DISTRIBUTIONAL ECOLOGY AND HABITS OF SOME BOUGAINVILLE BIRDS (SOLOMON ISLANDS)

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Bougainville, the largest (ca. 8680 km^2) of the Solomon Islands, is located in the southwest Pacific Ocean about 600 km east of New Guinea and 600 km south of the equator (fig. 1). It is largely forested and has mountains rising up to about 2600 m, including active volcanoes. With 98 resident nonmarine bird species, Bougainville is second only to Guadalcanal among Pacific islands east of the Bismarck Archipelago in the diversity of its avifauna. Since the straits between many Solomon islands are less than 100 m deep, Bougainville must have formed part of a much larger island that extended from Buka in the northwest through the Shortland group, Choiseul, and Ysabel to Florida and possibly Guadalcanal in the southeast, during glacial periods of low sea level up to about 10,000 years ago. Thus, it is not surprising that only one endemic species is confined to Bougainville today, but the majority of endemic Solomon species are shared between Bougainville and other islands.

The avifauna of Bougainville was first explored by A. S. Meek in 1904 (discussed by Rothschild and Hartert 1905), later more thoroughly by the Whitney South Sea Expedition in 1927–29 (discussed in numerous papers by Mayr in American Museum Novitates), and more briefly by Poncelet in 1936–37 (discussed by Danis 1937a,b, 1938; White 1938). The results of these explorations were summarized in a book by Mayr (1945). Subsequent papers (Beecher 1945; Virtue 1947; Baker 1948; Filewood 1969, 1972) have added about a dozen more resident species. However, as pointed out by Mayr (1945), less published field information on ecology, behavior, and voice has been available for birds of the Solomons than of any other southwest Pacific island group. While the detailed observations of Cain and Galbraith (1956) rectify this gap for Guadalcanal, San Cristobal, Ugi, and Ulawa in the eastern Solomons, the only observations specifically from Bougainville are those by Beecher, Virtue, and Filewood for a number of species. Since populations of the same species on different Solomon islands often differ strikingly in their natural history, information specifically for Bougainville is desirable.

In August 1972 I observed birds between sea level and 1950 m at several localities in eastern Bougainville (Mt. Balbi, Rotokas, Wakunai, Panguna, Kieta, Aropa). The species accounts presented here serve four purposes: (1) my observations on the distributional ecology of 28 species endemic to the Solomons or Northern Melanesia, and of 15 other endemic races, are briefly summarized. (2) Additional records are provided for four species first recorded for Bougainville by Beecher, Virtue, or Filewood after the publication of Mayr's book. (3) Vocalizations of some Bougainville populations are described and, where possible, compared with vocalizations of populations of the same or related species which I heard on other Pacific islands. Often, there is marked geographical variation in vocalizations which may be relevant to questions of taxonomic affinities or geographical origins (cf. *Cacomantis variolosus*, *Rhipidura drownei*, and *Mino dumontii*, discussed below). In the text, wherever a reference citation is not explicitly given for a New Guinea song, it is taken from Diamond (1972a), and for songs on other islands, from my unpublished observations. In such cases the name of an island in parentheses after the name of a species does not necessarily convey the entire geographical range of the species but only the particular island where I heard the song. (4) Differences between Bougainville populations and conspecific populations on other islands with respect to spatial parameters of the niche are noted. Among southwest Pacific island populations, "niche shifts" are frequently observed (Diamond 1970a,b, 1973), i.e., a given species may expand or contract its altitudinal range, vertical foraging range, or habitat preference as a function of the competing species pool, particularly (though not only) in response to the presence or absence of congeners.

GENERAL OBSERVATIONS

Four general features of the Bougainville avifauna deserve mention.

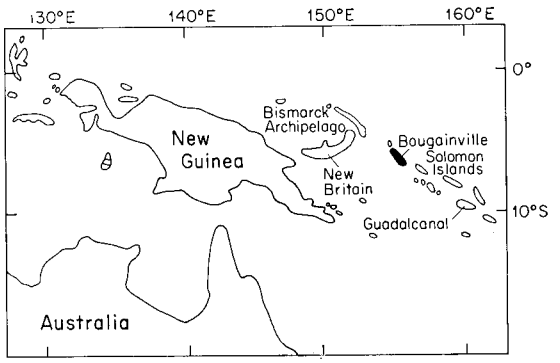

FIGURE 1. Map showing the location of Bougainville, one of the Solomon Islands, in the southwest Pacific Ocean.

