to several

endemic birds. Nine upland species are endemic to these highlands west of Cenderawasih, including White-striped Forest Rail (*Rallina leucospila*), Vogelkop Scrubwren (*Sericornis rufescens*), Vogelkop Whistler (*Pachycephala meyeri*), Vogelkop Melidectes (*Melidectes leucostephes*), Arfak Honeyeater (*Melipotes gymnops*), Grey-banded Mannikin (*Lonchura vana*), Vogelkop Bowerbird (*Amblyornis inornatus*), Western Parotia (*Parotia sefilata*), and Arfak Astrapia (*Astrapia nigra*) (Stattersfield et al. 1998). Eleven additional species have ranges that extend into other mountain ranges, but many of these have distinct subspecies in the western Papuan highlands.

The Foja and Cyclops mountains, and the North Coastal ranges (Bewani, Torricelli, and Prince Alexander ranges) form a biogeographically distinct region called the north Papuan mountains (Stattersfield et al. 1998). These are relatively low mountains, but they are separated from the Central Ranges and other mountains by vast stretches of lowland forest in the Sepik and Mamberamo river basins. There are three bird species that are endemic to the north Papuan mountains, including Mayr's Forest Rail (*Rallina mayri*), Mayr's Honeyeater (*Ptiloprora mayri*), and the Golden-fronted Bowerbird (*Amblyornis flavifrons*). There are an additional three restricted-range species that occur here and west Papuan highlands and parts of the Central Ranges (see Stattersfield et al. 1998).

The Adelbert Mountains and the Huon ranges (Finisterre, Saruwaged, Rawlinson mountains) are primarily oceanic terranes. Although these mountains can be very high (up to 4,100 m in the Finisterre), they are relatively young. The Huon terranes joined New Guinea as early as 10 mya or more (Pigram and Davies 1987; Pigram and Symonds 1991), but the mountains only began forming as recently as 3 mya or later (Abbott et al. 1997). There are only about six endemic bird species found on these mountains, including Huon Melidectes (*Melidectes foersteri*), Spangled Honeyeater (*Melipotes ater*), Fire-maned Bowerbird (*Sericulus bakeri*), Wahnes' Parotia (*Parotia wahnesi*), Huon Astrapia (*Astrapia rothschildi*), and the Emperor Bird of Paradise (*Paradisaea guilielmi*). Another five restricted-range species have ranges that extend into the Central Ranges.

The Central Cordillera extends from just south of Cenderawasih Bay east to Milne Bay in Papua New Guinea, and include the Snow (Maoke, Jayawijaya) Mountains, Star Mountains, Central Highlands, Eastern Highlands, and Southeast Highlands. There are 39 bird species endemic to the Central Cordillera. These include several species that occur only in high alpine grassland areas above ca 3,000 m elevation—a habitat that is absent from nearby islands outside New Guinea. These endemics include the Snow Mountain Quail (*Anurophasis monorhonyx*), Alpine Pipit (*Anthus gutturalis*), the Snow Mountain Robin (*Petroica archboldi*), the Snow Mountain Mannikin (*Lonchura montana*), and the Alpine Mannikin (*Lonchura monticola*).

#### Lowland Regions

Several distinct lowland regions also have isolated endemics and restricted-range species. These are often broken into only four major lowland areas: the Bintuni

lowlands, the north Papuan lowlands (comprising the Mamberamo and Sepik-Ramu basins), the south Papuan basin, and the Trans-Fly lowlands. The first three are ecologically similar but are separated by high mountains or large bays, and the Trans-Fly is ecologically separated from the adjacent south Papuan lowlands by its reduced and more strongly seasonal rainfall.

The Bintuni basin includes the islands of Misool and Salawati as well as the vast lowlands of the Vogelkop and Bomberai Peninsula. These support four endemic bird species, including the Red-billed Brush Turkey (*Talegalla cuvieri*), the Western Crowned Pigeon (*Goura cristata*), the Black Lory (*Chalcopsitta atra*), and the Olive-crowned Flowerpecker (*Dicaeum pectorale*). The Central Cordillera clearly restricts avian dispersal between the northern and southern watersheds of New Guinea, acting as a formidable barrier to bird movement. Thus the mountains define the northern and southern lowland basins. The north Papuan lowlands include the large Mamberamo River drainage, the Sepik River drainage, and the Ramu River drainage. There are only five species endemic to the north Papuan lowlands: the Brown Lory (*Chalcopsitta duivenbodei*), Edward's Fig-parrot (*Psittaculirostris edwardsii*), Salvadori's Fig-parrot (*Psittaculirostris salvadorii*), Brass's Friarbird (*Philemon brassi*), and the Pale-billed Sickbill (*Epimachus bruijnii*).

The southern lowlands are divided by ecological region into the south Papuan basin that is primarily rainforest, and the Trans-Fly that has a strongly seasonal climate with savannah and monsoon forest. Together, these two regions have only six endemic species. Species endemic to the south Papuan basin include the Striated Lorikeet (*Charmosyna multistriata*), the White-bellied Pitohui (*Pitohui incertus*), and the Greater Bird of Paradise (*Paradisaea apoda*); the species endemic to Trans-Fly include the Fly River Grassbird (*Megalurus albolimbatus*), the Grey-crowned Mannikin (*Lonchura nevermanni*), and the Black Mannikin (*Lonchura stygia*). We believe, however, that the real diversity of lowland taxa may be underappreciated by this species-level analyses.

Many lowland species show a surprising level of intraspecific morphological variation, and some lowland species have as many as 20 or more described subspecies. For example, the Variable Pitohui (*Pitohui kirhocephalus*) is tremendously variable in coloration and size, and has 20 described subspecies in New Guinea and the nearby continental islands; the Little Shrike-thrush (*Colluricincla megarrhyncha*) has up to 23 subspecies by some accounts, although the morphological variation is less pronounced (Rand and Gilliard 1967). We believe that this large number of subspecies may be due, in part, to biases of taxonomists working in Papua, because despite significant morphological variation among lowland populations, the populations have traditionally been lumped into single species rather than being split into multiple species. This has been done for two reasons. First, it is assumed that lowland populations are not isolated from other nearby lowland forests. Lowland forests form a continuous ring around the island, and even the most isolated valleys have corridors of lowlands connecting them to larger adjacent populations. Therefore, it was assumed that there was substantial interbreeding among the different subspecies or that their records were just points along a

continuous species cline. Second, at the time when many large taxonomic revisions were done, sampling was relatively sparse. Thus it was assumed that as more samples were made, more intergrading populations would be found in the forest corridors between the major basins. Splitting such taxa is common for isolated montane species, but has not been done in lowland taxa in part because there is a presumption that there must be some gene flow, and that intergrading populations would be found if there were greater sampling.

We surveyed the putative ranges of 120 subspecies from 28 avian polytypic species (based on Rand and Gilliard 1967), and plotted the ranges of the subspecies on a map of New Guinea (see Figure 4.9.1). Many subspecific boundaries appeared to coincide. For example, nearly 30 subspecies' ranges bordered on the Huon mountains, suggesting that Huon Peninsula is an important vicariance barrier (a barrier that prevents gene flow), and many more ranges were divided at the Vogelkop isthmus. Other discontinuities were more surprising: five subspecies' boundaries coincided with the border mountains in the north Papuan lowlands, and 15 subspecies' boundaries coincided with a hypothesized inland bay called the "Aure trough" (Pigram and Davies 1987). Many of these same natural boundaries were appreciated much earlier (Hartert et al. 1936) but have not received a great deal of comment in recent works.

We are actively examining genetic differentiation among these lowland basins. Our preliminary data suggest a significant split between the north and south coasts in several species, including *Colluricincla megarhyncha*, *Pitohui kirhocephalus*, the lowland owlet-nightjar, *Aegotheles bennettii* (Dumbacher and Fleischer 2001; Dumbacher et al. 2003), and certainly others. The genetic divergence among the *Pitohui kirhocephalus* groups is quite marked, and probably warrants splitting them into separate species: a western Papuan Island group, a south coast group, and a north coast group. Interestingly, members of both the north coast and south coast groups are present in the Bintuni Basin, suggesting that both of these groups may have invaded after the Bintuni terranes joined the main island of New Guinea.

It is easy to imagine the impact of a mountain range that forms and splits a population in two, or an inland bay that separates coastal populations. But more complex biogeographic processes may be taking place on the north coast of New Guinea, as a consequence of the Australian plate moving northward. We now believe that many of the northern islands (e.g., New Britain and New Ireland) are on course to collide with New Guinea in the future. Because birds are good over-ocean dispersers relative to many other vertebrates, they are capable of moving to offshore islands or volcanic island arcs as they become closer to the mainland (Diamond 1973). Once on these islands, birds can evolve independently and potentially become different enough to become new species. Later, when the island collides with the mainland, the island species will come into contact with the mainland species. Some will merge into one gene pool, some may go extinct, and

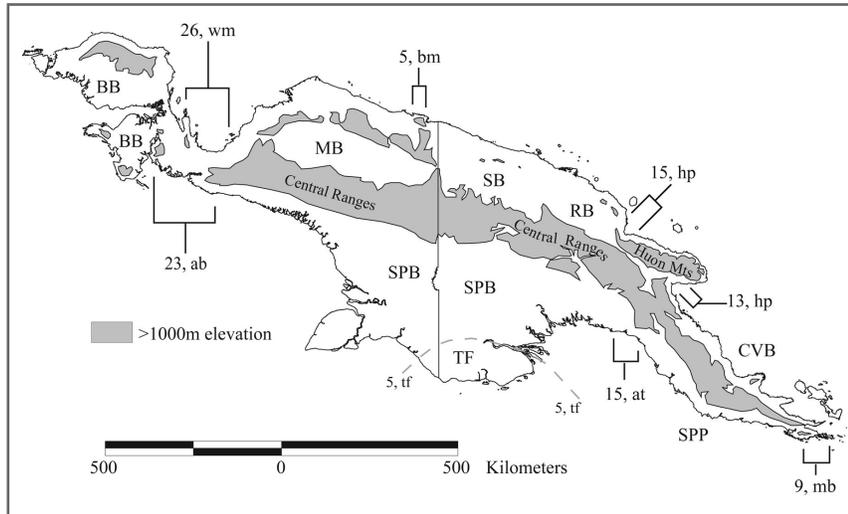


Figure 4.9.1. Map of New Guinea lowlands. Areas over 1,000 m elevation are shown in gray. BB: Bintuni Basin; MB: Meervlakte Basin; SB: Sepik Basin; RB: Ramu Basin; CVB: Cape Vogel Basin; SPP: Southeast Papuan Peninsula; SPB: South Papuan Basin; TF: Trans-Fly lowlands. We surveyed the ranges of 120 subspecies from 28 avian polytypic species, and the numbers on this figure correspond to the number of avian subspecies whose ranges terminate at this locality. Lowercase letters following the numbers denote hypothesized geologic barriers or dispersal routes at these localities. at: Aure Trough; mb: Milne Bay Break; hp: Huon Peninsula; bm: border mountains; wm: Wandammen Mts; ab: Aetna Bay. Dashed gray line depicts extent of the Trans-Fly (tf) lowlands. The vertical line down the center is the political boundary between Papua, Indonesia (to the west), and Papua New Guinea (to the east).

some may persist as different species for long periods or even spread across the mainland. We believe that the processes of island formation, island colonization, and island accretion can account for some of the rich biodiversity of Papua, especially in the northern basins and northern mountain ranges, such as the Huon, Adelbert, Torricelli, and others. Likewise, New Guinea has served as a bird colonization source for thousands of islands throughout the tropical Pacific. Detecting such histories may be difficult, because for any single case, there will be alternative historical explanations.