1. *Number of montane species.* On many southwest Pacific islands, the number of montane species (i.e., bird species confined to the mountains and absent at sea level) has been found empirically to equal approximately 0.089 LS/1000, where L is the island's elevation in meters and S is the number of resident nonmarine species occurring at sea level (Diamond 1972b, 1973). Of the species I observed on Bougainville, the following 10 were confined to the mountains: *Ptilinopus solomonensis, Gymnophaps solomonensis, Vini meeki, Phylloscopus trivirgatus, Rhipidura drownei, Petroica multicolor, Pachycephala pectoralis, Pachycephala implicata, "Stresemannia" bougainvillei,* and *Zosterops ugiensis* (see appendix for common names). The records of the Whitney South Sea Expedition (as summarized in Mayr 1945, and in the expedition journals) show that six additional species which I failed to observe are also montane: *Columba vitiensis, Columba pallidiceps, Reinwardtoena crassirostris, Micropsitta bruijnii, Coracina caledonica,* and *Turdus poliocephalus.* My failure to encounter these species may have been due to the fact that, several months prior to my visit, a cyclone had blown down most large trees above 900 m in the area of Mt. Balbi that I studied. Thus, out of the 98 breeding species recorded for Bougainville, 16 are montane, and the remaining 82 descend to sea level. Since the elevation of Bougainville is approximately 2600 m, the number of montane species predicted by the above formula is (0.089) (82) (2600)/1000 = 19, close to the 16 found. Thus, the diversity of Bougainville's montane avifauna is as expected from its elevation, by comparison with other Pacific islands.

It is interesting that 9 of the 16 species that are montane on Bougainville (*Ptilinopus solomonensis, Columba vitiensis, Columba pallidiceps, Reinwardtoena crassirostris, Coracina caledonica, Turdus poliocephalus, Phylloscopus trivirgatus, Petroica multicolor,* and *Pachycephala pectoralis*) descend to sea level on smaller, less species-rich islands of the southwest Pacific. Thus, their confinement to the mountains of Bougainville does not reflect inability to survive at sea level but, instead, competition from other species in species-rich avifaunas.

2. *Altitudinal sequences.* On New Guinea and other species-rich, mountainous islands of the southwest Pacific, there are numerous instances in which pairs, triplets, and even quartets of congeneric species replace each other abruptly with altitude, at transition altitudes that do not coincide with an abrupt change in vegetation (Diamond 1970a, 1972a, 1973; see Terborgh 1971 for analogous cases in Peru). Bougainville has no such triplets or quartets but does have six pairs. Citing the high-altitude form first in each case, these are: *Vini meeki* > *V. placentis, Micropsitta bruijnii* > *M. finschii, Rhipidura drownei* > *R. rufifrons, Pachycephala implicata* > *P. pectoralis, Zosterops ugiensis* > *Z. metcalfei,* and (one-for-two replacement) *Ptilinopus solomonensis* > *P. viridis* and *P. superbus.* In the cases of *Ptilinopus, Rhipidura, Pachycephala,* and *Zosterops,* I was able to observe that the altitudinal ranges of the respective forms abut or come close to abutting with little or no overlap, suggesting that the sharpness of the transition is due to competition. Further evidence for a role of competition is available for one of the species in all four cases: on islands lacking the other species of the pair, the montane species *Ptilinopus solomonensis* descends to sea level (numerous examples in Mayr 1945 and elsewhere), and *Zosterops ugiensis* descends to at least 500 m but not to sea level on Guadalcanal and San Cristobal (Cain and Galbraith 1956), while the lowland species *Rhipidura rufifrons* and *Pachycephala pectoralis* ascend on Goodenough (Mayr and Van Deusen 1956) and on New Britain (my observations), respectively, to at least 1600 m, more than 600 m above their ceiling on Bougainville. Proof of the converse expansions is impossible to obtain because the montane species *Rhipidura drownei* and *Pachycephala implicata* occur on no island not shared by their congener, and the lowland species *Ptilinopus viridis, P. superbus,* and *Zosterops metcalfei* occur on no high island not shared by their congener. In the case of *Vini,* it appeared to me that there was a wide gap between the ceiling of *V. placentis* and the floor of *V. meeki,* suggesting that the

sequence was not maintained simply by one-to-one competition (cf. Terborgh 1971 for analogous gaps in Peruvian sequences, and Diamond 1969:43 for an analogous gap in a New Guinea sequence). In the case of *Micropsitta*, I do not know whether there is a gap.

3. *Size sequences.* When closely related bird species with similar diets and foraging techniques are found to coexist in the same habitat at the same altitude, they frequently differ in weight by approximately a factor of 2 (Diamond 1972a:42–44, and 1973, fig. 9). The size difference permits coexistence partly because the lighter bird can forage onto finer twigs, and partly because the heavier bird takes on the average larger food particles. On New Guinea some size sequences extend to eight members, each heavier than the next. Among Bougainville birds there are five such sequences (among fruit pigeons, lories, kingfishers, starlings, and honeyeaters), each involving up to four species. Details and approximate weights are given below under individual species. Since I weighed no birds on Bougainville itself, the weights cited are based on the same race or another race with similar winglength on other islands of Northern Melanesia (from Mayr 1931; Galbraith and Galbraith 1962; and my unpublished measurements).

4. *Mixed foraging flocks.* In the New Guinea region the occurrence of multi-species insectivorous foraging flocks, such as have been reported from most parts of the tropics, seems erratic (Diamond 1972a:81). It is therefore worth recording explicitly the presence of such flocks in Bougainville forests in August 1972. The flocks always included *Monarcha castaneiventris*, usually *Rhipidura cockerelli* and *R. rufifrons*, often *Monarcha barbata* and *Coracina holopolia*, and occasionally *Myiagra ferrocyanea*, *Zosterops metcalfei*, *Chrysococcyx lucidus*, and *Coracina papuensis*. *Pachycephala pectoralis*, which is absent at sea level and lives at 600–900 m, was always present in flocks seen within this altitudinal range. Except for *Z. metcalfei*, which probably takes much fruit as well as insects, these species are either largely or exclusively insectivorous. All are Bougainville residents except for *Chrysococcyx lucidus*, a winter visitor from New Zealand. Most of the individuals foraged more than 6 m above the ground, except that *Rhipidura rufifrons* remained lower. Flocks were observed from sea level to about 850 m, which is close to the upper altitudinal limit of all 10 species that I met in the flocks. *Monarcha castaneiventris*, in addition to being an invariant member of the flocks, was often the noisiest and most numerous member and may have served as a nuclear species with which other birds associated.

It is possible that these multi-species insectivorous flocks are a "dry-season," post-breeding phenomenon, as Fogden (1972) documented in detail for Borneo. As summarized by Brookfield and Hart (1966), annual rainfall at sea level on the east coast of Bougainville decreases from 3000 mm at Kieta to 2400 mm at Hakau Plantation (about 40 km N of Wakunai, Rotokas, and Mt. Balbi). The west side of Bougainville is wetter. Rainfall surely increases with altitude, though no measurements are available at higher elevations. February through April tend to be relatively wet months, September relatively less wet, but the differences are not marked. The ratio of rainfall in the wettest month to rainfall in the driest month is only 1.5 at Kieta, 2.4 at Hakau. Thus, my observations were made several months after the end of the wettest period. In practice, it rained virtually uninterruptedly while I was above 900 m but rained only intermittently while I was in the lowlands.

SPECIES ACCOUNTS

Accipiter novaehollandiae, Rufous-breasted Hawk and *Accipiter albogularis*, Pied Hawk. These two fairly common hawks are of similar size (*A. albogularis* slightly larger), and sometimes occur in close proximity. They differ ecologically in that *A. albogularis* occurs more commonly at higher elevations (up to at least 1800 m) and in forest and feeds mainly on birds, while *A. novaehollandiae* occurs primarily below 900 m and outside forest and feeds mainly on reptiles and insects. In habitat and diet *A. albogularis* is the equivalent of *A. melanochlamys* of New Guinea, which belongs in the same superspecies (Mayr 1957).