Several species or groups have strong ecological preferences that limit their geographic distribution. One species, the Greater Melampitta, *Melampitta gigantea*, inhabits limestone karst habitat that is limited but widespread. These melampittas prefer to build nests in cave tunnels at the bottom or sides of limestone sinkholes,

from which they emerge during the day to forage (Diamond 1983; J. Dumbacher, pers. obs.). *Melampitta*'s distribution is likely limited somewhat by the availability of suitable habitat, although it has been recorded in non-karst regions in the Bewani Mountains. Similarly, the finch *Lonchura montana* occurs in montane grasslands and is generally restricted to those habitats.

But often in tropical environments, bird species have patchy distributions even with respect to their preferred habitat, and this is especially true in Papua. The causes of the patchiness may be due to historical vicariance or barriers to gene flow (Hedges 2001a,b,c), ecological exclusion of similar competitive species in different areas (Diamond 1973), or simply to the natural process of local extinctions and recolonization (Diamond 1973). The significance of patchiness is discussed in detail in Diamond (1973).

### *Ecology*

Most Papuan bird species live in just one of the main habitat categories (described in detail in other chapters): marine, mangrove, aquatic, savanna, wet tropical forest (lowland through upper montane), and alpine habitats (Table 4.9.2). Some species may occur across habitat types, particularly aerial hunters such as swifts and raptors, but most species have fairly specific habitat requirements. To some extent, the overall diversity of birds in a region depends on the diversity and extent of available habitats and the niches contained therein. Many neotropical sites have greater niche diversity than New Guinea (Pearson 1977; Ridgely et al. 2005).

**Table 4.9.2.** Primary habitat preferences of Papuan birds

Preferred habitat	Number of species	Percent of Papuan species
Pelagic	16	2.4
Aquatic (incl. lowland and montane freshwater)	64	9.7
Coastal (incl. nearshore, beach, mangrove, coastal forest, estuary)	65	9.9
Savannas	59	9
Grasslands (incl. lowland and montane grasslands)	47	7.2
Lowland rainforest	212	32.3
Hill forest	55	8.4
Montane forest	130	19.8
Alpine	6	0.9
Towns/other	3	0.5

#### ELEVATION

It is well known from studies around the world (e.g., Kitayama 1992a,b) that forest composition and habitat change with elevation, though the proximate causes of these changes are not always apparent (Ashton 2003). The rugged Central Cordillera running the length of New Guinea creates a fairly complex mix of forest vegetation types within relatively small areas (Hyndman and Menzies 1990; Johns 1976; Paijmans 1970, 1976). Elevation generally affects distribution of birds (Lomolino 2001; Patterson et al. 1998; Rahbek 1997; Sanchez-Cordero 2001), and this is true for New Guinea as well (Beehler 1982; Diamond 1972, 1973). Diamond (1972) describes in detail how elevation helps partition bird communities along elevational gradients on Mt Karimui, PNG. He found that many genera contain species that segregate by elevation; good examples include the species of *Ptilorrhoa*, *Rhipidura*, *Sericornis*, and *Crateroscelis*. It is logical that closely related congeners would share similar niches and ecological requirements and thus would compete (Diamond 1978); the principal of competitive exclusion (Hardin 1960) would lead them to segregate.

#### DIET AND GUILDS

The morphology, physiology, and behaviors of birds are strongly influenced by their diets (Brandl et al. 1994; Karasov and Levey 1990; McNab 1988). In New Guinea, relatively few studies have examined relationships between diet and morphology, behavior, and physiology (McNab 2005; Wooller and Richardson 1988; Wooller et al. 1990), but these suggest that adaptations for different diets are similar to those found in other birds worldwide.

Although it is difficult to unambiguously break the continuum of avian feeding preferences into discrete categories, a rough breakdown reveals some general trends (Table 4.9.3). The species that are strongly insectivorous (listed as insectivores under heading of carnivore in Table 4.9.3) comprise over 42% of the avifauna of Papua. Those terrestrial species that would be considered typical carnivores, specializing on vertebrate prey, comprise just over 7% of the Papuan avifauna. The following sections address the major trophic groups.

#### Carnivores and Predation

Because of the absence of large mammalian predators in New Guinea, large raptors probably play an unusually important role on the island. There are 40 species of raptors (including owls) in Papua. Most notably, the New Guinea Harpy Eagle (*Harpyopsis novaeguineae*) is one of the largest terrestrial predators on the island of New Guinea; only some varanids and snakes are larger. It occurs from near sea level to the tree line at 3,200 m, and feeds predominantly on ringtails, cuscus, and forest wallabies, though it preys on other mammals, megapodes, reptiles, and juvenile cassowaries as well (Beehler et al. 1992; Watson and Asoyama 2001). The status of raptors in Papua is not well known, but presumably most are not as threatened as raptors from the more densely populated parts of Indonesia (van Balen 1998).

Table 4.9.3. Trophic specializations of Papuan birds

Primary dietary category	Number of species
Carnivores (n = 410)	
Insectivore (and some other invertebrates)	214
Insectivore (and some vertebrates)	26
Insectivore (and some fruit and seeds)	24
Insectivore (and some nectar)	10
Aquatic and marine invertebrates	44
Terrestrial vertebrates (and some insects)	47
Fish (and some invertebrates)	45
Frugivores (n = 121)	
Fruits	39
Fruit and insects (and some vertebrates)	54
Fruit and seeds (and some insects)	28
Granivores (n = 37)	
Seeds	22
Seeds and insects (and some fruit)	15
Herbivores (n = 17)	
Plant matter and insects (incl. aquatic)	17
Nectarivores (n = 49)	
Nectar	6
Nectar and fruit	19
Nectar and insects (and some fruit)	24
Omnivores (n = 18)	
Unclassifiable*	8

Note: Bird species of Papua for which we have data (see Appendix 8.2) assigned broad dietary categories.

\* Combines three or more of the above categories, without an obvious strong emphasis on one

Source: summarized in Coates 1985, 1990; personal observations.

Among the carnivores (Table 4.9.2) we have included the piscivores (fish eaters). Papua has at least 15 species of herons and egrets, most of which eat significant amounts of fish. Other piscivores include grebes, a pelican, a darter, cormorants, osprey, terns, and some kingfishers. All of these are vulnerable to transformation of wetlands for agricultural purposes, sedimentation from mining, or the damming of rivers. Transformation of wetlands to rice production does not provide good habitat for piscivorous ardeids, though paddies can be suitable for the introduced Cattle Egret (Richardson and Taylor 2003).

As top predators in the aquatic food chain, piscivorous birds are known to accumulate certain toxins that humans release into the environment, particularly organochlorides. During the period of unregulated DDT use in the United States, populations of piscivores such as pelicans, Bald Eagles, and cormorants plummeted in numbers due to the egg shell thinning caused by toxic accumulations of organochlorides in the laying females (Hickey and Anderson 1968). Use of these

pesticides was banned in the United States, but they are still used in many parts of the world. When properly applied these pesticides can be a potent weapon in the fight against malaria and other mosquito-borne diseases. However, without proper application, damage to birds can be unnecessarily high. In some parts of the world, populations of piscivorous birds are still suffering from the release of organochlorides to the aquatic environment (Connell et al. 2002, 2003; De Luca-Abbott et al. 2001). There are few data or tests from Papua, but given the push to increase industrial agricultural outputs of rice and oil palm, it seems prudent to voice concern over how pesticides will be applied.

#### Pelagic and Migrant Species

Very little is known of the pelagic birds (species that live in the open ocean) that occur near Papua. The most relevant data come from the seas to the west of Papua (e.g., Cadee 1985). As far as we know, there are no breeding colonies of Procellariiform species in Papua, but several pelagic terns and boobies are known to breed in eastern Indonesian waters. Because many of the pelagic species found in the oceans off Papua are widespread and better known from other parts of the Indian and Pacific oceans, relatively little attention has been devoted to them, in favor of attention to the endemic and unique terrestrial avifauna.

Seventy-five species of migratory birds are listed under treaties to protect migratory birds between Australia and Japan (Japan-Australia Migratory Bird Agreement) and Australia and China (China-Australia Migratory Bird Agreement). All of these migratory species are known to, or could be expected to, also pass through or stay in Papua for at least some short period. Additionally, there are roughly an additional 65 species of terrestrial and aquatic species that are known to, or could be reasonably expected to, move between New Guinea and Australia (Dingle 2004) (Appendix 8.2). The number of birds moving between Australia and New Guinea is large enough that conservation of some “Australian” species requires more information about and management in the New Guinea “wintering” grounds (Legge et al. 2004).

#### Frugivores and Seed Dispersal

The avifauna of the Papua, and New Guinea in general, has an exceptionally high number of frugivorous species (Pearson 1977) that play crucial roles as dispersers of seeds. Some scientists have speculated that in the absence of many potential mammalian competitors (e.g., primates, squirrels) frugivorous birds have diversified more here than in other tropical regions. Roughly 90% of the woody plants in the New Guinea rainforests produce fleshy diaspores that appear to be adapted for dispersal by birds and Pteropodid fruit bats (Mack and Wright 2005). In the absence of dispersal by birds, many plant species would not be able to sustain their populations (Mack et al. 1999; Mack and Wright 2005). For a combination of reasons, many trees from Papuan rainforests have unusually large diaspores (Mack 1993). Thus a relatively small number of bird species—the three cassowaries *C. casuarius*, *C. unappendiculatus*, and *C. bennetti* and the hornbill *Rhyticeros plicatus*

*tus*—are inordinately important for the maintenance of diverse floras in Papuan forests (Mack and Wright 2005). If the birds become extirpated, one could expect a gradual loss of plant diversity. Where these four bird species are heavily hunted there is the potential for extirpation. Fortunately, at least some of these species appear to have large ranges and seasonal movements that might reduce the risk of local extirpation. Some tropical forest trees, particularly in the Myristicaceae and Meliaceae, have fairly narrow sets of frugivorous birds that can extract seeds from their capsules, so maintenance of these tree species populations depends on the conservation of a small number of frugivorous bird species (Beehler and Dumbacher 1996).

The frugivorous avifauna includes a large number of pigeons and doves. At some localities 20 or more species of columbids can be sympatric (Beehler et al. 1995; Bell 1982b; Mack and Wright 1996). This presents a classic example of niche partitioning, with species in closely related taxa (e.g., *Ptilinopus* spp.) dividing up the fruit resource based on where they forage and their body size (Bell 1983a; Diamond 1973, 1978; Frith et al. 1976; Pratt 1984; Pratt and Stiles 1983; Terborgh and Diamond 1970). Since these seminal papers, little research had been conducted with columbids or the issues of niche partitioning by frugivores in New Guinea. Intensive study in this region of the ecology of pigeons, and especially their competitive interactions and resource partitioning, would be highly rewarding (Pratt 1984; Pratt and Stiles 1983).

Figs (*Ficus* spp.: Moraceae) present a special fruit resource for tropical frugivores (Shanahan et al. 2001). In Papua several bird species specialize in consuming figs (Beehler 1982, 1989; Beehler and Dumbacher 1996), including the Vulturine Parrot (Mack and Wright 1998), the Manucodes (Beehler 1985; Frith and Beehler 1998), and some cuckoo-shrikes. Figs provide a nutritious resource that is often reliable due to its asynchronous fruiting phenology (Beehler 1985; O'Brien et al. 1998), and the movements of birds tracking figs or other fruit resources can play an important role in forest generation (Kinnaird et al. 1996). Protection of keystone fruit resources and other important fruiting species could be important to help promote forest regrowth and recovery after logging (Hamann and Curio 1999; Holbrook et al. 2002).

#### Nectarivores and Pollination

An important component of the avifauna of Papua consists of nectarivorous birds, particularly the large radiations of honeyeaters (Meliphagidae: 55 spp.) and lorries (Loriinae: 19 spp.). Based on what is known from other tropical forests and the large number of ornithophilous flowers in Papuan forests, it is safe to assume nectarivorous birds play a crucial, but not well understood, role. In one of the few studies of nectar feeding birds in PNG, roughly 20% of the flowering trees in a plot were visited by nectar feeding birds (Brown and Hopkins 1996) and 13% of the bird species at the site fed upon nectar (Brown and Hopkins 1995). The proportion of rainforest trees that are visited by nectarivorous birds and are probably pollinated by them is higher in New Guinea than in most tropical forests. This

difference is probably due to the taxonomic affinities of nectarivores in different regions. In Papua, most nectarivorous birds are honeyeaters and lorries that feed mostly on canopy trees, whereas in Latin America, most are hummingbirds that feed mostly on herbs, vines, and epiphytes (Brown and Hopkins 1995).

This difference in the ecology of New Guinea forests and neotropical forests is quickly apparent to anyone who has visited both. The large number of nectarivorous birds that congregate in flowering trees in New Guinea are a diverse mixture of many genera with dramatically different morphologies, from tiny myzomelids to large lorries. In the cases of neotropical ornithophilous trees, most avian visitors are small hummingbirds and other small passerines (e.g., *Chlorospiza*, *Dacnis*). In New Guinea competition may be reduced by honeyeater species using different strategies within the same tree (Collins and Paton 1989) and by the birds' different morphologies (Paton and Collins 1989). But, as evinced by the fighting and displacements by different species in such aggregations, competition is strong. Indeed, two *Myzomela* species that have only recently (300 years) come into contact exhibit evidence of character displacement, probably as a result of competition for nectar resources (Diamond et al. 1989). Competition by birds affects pollen movement, seed set, and outcrossing (Ramsey 1988, 1989), but is unexamined in New Guinea where it could have important implications for economically important tree species (Brown and Hopkins 1995).

In New Guinea there is little evidence of fairly tight mutualisms between any plant and a bird species or genus (Brown and Hopkins 1995). Most New Guinea nectarivores probably feed upon a diversity of plant taxa and flower types, which is more typical of plant-pollinator systems (Waser et al. 1996). However, this does not imply birds are not important as pollinators, and it will be important to conserve the full suite of nectarivores in a rainforest in order to ensure plant reproduction continues successfully (Bawa and Krugman 1991; Bond 1994; Kearns et al. 1998). It is difficult to assess the importance of birds as pollinators because virtually no studies have examined birds and pollination in the region. We are unaware of any study in the New Guinea region that explicitly quantifies how seed sets are affected by avian pollinators.

Nectar-feeding birds can become abundant locally when key plants are in flower, then emigrate when flowering terminates (McGoldrick and MacNally 1998). The scale of local movements of such birds tracking resource availability in New Guinea is unknown, but eruptions of nomadic or migratory nectarivorous birds seem timed with large flower crops that were often asynchronous with less copiously-flowering species (Bell 1982a; Brown and Hopkins 1996). Given the right circumstances of nectar production and density of flowers, nectar resources can be temporarily defended by aggressive nectarivores (Beehler 1994), as sometimes also happens with fruit resources (Pratt 1984). Detailed long-term studies of bird populations, coupled with phenological studies, are needed to elucidate what appears to be complex patterns of movements by nectar-feeding birds, particularly lorikeets.

## Insectivores

The large number of insectivorous species at any one site would lead one to suspect competition could be intense. However, insects and the places they occur are extremely diverse and thus provide many distinct foraging niches that different species of insect feeding birds could specialize upon. In New Guinea this seems to be the case, with species sorting by size, substrate, and vertical distribution (Bell 1982c, 1983a; Croxall 1977). Birds have a variety of hunting styles, from aerial hawking species (e.g., swifts), to ground-dwelling species that search the forest litter for insects (e.g., Pittas).

Just as frugivores and nectarivores provide economically valuable ecosystem services as seed dispersers and pollinators, insectivorous birds provide a vital service in control of insect pests. Birds can play a role in pest management of simple temperate agricultural systems (Mols and Visser 2002; Tremblay et al. 2001). More recently there has been evidence that insectivorous birds are important for regulating insect pests in tropical agroforestry, cacao, and coffee plantations (Perfecto et al. 2004, Philpott et al. 2004). However, only recently has evidence emerged that birds can be important in reducing insect pests in tropical forests (van Bael et al. 2003; van Bael and Brawn 2005). Although data from New Guinea are not available, given the great density and diversity of insectivorous birds in the region (Table 3.9.2) and at specific sites (Bell 1982b; Mack and Wright 1996), insectivorous birds are probably economically important in Papua for the role they play controlling insect pests in agricultural and agroforestry systems.

## BIRDS OF PARADISE (PARADISAEIDAE)

The study of avian behavior in the New Guinea region is dominated by studies of the birds of paradise. This short chapter cannot cover the detailed studies of birds of paradise by B. Beehler, C. Frith, D. Frith, T. Gilliard, M. LeCroy, J. Diamond, T. Pratt, M. Pruett-Jones, and S. Pruett-Jones, but all the work is comprehensively summarized and synthesized in Frith and Beehler (1998). The birds of paradise have been the focus of so much study because they are models for studies of strong sexual selection (Diamond 1981), hybridization (Fuller 1995), courtship and lek display behaviors (Beehler 1988; Frith and Frith 1988; Pruett-Jones and Pruett-Jones 1988), sexual dimorphism and extravagant male plumages (Frith 1981), frugivory (Beehler 1989), and polygamy (Beehler 1987). There is much traditional lore about the birds (Healey 1993) and local people use their feathers as adornment (Swadling 1995).

Within the birds of paradise there is great diversity. Taxa range from primarily monogamous (e.g., *Manucodia* spp.) to promiscuous polygamous species (e.g., *Paradisaea* spp.). There are highly frugivorous taxa (e.g., *Paradisaea* spp.) and others that are nearly wholly insectivorous (e.g., *Drepanornis albertisi*). A few are territorial while most do not appear to defend territories. Males may display as isolated individuals, or in collective display areas called leks, in which many males display within close proximity with interactive dances and vocal behavior. The stronger the sexual selection in a species (i.e., females selecting a small proportion

of the males for the majority of copulations), the stronger the selection for specialized plumage, dances, and vocalizations (Christidis and Schodde 1993; Diamond 1981; Emlen and Oring 1977). This selection appears to have led to a fairly rapid evolution of diverse morphologies, but with relatively little genetic divergence. Thus the phylogenetic branches between quite different-looking taxa are short and poorly resolved (Nunn and Cracraft 1996), suggesting that some taxa have evolved more rapidly in morphological and behavioral characters than in other characters. The large number of recorded hybrids (Frith and Beehler 1998; Fuller 1995), even among different genera of birds of paradise (e.g., Frith and Frith 1996), supports this conclusion.

#### BOWERBIRDS (PTILONORHYNCHIDAE)

The second avian family that has received great attention from ornithologists (e.g., G. Borgia, J. Diamond, C. Frith, D. Frith, T. Gilliard, M. Pruett-Jones, and S. Pruett-Jones) is the bowerbird family (Ptilonorhynchidae), much of which has been incorporated in an excellent review of the family (Frith and Frith 2004). The bowerbirds are exceptional because in many species the males construct structures that act as attractions, display arenas, and courting grounds. These “bowers” can be anything from a cleared area with a few leaves placed for decoration, up to massive structures of twigs, decorated with hundreds of colorful items like fruit or flowers, that take months to construct.

One of the notable things about the bowerbirds is how they use ornaments around their bower as attractants to females. Often these ornaments are hard-to-find, colorful items that are replaced often as they fade or spoil (e.g., flower petals and colored fruits). Males spend considerable effort collecting these articles and defending their decorations from marauding male conspecifics, so the degree of decoration can act as a measure of male quality to a potential female mate (Diamond 1982a; Diamond 1986; Hunter and Dwyer 1997).

#### NIDIFICATION

Most tropical passerine birds lay only two eggs at a time, but might have several nesting attempts in a year if the first is unsuccessful. Rates of nest predation are typically high in rainforests and rainforest birds may re-nest several times before successfully fledging. The nidification (i.e., nest building) of many Papuan bird species has not been described (Coates 1985, 1990), and there are very few detailed studies of nesting biology and nest success (e.g., Frith and Frith 1993, 1994).

A little appreciated ecological role of some birds in Papua is that some, most notably Psittacids, excavate and enlarge cavities in trees. Because there are no woodpeckers in the region’s rainforests, the wide diversity of species that occupy nest holes (from rats to arboreal marsupials to hornbills) might rely on the relatively few avian species that actively excavate cavities. For many species, suitable cavity nest sites could be a major limiting factor to populations (Gibbs et al. 1993). One consequence of logging operations can be the removal of large trees that have cavities. The hunting practice of chopping down trees with cavities in them to

extract prey also reduces availability of snags and nesting cavities. Reduction of snag and cavity availability through these activities could have serious deleterious effects on hole-nesting species of birds, especially parrots (Monterrubio et al. 2002; Seixas and Mourao 2002), and mammals (Laurance and Laurance 1996). These effects have not yet been assessed in New Guinea.

Undoubtedly the New Guinea birds with the most fascinating nesting biology are the megapodes. This family of birds is unique in that all species use some form of environmental heat to incubate their eggs—neither the male or female broods the eggs, which makes them similar to the putative ancestor to modern birds. Much of what is known about megapodes has been summarized by Jones et al. (1995), although there has been some more recent work in the New Guinea area since the book was published (Sinclair 2000, 2001; Sinclair et al. 2002). Some species use their large, strong feet to scrape together large mounds of forest leaf litter, which generates heat in the center as it decomposes. The eggs are laid in the heart of these large mounds, covered, and allowed to incubate. In other species, the female lays her eggs in earth heated by geothermal sources or, in some instances, in solar-heated sand. In all cases, the young hatch, dig their way to the surface, and then are completely self sufficient. Some young can fly within 24 hours of emerging from their subterranean nest site, making them the most precocial birds in the world, with absolutely no post-hatching parental care.

Because the chick develops completely without parental care, the female invests a great deal in egg yolk. Megapode eggs are the most nutritious eggs laid by birds. This, combined with the conspicuous and specialized places where they lay their eggs, means that human hunters highly prize megapode eggs. They are a nutritious delicacy for people across New Guinea, so megapodes are under heavy pressure from people wherever they live near humans. Indeed the Maleo, a megapode species from Sulawesi, is highly endangered from over-exploitation (Baker and Butchart 2000; Butchart and Baker 2000). Megapodes were once much more numerous and diverse across the Pacific region, but human hunters and possibly rats helped wipe them out in many places, and many species have already gone extinct (Steadman 1991; Steadman et al. 1999, 2002). Without proper management, many other megapode species could follow the Maleo to extinction. The Waigeo Brush Turkey (*Aepyodius bruijnii*), a megapode endemic to upland Waigeo Island, Papua, is one of the most highly endangered species in the region.

#### MIXED-SPECIES FLOCKS

Around the world many birds form mixed species flocks (Ficken 2000; Ragusa-Netto 2002; Styring and Ickes 2001; Thiollay 1999, 2002; Vuilleumier 1967) and the birds of New Guinea are no different. Flocks can be aggregations at locally rich resources, as is common with nectar- and fruit-eating species. At the dense fruit or nectar resource many species can compete through exploitative and interference competition (Terborgh and Diamond 1970). Where resources become sufficiently abundant, it is possible that normally nonterritorial species temporarily defend

resources sufficiently rich to justify defense (Pratt 1984). How long such nectarivores and frugivores remain at the resource helps determine rates of pollen flow and seed dispersal (Pratt and Stiles 1983).

But of perhaps greater interest are the groups of primarily insectivorous species that seem to move in loose parties through the forest but that employ different strategies to find insects. Some search foliage, some examine limbs and trunks, while others sally and grab flying insects (Bell 1983b). Whether joining flocks improves survivorship is difficult to tell, because many variables must be controlled, but at least in some cases survivorship for neotropical flocking species is higher than for non-flocking species (Jullien and Clobert 2000). Higher survivorship could be due to greater vigilance and predator avoidance (Thiollay 1999), or that foraging birds act as “beaters,” flushing insects that other individuals capture, thereby conferring a foraging advantage to insectivores that travel in groups rather than solo.

### Systematics

Avian systematics is experiencing a revolution as a result of recent advances in molecular biology. Although there are still relatively few studies that focus exclusively on Papuan birds, many studied avian groups have important centers of diversity in Indonesia and Australia. Study of these groups should help clarify our understanding of the evolution of avian diversity across the region.

Among the most recent and important are two studies that examine the systematics of the Passeriform radiation (songbirds, or perching birds; Barker et al. 2002, 2004). Their work shows that the basal Oscine lineages appear to have evolved in Australasia, and that many of the most basal groups (Menuridae, Ptilonorhynchidae, Climacteridae, Meliphagoideae) have centers of diversity in Australasia, often centering on or near New Guinea. Twelve species of berrypecker, placed in two families, Melanocharitidae and Paramythiidae (Sibley and Monroe 1990), are the only widely recognized bird families endemic to New Guinea, although some other Papuan radiations may soon be recognized as families (e.g., Cnemophilinae, *sensu* Barker et al. 2004).

The number of species recognized in Papua is liable to change substantially when modern phylogenetic analyses are undertaken. This is only in part the result of the much narrower species definition that is replacing the broader polytypical concept that dominated in the 1960s and 1970s. For example, within two New Guinean genera (*Aegotheles* and *Pitohui*) that have been studied using modern phylogenetic techniques, three to four new species have been revealed (Dumbacher and Fleischer 2001; Dumbacher et al. 2003; Pratt 2000). Many more groups currently viewed as species will likely be found to be composed of genetically well-differentiated taxa that have been unrecognized because they are morphologically similar or poorly represented in systematic collections. Additional species, particularly pelagic species, might be expected to occur in Papua, but have not yet been recorded.

There are probably relatively few new species remaining to be discovered in Papua, but scientists are likely to name new species of birds based on examination of specimens. Collection of additional specimens or closer examination of existing specimens is likely to reveal differences that have not been appreciated. A recent example is the Starry Owlet-nightjar (*Aegotheles tatei*), that has been elevated to species, based on a study of several definitive morphological characters that revealed significant differences. Several other groups probably need revision (e.g., *Chaetorhynchus*, Petroicidae, *Melampitta*, Pachycephalidae, and *Ptilorrhoa*).

### *Research Needs*

Field research has declined in Papua since the 1960s. Its avifauna is one of the least-studied in the world partly because of the inaccessibility of much of the region, but also because of the shortage of experienced ornithologists adequately familiar with the avifauna (Beehler et al. 1995). What recent knowledge we have of the Papuan birds comes mostly from research in the PNG side of the island.

Some survey work is still being completed in PNG, but surveys in PNG are poor substitutes for elucidating the distribution of birds in Papua. Very few formal surveys have been published from Papua in the past twenty years (Diamond 1982b; Mack and Alonso 2000; Richards and Suryadi 2002) and only a handful of informal accounts from short visits by ornithologists and birdwatchers have appeared (e.g., Eastwood 1996; Gibbs 1994; Melville 1979, 1980). A large amount of information was collected when planning protected areas in Papua (Petocz et al. 1983; J. Diamond, unpub. data), but these were mostly short surveys in areas proposed as protected areas. Thus, despite some recent fieldwork, there is still considerable room for improvement in the state of the overall knowledge of avian distributions in Papua. Better knowledge of distributions of birds (as well as other taxa) is needed to guide land use planning and conservation actions (e.g., Benayas and de la Montana 2003). Without a fundamental knowledge of the distribution of biodiversity in Papua, site-based conservation interventions can be little more than best guesses (Supriatna 1999).

The second major deficiency in knowledge that will hamper conservation and management needs comes from ignorance of basic natural history and ecology. For management of hunting offtake (e.g., megapode egg harvesting), it is necessary to know basic natural history—population density, home range size, longevity, age of first reproduction, and annual reproductive output (Alvard et al. 1997; Novaro et al. 2000; Robinson et al. 1999; Sanderson et al. 2002). Traditional use of cassowaries is probably not sustainable in many areas, but we lack the basic natural history data to conduct population viability analyses and to make informed management decisions (Johnson et al. 2004). Basic ecological knowledge is required in order to manage ecosystems, both in protected areas and in other land use zones, in order to minimize impact (Brussard 1991).

The third area in which research would be beneficial is the realm of pure science. Many important scientific innovations are derived from studies of birds in

New Guinea (Diamond 1973; Diamond et al. 1989; Mayr 1963; Mayr and Diamond 1976; Wallace 1869). Because New Guinea has a unique biota with an evolutionary history independent of most of the rest of the world, it offers a special opportunity both to test ideas that are derived from other areas without merely being pseudoreplication (Hurlbert 1984) and to generate novel ideas that can be applied to other parts of the world (Westoby 1988). Better knowledge of avian distributions can help elucidate the complex evolutionary history and biogeography of the region (Heads 2001a,b, 2002). We do not have good basic distributional data for any widespread group of organisms in New Guinea except the birds, so improved knowledge of avian distributions provides the best hope for generating novel findings in the fields of biogeography and evolutionary biology.

### Conservation

Papua is home to a substantial number of endemic species that are primarily confined to small islands (e.g., *Aepyodius bruijnii*, *Megapodius wallacei*, *Eos cyanogenia*, *Centropus chalybeus*, *Myiagra atra*, *Monarcha julianae*) or, in some cases, to small areas on the mainland, particularly certain montane species (e.g., *Anurophasis monorhonyx*, *Sericornis rufescens*, *Petroica archboldi*, *Lonchura teerinki*). Many of these endemics are included among the 129 species from the New Guinea region listed by the IUCN and BirdLife International at some level of conservation concern, and 74.4% of the listed species are endemic to the New Guinea region (Appendix 8.2). Papua still has a relatively small human population and large areas of intact forest, but conservation of this province is threatened by Indonesia's rapid human population growth and increasing exploitation of natural resources. Conservation threats to birds in Papua can be classified in five general categories, each of which we discuss below.

#### TRADITIONAL AND SUBSISTENCE USE OF BIRDS

The people of Papua have developed hundreds of distinct cultures, each with its own traditions, myths, and uses of wildlife, in which birds play a central role. Traditional adornment for ceremonies, weddings, and rituals often includes bird plumage, sometimes in large quantities (Healey 1986; Heaney 1982). The group most used for traditional adornment, the birds of paradise, was also at one time very heavily exploited for the millinery trade overseas. At the peak of the trade, export of bird of paradise plumes was measured in tons of feathers per year, yet no species went extinct (Swadling 1995). This is because only fully-plumaged males were taken and subadult males could reproduce in their absence, and because the most desired species (*Paradisaea* spp.) are typically widespread from the lowlands to middle elevations. Traditional plume usage is liable to have an impact on species that are strongly and widely desired (e.g., *Harpyopsis novaeguineae*, *Psittirichas fulgidus*, *Epimachus fastuosus*; Mack and Wright 1998; Watson and Aoyama 2001) or which might be less desired, but have restricted ranges or populations (e.g., *Cicinnurus respublica*).

Although larger mammals are particularly targeted by subsistence hunting, many bird species also face serious pressure from hunting (Mack and West 2005). Because the human population is growing rapidly in Papua and there is little domestic livestock or access to commercially produced meat, wildlife faces inordinate pressure from subsistence hunting. In most of rural and montane New Guinea the majority of people obtain a significant portion of their dietary protein from wild game (see Dwyer 1974, 1982, 1983; Morren 1986). Much of this comes from birds. There are very few data on consumption of small birds, which are often consumed before researchers can register the event. This kind of hunting seems to have a significant effect on small bird populations around many human population centers (Mack, pers. obs.) but is unlikely to threaten small bird species that are fairly widespread.

The birds most threatened directly by subsistence hunting and egg-taking are cassowaries (3 spp.), Goura pigeons (3 spp.) and other large terrestrial pigeons, hornbills (1 sp.), megapodes (9 spp.), and waterfowl (at least 1 sp.). Larger ground-nesting birds such as terns, waterfowl, and shorebirds probably suffer high nest predation wherever they nest near human population centers. Many of the larger birds are reasonably secure from traditional hunting with bow and arrow but they are vulnerable to shotguns and, in the case of cassowaries, snares. Thus technological innovations like shotguns and wire can have serious impacts when introduced.

Megapodes are particularly vulnerable to depletion. Megapodes produce large and highly nutritious eggs and lay them in conspicuous mounds of rotting vegetation or in geothermally heated rookeries well known to local hunters. Such highly concentrated, easily located, and nutritious eggs are heavily exploited across the region. However, megapode eggs can be sustainably harvested with proper scientifically based management. Not coincidentally, one of the rarest birds in Papua is a megapode, *Aepyodius bruijnii*. This species is close to extinction, almost certainly due to past harvest practices that were unsustainable. It is reasonable to expect that other species and populations of megapodes will face the same fate if management practices do not begin soon.

#### AGRICULTURAL CONVERSION

Agricultural conversion includes both large-scale industrial production and small-scale subsistence. Large areas of Papua have already been cleared for industrial agriculture or are planned to be cleared for plantations (Supriatna 1999). In the lowlands, conversion is primarily for oil palm plantations. Oil palm plantations are essentially sterile in terms of biodiversity, and they also pollute freshwater systems. Because they are monocultures, they have little biological or structural variability and thus make a poor substrate for bird populations. Sometimes some predatory birds, especially owls, do well in oil palm plantations due to the large numbers of rats supported by the palm nuts, but overall, oil palm plantations do not support substantial diversity.

INDUSTRIAL LOGGING

Large-scale logging presents a major threat to many birds in Papua. Impacts derive from the direct effects of cutting and extracting timber, and indirect effects such as elevated hunting and introduction of pests. The magnitude of direct effects will vary according to the intensity of the extraction and the practices used. At the most damaging extreme is clear-felling, in which the majority of trees are removed (e.g., for pulp wood). This type of logging is presently rare in Papua, but projections of future demand from Asia, particularly China, suggest the demand for New Guinea pulp could increase.

At the other end of the spectrum is small-scale, environmentally friendly selective logging. Many conservationists are developing practices for reduced impact forestry and at the same time developing markets for certified lower-impact timber. There is still a great deal to learn about how to minimize the impact of logging, and we need data on the effects of different forestry practices. Nonetheless, some information is available, particularly from tropical forests in other parts of the world.

Many bird species depend on hollow trees and snags for roosting and nesting sites (Gibbs et al. 1993). Logging practices that reduce damage to roost trees can help maintain populations of parrots and other cavity-nesting organisms in Australia (Brigham et al. 1998; Gibbons and Lindenmayer 2002). The impacts of moderate levels of timber removal on Papuan birds are difficult to measure, partly due to the inherent problems associated with censusing birds in rainforests (Driscoll 1984). However evidence suggest that while some bird species increase in regrowth and others decrease after logging, large tracts of second growth have depauperate avifaunas (Driscoll 1984).

Because many birds of the New Guinea rainforests depend on either nectar or fruit as dietary staples, logging practices that reduce nectar- and fruit-bearing trees can have substantial effects on a large number of bird species. This impact will be more dramatic if keystone fruit or nectar resources are removed (van Schaik et al. 1993). Keystone resources are loosely defined as resources upon which a disproportionate number of species are strongly dependent, and whose removal would have large, cascading effects on the ecosystem (Paine 1995; Simberloff 1998). For example, figs or other fruits that are available during times of low overall fruit availability act as keystone resources (Kinnaird et al. 1999; Patel 1997; Peres 2000; Shanahan et al. 2001). Low impact logging should be designed to protect keystone resources so that key fruit and nectar resources are sufficient to maintain bird populations. Although data are sparse from Papua, it appears that keystone fruit resources would at least include some species of *Ficus*, *Elmerrillia*, and *Calophyllum*, but it is extremely difficult to clearly identify keystone fruit resources in New Guinea as some are important in different years or different seasons (Wright 2005).

Regeneration after logging can be enhanced if bird populations are robust and able to maintain natural patterns of seed dispersal. Birds and other frugivores move seeds into disturbed areas and thus enhance forest regeneration (Gorchov

et al. 1993; Holbrook et al. 2002; Wunderle 1997). Thus birds and other seed dispersing animals can assist revegetation of logged areas through natural processes that would be costly for humans to undertake. In the mountainous terrain of Papua, seed dispersing frugivores like cassowaries are essential in order to move seeds uphill. In the absence of dispersers, many plant populations will shift downhill over time merely by the agency of gravity moving seeds of each successive generation downhill (Mack et al. 1999).

#### COMMERCIAL BIRD TRADE

Few data exist on the numbers of birds exported from Papua for the live bird trade, but what information there is suggests a considerable trade in live birds from Papua into the markets of Southeast Asia (Nash 1992, 1994; Rumbiak 1984). The international live animal trade is a contributing factor in the conservation status of hundreds of threatened and endangered species on the IUCN Red List (IUCN 2002). Large numbers of birds in Southeast Asia move through the major bird markets of Jakarta, Singapore, and Hong Kong. For some, particularly parrots and lorries, the live pet trade might present a significant threat. Closer monitoring of the markets and exportations from Papua is needed.

#### INTRODUCED EXOTIC SPECIES

New Guinea is fortunately free of many of the catastrophic introductions that have devastated many bird populations around the world. Introduced birds brought avian malarias to Hawaii that helped bring about the extinction of many native bird species (Warner 1968). On Guam, the inadvertent introduction of the Brown Tree Snake (*Boiga irregularis*) from the New Guinea region has caused the extinction of several endemic species (Fritts and Rodda 1998; Rodda et al. 1997). Throughout the Pacific, the introduction of the Polynesian rat to remote islands has caused a massive pulse of avian extinctions (Kirch et al. 1992; Owens and Bennett 2000). On Vanuatu, the introduced fire ant *Wasmannia* is wiping out birds that have altricial nestlings. These are just a few examples; many conservationists see the transportation and introduction of invasive exotic species as one of the biggest global threats to biodiversity. Although it may be possible to correct many environmental wrongs through rehabilitation, reintroduction, or restoration, it is almost impossible to eradicate an invasive species once it becomes established.

There are few data for New Guinea on introduced and invasive species. Invasive plants and fungi of significant economic impact have received some attention. But the roles of introduced *Rattus*, cats, and other species likely to impact birds have received little attention. The numbers of invasive species that directly impact birds are probably lower than some areas, such as New Zealand or Australia, where many birds are threatened by stoats, cats, rats, and other predators. But conservationists, policy makers, and enforcement agencies should not be complacent. The figures for New Guinea are low, not because it is harder for invasive species to establish in New Guinea, but because there has been less economic activity and

commerce of the sort that brings invasive species. As commerce increases in Papua and there is more exchange with the outside world, more exotic species will land in Papua. Strict customs and quarantine regulations coupled with effective enforcement are needed.

In Papua there is currently deep concern over the introduction of macaques, in the Jayapura area (Chapter 7.7). This species has had devastating effects on the native fauna and flora of other islands to which it has been introduced (e.g., the Mascarene Islands). The monkeys compete with other animals by consuming fruits and other resources and directly prey upon some animals, particularly nesting birds. Because New Guinea does not have any native placental predatory mammals, release of species such as cats or monkeys would pose a significant threat to the birds of Papua.

#### Literature Cited

- Abbott, L.D., E.A. Silver, R.S. Anderson, R. Smith, J.C. Ingle, S.A. Kling, D. Haid, E. Small, J. Galewsky, and W. Sliter. 1997. Measurement of tectonic surface uplift rate in a young collisional mountain belt. *Nature* 385: 501–507.
- Alvard, M.S., J.G. Robinson, K.H. Redford, and H. Kaplan. 1997. The sustainability of subsistence hunting in the neotropics. *Conserv Biol* 11: 977–982.
- Ashton, P.S. 2003. Floristic zonation of tree communities on wet tropical mountains revisited. *Perspect Plant Ecol Evol Syst* 6: 87–104.
- Baker, G.C., and S.H.M. Butchart. 2000. Threats to the maleo *Macrocephalon maleo* and recommendations for its conservation. *Oryx* 34: 255–261.
- Barker, F.K., G.F. Barrowclough, and J.G. Groth. 2002. A phylogenetic hypothesis for passerine birds: taxonomic and biogeographic implications of an analysis of nuclear DNA sequence data. *Proc R Soc Lond B Biol Sci* 269: 295–308.
- Barker, K.F., A. Cibois, P. Schikler, J. Feinstein, and J. Cracraft. 2004. Phylogeny and diversification of the largest avian radiation. *Proc Natl Acad Sci U.S.A.* 101: 11040–11045.
- Bawa, K.S., and S.L. Krugman. 1991. Reproductive biology and genetics of tropical trees in relation to conservation and management. Pp. 119–136 in Gomez-Pompa, A., T.C. Whitmore, and M. Hadley (eds.) *Rain Forest Regeneration and Management*. Parthenon Publishing Co., Park Ridge, New Jersey.
- Beehler, B.M. 1982. Ecological structuring of forest bird communities in New Guinea. Pp. 837–860 in Gressitt, J.L. (ed.) *Biogeography and Ecology of New Guinea*. W. Junk, The Hague.
- Beehler, B.M. 1985. Adaptive significance of monogamy in the Trumpet Manucode *Manucodia keraudrenii* (Aves: Paradisaeidae). Pp. 83–99 in Gowaty, P.A., and D.W. Mock (eds.) *Avian Monogamy*. American Ornithologists' Union, Washington, D.C.
- Beehler, B.M. 1987. Birds of paradise and mating system theory—predictions and observations. *Emu* 87: 78–89.
- Beehler, B.M. 1988. Lek behavior of the Raggiana Bird of Paradise. *Nat Geog Soc Res Rep* 4: 343–358.
- Beehler, B.M. 1989. Patterns of frugivory and the evolution of birds of paradise. Proceedings of the XIX International Ornithological Congress: 816–826.

- Beehler, B.M. 1994. Canopy-dwelling honeyeater aggressively defends terrestrial nectar source. *Biotropica* 26: 459–461.
- Beehler, B.M., W. Crill, B. Jefferies, and M. Jefferies. 1992. New Guinea Harpy Eagle attempts to capture a monitor lizard. *Emu* 92: 246–247.
- Beehler, B.M., and J.P. Dumbacher. 1996. More examples of fruiting trees visited predominantly by birds of paradise. *Emu* 96: 81–88.
- Beehler, B.M., and B.W. Finch. 1985. *Species Checklist of the Birds of New Guinea*. Royal Australasian Ornithologists Union, Victoria.
- Beehler, B.M., T.K. Pratt, and D.A. Zimmerman. 1986. *Birds of New Guinea*. Princeton University Press, Princeton.
- Beehler, B.M., J.B. Sengo, C. Filardi, and K. Merg. 1995. Documenting the lowland rainforest avifauna in Papua New Guinea—effects of patchy distributions, survey effort and methodology. *Emu* 95: 149–161.
- Bell, H.L. 1982a. A bird community of lowland rain forest in New Guinea. 2. Seasonality. *Emu* 82: 65–74.
- Bell, H.L. 1982b. A bird community of lowland rainforest in New Guinea. 1. Composition and density of the avifauna. *Emu* 82: 24–41.
- Bell, H.L. 1982c. A bird community of New Guinean lowland rainforest. 3. Vertical distribution of the avifauna. *Emu* 82: 143–162.
- Bell, H.L. 1983a. A bird community of lowland rainforest in New Guinea. 6. Foraging ecology and community structure of the avifauna. *Emu* 84: 142–158.
- Bell, H.L. 1983b. A bird community of lowland rainforest in New Guinea. 5. Mixed-species flocks. *Emu* 82: 256–275.
- Benayas, J.M.R., and E. de la Montana. 2003. Identifying areas of high-value vertebrate diversity for strengthening conservation. *Biol Conserv* 114: 357–370.
- Bond, W.J. 1994. Do mutualisms matter? assessing the impact of pollinator and disperser extinction on plant extinction. *Philos Trans R Soc Lond B Biol* 344: 83–90.
- Brandl, R., A. Kristin, and B. Leisler. 1994. Dietary niche breadth in a local community of passerine birds, an analysis using phylogenetic contrasts. *Oecologia* 98: 109–116.
- Brigham, R.M., S.J.S. Debus, and F. Geiser. 1998. Cavity selection for roosting, and roosting ecology of forest-dwelling Australian Owlet-nightjars (*Aegotheles cristatus*). *Aust J Ecol* 23: 424–429.
- Brown, E.D., and M.J.G. Hopkins. 1995. A test of pollinator specificity and morphological convergence between nectarivorous birds and rainforest tree flowers in New Guinea. *Oecologia* 103: 89–100.
- Brown, E.D., and M.J.G. Hopkins. 1996. How New Guinea rainforest flower resources vary in time and space: implications for nectarivorous birds. *Aust J Ecol* 21: 363–378.
- Brussard, P.F. 1991. The role of ecology in biological conservation. *Ecol Appl* 1: 6–12.
- Bulmer, S. 1982. Human ecology and cultural variation in prehistoric New Guinea. Pp. 169–206 in Gressitt, J.L. (ed.) *Biogeography and Ecology of New Guinea*. W. Junk, The Hague.
- Butchart, S.H.M., and G.C. Baker. 2000. Priority sites for conservation of maleos (*Macrocephalon maleo*) in central Sulawesi. *Biol Conserv* 94: 79–91.
- Cadee, G.C. 1985. Some data on seabird abundance in Indonesian waters, July–August 1984. *Ardea* 73: 183–188.
- Christidis, L., and R. Schodde. 1993. Sexual selection for novel partners, a mechanism for accelerated morphological evolution in the Birds-of-Paradise Paradisaeidae. *Bull Brit Orn Club* 113: 169–172.
- Coates, B.J. 1985. *Birds of Papua New Guinea: Non-passerines*. Dove, Alderley.

- Coates, B.J. 1990. *Birds of Papua New Guinea: Passerines*. Dove, Alderley.
- Collins, B.G., and D.C. Paton. 1989. Consequences of differences in body mass, wing length and leg morphology for nectar-feeding birds. *Aust J Ecol* 14: 269–289.
- Connell, D.W., C.N. Fung, T.B. Minh, S. Tanabe, P.K.S. Lam, B.S.F. Wong, M.H.W. Lam, L.C. Wong, R.S.S. Wu, and B. Richardson. 2003. Risk to breeding success of fish-eating ardeids due to persistent organic contaminants in Hong Kong: evidence from organochlorine compounds in eggs. *Water Res* 37: 459–467.
- Connell, D.W., B.S.F. Wong, P.K.S. Lam, K.F. Poon, M.H.W. Lam, R.S. Wu, B.J. Richardson, and Y.F. Yen. 2002. Risk to breeding success of ardeids by contaminants in Hong Kong: evidence from trace metals in feathers. *Ecotoxicology* 11: 49–59.
- Cracraft, J., and J. Feinstein. 2000. What is not a bird of paradise? molecular and morphological evidence places Macgregoria in the Meliphagidae and Cnemophilinae near the base of the corvoid tree. *Proc R Soc Lond B* 267: 233–241.
- Croxall, J.P. 1977. Feeding behaviour and ecology of New Guinea rainforest insectivorous passerines. *Ibis* 119: 113–146.
- Davies, H.L., R.D. Winn, and P. KenGemar. 1996. Evolution of the Papuan Basin—a view from the orogen. Pp. 53–62 in Third PNG Petroleum Convention, Port Moresby, Papua New Guinea.
- De Luca-Abbott, S.B., B.S.F. Wong, D.B. Peakall, P.K.S. Lam, L. Young, M.H.W. Lam, and B.J. Richardson. 2001. Review of effects of water pollution on the breeding success of waterbirds, with particular reference to ardeids in Hong Kong. *Ecotoxicology* 10: 327–349.
- Diamond, J.M. 1966. Zoological classification system of a primitive people. *Science* 151: 1102–1104.
- Diamond, J.M. 1972. *Avifauna of the Eastern Highlands of New Guinea*. Nuttall Ornithological Club, Cambridge.
- Diamond, J.M. 1973. Distributional ecology of New Guinea birds. *Science* 179: 759–769.
- Diamond, J.M. 1978. Niche shifts and the rediscovery of interspecific competition. *Am Sci* 66: 322–331.
- Diamond, J.M. 1981. Birds of paradise and the theory of sexual selection. *Nature* 293: 257–258.
- Diamond, J.M. 1982a. Evolution of the bowerbirds' bowers: animal origins of the aesthetic sense. *Nature* 297: 99–102.
- Diamond, J.M. 1982b. Rediscovery of the Yellow-fronted Gardner Bowerbird. *Science* 216: 431–434.
- Diamond, J.M. 1983. *Melampitta gigantea*: possible relation between feather structure and underground roosting habits. *Condor* 85: 89–91.
- Diamond, J.M. 1985. New distributional records and taxa from the outlying mountain ranges of New Guinea. *Emu* 85: 65–91.
- Diamond, J.M. 1986. Animal art: variation in bower decorating style among male bowerbirds *Amblyornis inornatus*. *Proc Natl Acad Sci U.S.* 89: 3042–3046.
- Diamond, J.M. 1987. Bower building and decoration by the bowerbird *Amblyornis inornatus*. *Ethnology* 74: 177–204.
- Diamond, J., S.L. Pimm, M.E. Gilpin, and M. Lecroy. 1989. Rapid evolution of character displacement in Myzomelid honeyeaters. *Am Nat* 134: 675–708.
- Dingle, H. 2004. The Australo-Papuan bird migration system: another consequence of Wallace's Line. *Emu* 104: 95–108.
- Dow, D.B. 1977. A geological synthesis of Papua New Guinea. *Bull Aust Bur Min Res* 201.
- Dow, D.B., and R. Sukamto. 1984. Late Tertiary to Quaternary tectonics of Irian Jaya. *Episodes* 7: 3–9.

- Driscoll, P.V. 1984. The effects of logging on bird populations in lowland New Guinea rainforest. Ph.D. diss., University of Queensland, Brisbane.
- Dumbacher, J.P., and R.C. Fleischer. 2001. Phylogenetic evidence for colour-pattern convergence in toxic pitohuis: Müllerian mimicry in birds? *Proc R Soc Lond B* 268: 1971–1976.
- Dumbacher, J.P., T.K. Pratt, and R.C. Fleischer. 2003. Phylogeny of the owlet-nightjars (Aves: Aegothelidae) based on mitochondrial DNA sequence. *Mol Phyl Evol* 29: 540–549.
- Dwyer, P.D. 1974. The price of protein: five hundred hours of hunting in the New Guinea highlands. *Oceania* 44: 278–293.
- Dwyer, P.D. 1982. Prey switching: a case study from New Guinea. *J Anim Ecol* 51: 529–542.
- Dwyer, P.D. 1983. Etolo hunting performance and energetics. *Human Ecol* 11: 145–174.
- Eastwood, C. 1996. A trip to Irian Jaya. *Muruk* 8: 12–23.
- Emlen, S.T., and L.W. Oring. 1977. Ecology, sexual selection, and evolution of mating systems. *Science* 197: 215–223.
- Feld, S. 1990. *Sound and Sentiment: Birds, Weeping, Poetics, and Song in Kaluli Expression*. University of Pennsylvania Press, Philadelphia.
- Ficken, M.S. 2000. Call similarities among mixed species flock associates. *Southwestern Nat* 45: 154–158.
- Frith, C.B. 1971. Some undescribed nests and eggs of New-Guinea birds. *Bull Brit Orn Club* 91: 46–49.
- Frith, C.B. 1981. Displays of Count Raggi's Bird of Paradise *Paradisaea raggiana* and congeneric species. *Emu* 81: 193–201.
- Frith, C.B., and B.M. Beehler. 1998. *The Birds of Paradise: Paradisaeidae*. Oxford University Press, Oxford.
- Frith, C.B., and D.W. Frith. 1993. The nesting biology of the Ribbon-tailed Astrapia *Astrapia mayeri* (Paradisaeidae). *Emu* 93: 12–22.
- Frith, C.B., and D.W. Frith. 1994. The nesting biology of Archbold's Bowerbird *Archboldia papueis* and a review of that of other bowerbirds (Ptilonorhynchidae). *Ibis* 136: 153–160.
- Frith, C.B., and D.W. Frith. 1996. Description of the unique *Parotia lawesii* and *Paradisaea rudolphi* hybrid bird of paradise (Paradisaeidae). *Rec Aust Mus* 48: 111–116.
- Frith, C.B., and D.W. Frith. 2004. *The Bowerbirds: Ptilonorhynchidae*. Oxford University Press, Oxford.
- Frith, D.W., and C.B. Frith. 1988. Courtship display and mating of the Surperb Bird of Paradise *Lophorhina surperba*. *Emu* 88: 183–188.
- Frith, H.J., F.H.J. Crome, and T.O. Wolfe. 1976. Food of the fruit-pigeons in New Guinea. *Emu* 76: 49–58.
- Fritts, T.H., and G.H. Rodda. 1998. The role of introduced species in the degradation of island ecosystems: a case history of Guam. *Ann Rev Ecol Syst* 29: 113–140.
- Fuller, E. 1995. *The Lost Birds of Paradise*. Swan Hill Press, Shrewsbury, England.
- Gibbons, O., and D.B. Lindenmayer. 2002. *Tree Hollows and Wildlife Conservation in Australia*. CSIRO Publishing, Collingwood, Victoria.
- Gibbs, D. 1994. Undescribed taxa and new records from the Fakfak Mountains, Irian Jaya. *Bull Brit Orn Club* 114: 4–12.
- Gibbs, J.P., M.L. Hunter, and S.M. Melvin. 1993. Snag availability and communities of cavity-nesting birds in tropical versus temperate forests. *Biotropica* 25: 236–241.
- Gorchov, D.L., F. Cornejo, C. Ascorra, and M. Jaramillo. 1993. The role of seed dispersal

- in the natural regeneration of rain forest after strip-cutting in the Peruvian Amazon. *Vegetatio* 107/108: 339–349.
- Hall, R. 2001. Cenozoic reconstructions of SE Asia and the SW Pacific: changing patterns of land and sea. Pp. 35–56 in Metcalfe, I., J.M.B. Smith, M. Morwood, and I.D. Davidson (eds.) *Faunal and Floral Migrations and Evolution in SE Asia-Australasia*. Swets & Zeitlinger Publishers, Lisse, Netherlands.
- Hall, R. 2002. Cenozoic geological and plate tectonic evolution of SE Asia and the SW Pacific: computer-based reconstructions, model and animations. *J Asian Earth Sci* 20: 353–431.
- Hamann, A., and E. Curio. 1999. Interactions among frugivores and fleshy fruit trees in a Philippine submontane rainforest. *Conserv Biol* 13: 766–773.
- Hardin, G. 1960. The competitive exclusion principle. *Science* 131: 1292–1297.
- Hartert, E., K. Paludan, L. Rothschild, and E. Stresemann. 1936. Die Vogel des Weyland-Gebriges und seines Vorlandes. *Mitteilungen aus dem Zoolischen Museum* 21: 11–186.
- Heads, M. 2001a. Birds of paradise (Paradisaeidae) and bowerbirds (Ptilonorhynchidae): Regional levels of biodiversity and terrane tectonics in New Guinea. *J Zool* (London) 255: 221–339.
- Heads, M. 2001b. Birds of paradise, biography and ecology in New Guinea: a review. *J Biogeogr* 28: 893–925.
- Heads, M. 2001c. Regional patterns of biodiversity in New Guinea plants. *Bot J Linn Soc* 136: 67–73.
- Heads, M. 2002. Birds of paradise, vicariance biogeography and terrane tectonics in New Guinea. *J Biogeogr* 29: 1–23.
- Healey, C.J. 1986. Men and birds in the Jimi Valley. The impact of man on birds of paradise in the Papua New Guinea highlands. *Muruk* 1: 34–71.
- Healey, C. 1993. Folk taxonomy and mythology of birds of paradise in the New Guinea highlands. *Ethnology* 32: 19–34.
- Heaney, W. 1982. The changing roles of birds of paradise plumes in bridewealth in the Wahgi Valley. Pp. 227–231 in Morauta, L., J. Pernetta, and W. Heaney (eds.) *Traditional Conservation in Papua New Guinea, Implications for Today*. Institute of Applied Social and Economic Research, Boroko.
- Hickey, J.J., and D.W. Anderson. 1968. Chlorinated hydrocarbons and eggshell changes in raptorial and fish-eating birds. *Science* 162: 271–273.
- Holbrook, K.M., T.B. Smith, and B.D. Hardesty. 2002. Implications of long-distance movements of frugivorous rain forest hornbills. *Ecography* 25: 745–749.
- Hunter, C.P., and P.D. Dwyer. 1997. The value of objects to Satin Bowerbirds *Ptilonorhynchus violaceus*. *Emu* 97: 200–206.
- Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecol Monogr* 54: 187–211.
- Hyndman, D.C., and J.I. Menzies. 1990. Rain forests of the Ok Tedi headwaters, New Guinea: an ecological analysis. *J Biogeogr* 17: 241–273.
- IUCN. 2002. *IUCN Red List of Threatened Species*. IUCN, Gland, Switzerland.
- Johns, R.J. 1976. A classification of the montane forests of Papua New Guinea. *Science in New Guinea* 4: 105–128.
- Johnson, A., R. Bino, and P. Igag. 2004. A preliminary evaluation of the sustainability of cassowary (Aves: Casuariidae) capture and trade in Papua New Guinea. *Anim Conserv* 7: 129–137.
- Jones, D.N., R.J. Dekker, and C.S. Roselaar. 1995. *The Megapodes*. Oxford University Press, Oxford.

- Jullien, M., and J. Clobert. 2000. The survival value of flocking in neotropical birds: reality or fiction? *Ecology* 81: 3416–3430.
- Karasov, W.H., and D.J. Levey. 1990. Digestive trade-offs and adaptations of frugivorous passerine birds. *Physiol Zool* 63: 1248–1270.
- Kearns, C.A., D.W. Inouye, and N.M. Waser. 1998. Endangered mutualisms: the conservation of plant-pollinator interactions. *Ann Rev Ecol Syst* 29: 83–112.
- Kinnaird, M.F., T.G. O'Brien, and S. Suryadi. 1996. Population fluctuation in Sulawesi red-knobbed hornbills: tracking figs in space and time. *Auk* 113: 431–440.
- Kinnaird, M.F., T.G. O'Brien, and S. Suryadi. 1999. Importance of figs to Sulawesi's imperiled wildlife. *Trop Biodiv* 6: 5–18.
- Kirch, P.V., J.R. Flenley, D.W. Steadman, F. Lamont, and S. Dawson. 1992. Ancient environmental degradation. *Res Explor* 8: 166–179.
- Kitayama, K. 1992a. An altitudinal transect study of the vegetation on Mount Kinabalu, Borneo. *Vegetatio* 102: 149–171.
- Kitayama, K. 1992b. Comparative vegetation analysis on the wet slopes of two tropical mountains: Mt Haleakala, Hawaii and Mt. Kinabalu, Borneo. Ph.D. diss., University of Hawaii.
- Kocher-Schmid, C. 1991. *Of People and Plants: A Botanical Ethnography of Nokopo Village, Madang and Morobe Provinces, Papua New Guinea*. Ethnologisches Seminar der Universität und Museum für Völkerkunde, in Kommission bei Wepf und Co., Basel.
- Kocher-Schmid, C. 1993. Birds of Nokopo. *Muruk* 6: 1–15.
- Laurance, W.F., and S.G.W. Laurance. 1996. Responses of five arboreal marsupials to recent selective logging in tropical Australia. *Biotropica* 28: 310–322.
- Legge, S., S. Murphy, P. Igag, and A.L. Mack. 2004. Territoriality and density of an Australian migrant, the Buff-breasted Paradise Kingfisher, in the New Guinean non-breeding grounds. *Emu* 104: 15–20.
- Lomolino, M.V. 2001. Elevation gradients of species-density: historical and prospective views. *Global Ecol Biogeogr Lett* 10: 3–13.
- Mack, A.L. 1993. The sizes of vertebrate-dispersed fruits: a neotropical-paleotropical comparison. *Am Nat* 142: 840–856.
- Mack, A.L., and L.E. Alonso (eds.). 2000. A biological assessment of the Wapoga River area of northwestern Irian Jaya, Indonesia. RAP Bulletin of Biological Assessment 14. Conservation International, Washington, D.C.
- Mack, A.L., K. Ickes, J.H. Jessen, B. Kennedy, and J.R. Sinclair. 1999. Ecology of *Aglaia mackiana* (Meliaceae) seedlings in a New Guinea rain forest. *Biotropica* 31: 111–120.
- Mack, A.L., and P. West. 2005. Ten thousand tonnes of small animals: wildlife consumption in Papua New Guinea, a vital resource in need of management. Resource Management in Asia-Pacific Working Paper 61: 1–23.
- Mack, A.L., and D.D. Wright. 1996. Notes on the occurrence and feeding of birds at Crater Mountain Biological Research Station, Papua New Guinea. *Emu* 96: 89–101.
- Mack, A.L., and D.D. Wright. 1998. The Vulturine Parrot, *Psitttrichas fulgidus*, a threatened New Guinea endemic: notes on its biology and conservation. *Bird Conserv Intl* 8: 185–194.
- Mack, A.L., and D.D. Wright. 2005. The frugivore community and the fruiting plant flora in a New Guinea rainforest: identifying keystone frugivores. Pp. 184–203 in Dew, L., and J.P. Boubli (eds.) *Tropical Fruits and Frugivores: The Search for Strong Interactors*. Springer, The Netherlands.
- Majnep, I.S., and R. Bulmer. 1977. *Birds of My Kalam Country*. Auckland University Press, Auckland.

- Mayr, E. 1941. *List of New Guinea Birds: A Systematic and Faunal List of the Birds of New Guinea and Adjacent Islands*. American Museum of Natural History, New York.
- Mayr, E. 1963. *Animal Species and Evolution*. Harvard University Press, Cambridge, Massachusetts.
- Mayr, E., and J.M. Diamond. 1976. Birds on islands in the sky: origin of the montane avifauna of northern Melanesia. *Proc Natl Acad Sci U.S.* 73: 1765–1769.
- McGoldrick, J.M., and R. MacNally. 1998. Impact of flowering on bird community dynamics in some central Victorian eucalypt forests. *Ecol Res* 13: 125–139.
- McNab, B.K. 1988. Food habits and the basal rate of metabolism in birds. *Oecologia* 77: 343–349.
- McNab, B.K. 2005. Food habits and the evolution of energetics in birds of paradise (Paradisaeidae). *J Comp Physiol B Biochem Syst Environ Physiol* 175: 117–132.
- Mees, G.F. 1980. Supplementary notes on the avifauna of Misool. *Zool Meded* 55: 1–10.
- Mees, G.F. 1982. Birds from the lowlands of southern New Guinea (Merauke and Koembe). *Zoologische Verhandelingen* 191: 1–188.
- Melville, D. 1979. Ornithological notes on a visit to Irian Jaya. *PNG Bird Society Newsletter* 161: 3–22.
- Melville, D. 1980. Some observations on birds in Irian Jaya, New Guinea. *Emu* 80: 89–91.
- Mols, C.M.M., and M.E. Visser. 2002. Great tits can reduce caterpillar damage in apple orchards. *J Appl Ecol* 39: 888–899.
- Monterrubio, T., E. Enkerlin-Hoeflich, and R.B. Hamilton. 2002. Productivity and nesting success of Thick-billed Parrots. *Condor* 104: 788–794.
- Morren, G.E.B. 1986. *The Miyanimin: Human Ecology of a Papua New Guinea Society*. UMI Research Press, Ann Arbor.
- Nash, S.V. 1992. Parrot trade records for Irian Jaya, Indonesia, 1985–1990. *TRAFFIC Bulletin* 13: 42–45.
- Nash, S.V. 1994. Further parrot trade records for Irian Jaya, Indonesia. *TRAFFIC Bulletin* 14: 121–124.
- Novaro, A.J., K.H. Redford, and R.E. Bodmer. 2000. Effect of hunting in source-sink systems in the neotropics. *Conserv Biol* 14: 713–721.
- Nunn, G.B., and J. Cracraft. 1996. Phylogenetic relationships among the major lineages of the birds-of-paradise (Paradisaeidae) using mitochondrial DNA gene sequences. *Mol Phyl Evol* 5: 445–459.
- O'Brien, T.G., M.F. Kinnaird, E.S. Dierenfeld, N.L. Conklin-Brittain, R.W. Wrangham, and S.C. Silver. 1998. What's so special about figs? *Nature* 392: 668–668.
- Ogilvie-Grant, W.R. 1915. Report on the birds collected by the British Ornithologists' Union expedition and Wollaston expedition in Dutch New Guinea. *Ibis Tenth Series, Jubilee Supplement no. 2*: 1–336.
- Owens, I.P.F., and P.M. Bennett. 2000. Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. *Proc Natl Acad Sci U.S.* 97: 12,144–12,148.
- Paijmans, K. 1970. An analysis of four tropical rain forest sites in New Guinea. *J Ecol* 58: 77–101.
- Paijmans, K. 1976. *New Guinea Vegetation*. National University Press, Canberra.
- Paine, R.T. 1995. A conversation on refining the concept of keystone species. *Conserv Biol* 9: 962–964.
- Patel, A. 1997. Phenological patterns of *Ficus* in relation to other forest trees in southern India. *J Trop Ecol* 13: 681–695.
- Paton, D.C., and B.G. Collins. 1989. Bills and tongues of nectar-feeding birds—a review

- of morphology, function and performance, with intercontinental comparisons. *Aust J Ecol* 14: 473–506.
- Patterson, B.D., D.F. Stotz, S. Solari, J.W. Fitzpatrick, and V. Pacheco. 1998. Contrasting patterns of elevational zonation for birds and mammals in the Andes of southeastern Peru. *J Biogeogr* 25: 593–607.
- Pearson, D.L. 1977. A pantropical comparison of bird community structure on six lowland rain forest sites. *Condor* 79: 232–244.
- Peres, C.A. 2000. Identifying keystone plant resources in tropical forests: the case of gums from *Parkia* pods. *J Trop Ecol* 16: 287–317.
- Perfecto, I., J.H. Vandermeer, G.L. Bautista, G.I. Nunez, R. Greenberg, P. Bichier, and S. Langridge. 2004. Greater predation in shaded coffee farms: the role of resident neotropical birds. *Ecology* 85: 2677–2681.
- Petocz, R., M. Kirenius, and Y. de Fretes. 1983. Avifauna of the reserves in Irian Jaya. World Wildlife Fund Report. World Wildlife Fund, Bogor, Indonesia.
- Philpott, S.M., R. Greenberg, P. Bichier, and I. Perfecto. 2004. Impacts of major predators on tropical agroforest arthropods: comparisons within and across taxa. *Oecologia* 140: 140–149.
- Pigram, C.J., and H.L. Davies. 1987. Terranes and the accretion history of the New Guinea orogen. *BMR J Aust Geol Geophys* 10: 193–211.
- Pigram, C.J., and P.A. Symonds. 1991. A review of the timing of the major tectonic events in the New Guinea orogen. *J So East Asian Earth Sci* 6: 307–318.
- Polhemus, D.A. 1996. Island arcs and their influence on Indo-Pacific biogeography. Pp. 51–56 in Keast, A., and S.E. Miller (eds.) *The Origin and Evolution of Pacific Island Biotas, New Guinea to Eastern Polynesia: Patterns and Processes*. Academic Publishing, Amsterdam.
- Pratt, T.K. 1982. Biogeography of birds in New Guinea. Pp. 815–836 in Gressitt, J.L. (ed.) *Biogeography and Ecology of New Guinea*. W. Junk, The Hague.
- Pratt, T.K. 1984. Examples of tropical frugivores defending fruit-bearing plants. *Condor* 86: 123–129.
- Pratt, T.K. 2000. Evidence for a previously unrecognized species of owl-nightjar. *Auk* 117: 1–11.
- Pratt, T.K., and E.W. Stiles. 1983. How long fruit-eating birds stay in the plants where they feed: implications for seed dispersal. *Am Nat* 122: 797–805.
- Pruett-Jones, S.G., and M.A. Pruett-Jones. 1988. The use of court objects by Lawes' Parotia. *Condor* 90: 538–545.
- Ragusa-Netto, J. 2002. Vigilance towards raptors by nuclear species in bird mixed flocks in a Brazilian savannah. *Studies on Neotropical Fauna and Environment* 37: 219–226.
- Rahbek, C. 1997. The relationship among area, elevation, and regional species richness in neotropical birds. *Am Nat* 149: 875–902.
- Ramsey, M.W. 1988. Differences in pollinator effectiveness of birds and insects visiting *Banksia menziesii* (Proteaceae). *Oecologia* 76: 119–124.
- Ramsey, M.W. 1989. The seasonal abundance and foraging behavior of honeyeaters and their potential role in the pollination of *Banksia menziesii*. *Aust J Ecol* 14: 33–40.
- Rand, A.L., and E.T. Gilliard. 1967. *Handbook of New Guinea Birds*. Weidenfeld and Nicolson, London.
- Richards, S.J., and S. Suryadi (eds.). 2002. *A Biodiversity Assessment of Yongsu-Cyclops Mountains and the Southern Mamberamo Basin, Papua, Indonesia*. Conservation International, Washington, D.C.
- Richardson, A.J., and I.R. Taylor. 2003. Are rice fields in southeastern Australia an

- adequate substitute for natural wetlands as foraging areas for egrets? *Waterbirds* 26: 353–363.
- Ridgely, R.S., D. Agro, and L. Joseph. 2005. Birds of Iwokrama forest. *Proc Acad Nat Sci Phil* 154: 109–121.
- Robinson, J.G., K.H. Redford, and E.L. Bennett. 1999. Wildlife harvest in logged tropical forests. *Science* 284: 595–596.
- Rodda, G.H., T.H. Fritts, and D. Chiszar. 1997. The disappearance of Guam's wildlife. *Bioscience* 47: 565–574.
- Rumbiak, A.M. 1984. Observations on the trade in birds of paradise in Bomakia District of Kouh, Region of Merauke.
- Sanchez-Cordero, V. 2001. Elevation gradients of diversity for rodents and bats in Oaxaca, Mexico. *Global Ecol Biogeogr Lett* 10: 63–76.
- Sanderson, E.W., K.H. Redford, A. Vedder, P.B. Coppolillo, and S.E. Wardrecord. 2002. A conceptual model for conservation planning based on landscape species requirements. *Lands Urban Plan* 58: 41–56.
- Seixas, G.H.F., and G.D. Mourao. 2002. Nesting success and hatching survival of the Blue-fronted Amazon (*Amazona aestiva*) in the Pantanal of Mato Grosso do Sul, Brazil. *J Field Orn* 73: 399–409.
- Shanahan, M., S. So, S.G. Compton, and R. Corlett. 2001. Fig-eating by vertebrate frugivores: a global review. *Biol Rev* 76: 529–572.
- Sibley, C.G., and B.L.J. Monroe. 1990. *Phylogeny and Classification of Birds of the World*. Yale University Press, New Haven.
- Simberloff, D. 1998. Flagships, umbrellas, and keystones: is single-species management passe in the landscape era? *Biol Conserv* 83: 247–257.
- Sinclair, J.R. 2000. The behaviour, ecology and conservation of three species of megapode in Papua New Guinea. M.Sc. thesis, University of Otago, Otago.
- Sinclair, J.R. 2001. Temperature regulation in mounds of three sympatric species of megapode (Aves: Megapodiidae) in Papua New Guinea: testing the “Seymour Model.” *Aust J Zool* 49: 675–694.
- Sinclair, J.R., T.G. O'Brien, and M.F. Kinnaird. 2002. The selection of incubation sites by the Philippine Megapode, *Megapodius cumingii*, in North Sulawesi, Indonesia. *Emu* 102: 151–158.
- Stattersfield, A.J., M.J. Crosby, A.J. Long, and D.C. Wege. 1998. *Endemic Bird Areas of the World: Priorities for Biodiversity Conservation*. BirdLife International, Cambridge.
- Steadman, D.W. 1991. The identity and taxonomic status of *Megapodius stairi* and *M. burnabyi* (Aves, Megapodiidae). *Proc Biol Soc Wash* 104: 870–877.
- Steadman, D.W., G.K. Pregill, and D.V. Burley. 2002. Rapid prehistoric extinction of iguanas and birds in Polynesia. *Proc Natl Acad Sci U.S.* 99: 3673–3677.
- Steadman, D.W., J.P. White, and J. Allen. 1999. Prehistoric birds from New Ireland, Papua New Guinea: extinctions on a large Melanesian island. *Proc Natl Acad Sci U.S.* 96: 2563–2568.
- Styring, A.R., and K. Ickes. 2001. Woodpecker participation in mixed species flocks in peninsular Malaysia. *Wilson Bull* 113: 342–345.
- Supriatna, J. 1999. *The Irian Jaya Biodiversity Conservation Priority-setting Workshop: Final Report*. Conservation International, Washington, D.C.
- Swadling, P. 1995. *Plumes from Paradise: Trade Cycles in Outer Southeast Asia and Their Impact on New Guinea and Nearby Islands until 1920*. Robert Brown and Assoc., Coorparoo.
- Terborgh, J.W., and J.M. Diamond. 1970. Niche overlap in feeding assemblages of New Guinea birds. *Wilson Bull* 89: 29–52.

- Thiollay, J.M. 1999. Frequency of mixed species flocking in tropical forest birds and correlates of predation risk: an intertropical comparison. *J Avian Biol* 30: 282–294.
- Tremblay, A., P. Mineau, and R.K. Stewart. 2001. Effects of bird predation on some pest insect populations in corn. *Agric Ecosyst Environ* 83: 143–152.
- van Bael, S.A., and J.D. Brawn. 2005. The direct and indirect effects of insectivory by birds in two contrasting neotropical forests. *Oecologia* 143: 106–116.
- van Bael, S.A., J.D. Brawn, and S.K. Robinson. 2003. Birds defend trees from herbivores in a neotropical forest canopy. *Proc Natl Acad Sci U.S.A.* 100: 8304–8307.
- van Balen, S. 1998. Tropical forest raptors in Indonesia: recent information on distribution, status, and conservation. *J Raptor Res* 32: 56–63.
- van Schaik, C.P., J.W. Terborgh, and S.J. Wright. 1993. The phenology of tropical forests—adaptive significance and consequences for primary consumers. *Ann Rev Ecol Syst* 24: 353–377.
- Vuilleumier, F. 1967. Mixed species flocks in Patagonian forests with remarks on interspecies flock formation. *Condor* 69: 400–404.
- Wallace, A.R. 1869. *The Malay Archipelago and the Land of the Orang-utan and the Bird of Paradise*. Richard Clay and Sons, Suffolk.
- Wallace, A.R. 1876. *The Geographical Distribution of Animals: With a Study of the Relations of Living and Extinct Faunas as Elucidating the Past Changes of the Earth's Surface*. Macmillan, London.
- Warner, R.E. 1968. The role of introduced diseases in the extinction of the endemic Hawaiian avifauna. *Condor* 70: 101–120.
- Waser, N.M., L. Chittka, M.V. Price, N.M. Williams, and J. Ollerton. 1996. Generalization in pollination systems, and why it matters. *Ecology* 77: 1043–1060.
- Watson, M., and S. Asoyama. 2001. Dispersion, habitat use, hunting behavior, vocalizations, and conservation status of the New Guinea Harpy Eagle (*Harpyopsis novaeguineae*). *J Raptor Res* 35: 235–239.
- Westoby, M. 1988. Comparing Australian ecosystems to those elsewhere. *Bioscience* 38: 549–556.
- Wollaston, A.F.R. 1912. *Pygmies & Papuans: The Stone Age To-day in Dutch New Guinea*. Smith, Elder & Co., London.
- Wooller, F.L.S., and K.C. Richardson. 1988. Morphological relationships of passerine birds from Australia and New Guinea in relation to their diets. *Zool J Linn Soc* 94: 193–201.
- Wooller, R.D., K.C. Richardson, and D.R. Wells. 1990. Allometric relationships of the gastrointestinal tracts of insectivorous passerine birds from Malaysia, New-Guinea and Australia. *Aust J Zool* 38: 665–671.
- Wright, D.D. 2005. Diet, keystone resources, and altitudinal movement of dwarf casowaries in relation to fruiting phenology in a Papua New Guinean rainforest. Pp. 204–235 in Dew, J.L., and J. P. Boubli (eds.) *Tropical Fruits and Frugivores: The Search for Strong Interactors*. Springer, New York.
- Wunderle, J.M. 1997. The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. *Forest Ecol Mangt* 99: 223–235.