Haliaeetus sanfordi. Sanford's Eagle. A few soaring individuals of this eagle, which was previously reported for Bougainville by Beecher (1945) and Filewood (1969), were observed from the coast to elevations of 1200 m inland. The allospecies *H. leucogaster* occurs mainly at low elevations and near the coast on New Guinea.

Pandion haliaetus. Osprey. I saw one individual at Kieta Harbor. The osprey was first reported for Bougainville by Filewood (1969).

Megapodius freycinet. Incubator Bird. Solitary and fairly common from the coast to at least 600 m. Reliable local informants reported that this bird lays eggs in fallen, rotting trees of certain species, perhaps in order to utilize for incubation the heat engendered by decaying matter, as also suggested by the ob-

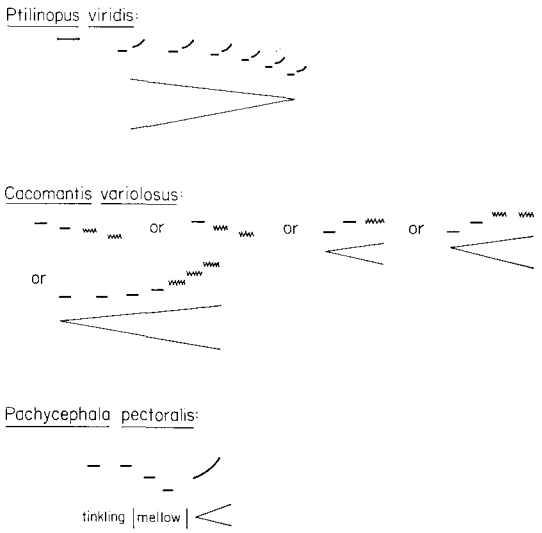

FIGURE 2. Vocalizations of three bird species on Bougainville Island.

servations of Cain and Galbraith (1956) on Guadalcanal and San Cristobal.

Porphyrio porphyrio. Purple Swamphen. Fairly common in grass, gardens, and early second-growth vegetation up to at least 600 m. As elsewhere in the southwest Pacific, the Purple Swamphen damages gardens on Bougainville by digging out taro.

Ptilinopus solomonensis. Yellow-bibbed Fruit Dove. This dove is common in the canopy of mountain forest from 900 to at least 1950 m and is the high-altitude equivalent of the two lowland fruit doves, *P. superbus* and *P. viridis.* It occurs at sea level on many other Solomon and Bismarck islands, but not on Bougainville (nor Guadalcanal or Malaita: Mayr 1945; Cain and Galbraith 1956). The call, a series of soft "hoo's" that accelerates slightly, differs from the call of the race *meyeri* of the New Britain area in that the pitch is lower (possibly related to the larger size of the Bougainville race) and the acceleration less marked.

Ptilinopus viridis. Red-throated Fruit Dove. Common in the canopy of lowland forest along with *P. superbus.* The typical call (fig. 2) is a soft series of "hoo's" that accelerates, drops slightly in pitch and volume, and accents the second note of each pair.

Ducula pistrinaria. Gray Pigeon. Fairly common in the canopy, from sea level to about 600 m. On Bougainville this pigeon occurs not only at the coast but also up to at least 16 km inland (cf. also Virtue 1947), although it is mainly coastal on other islands. The call, a series of hoarse barks that accelerate while dropping in pitch, is similar to calls of the Bismarck races *vanwyckii* (New Britain) and *rhodinolaema* (Long). The four lowland fruit-pigeons of Bougainville come in three sizes: *Ptilinopus viridis* (95–130 g), and *P. superbus* (105–133 g); *Ducula pistrinaria* (400–650 g); *D. rubricera* (650–800 g).

Gymnophaps solomonensis. Solomon Mountain Pigeon. Fairly common in the canopy of mountain forest, mainly above 750 m up to at least 1950 m. It was invariably met in flocks of up to 100 birds in a single tree, bursting explosively out of the treetop when disturbed. As with the allospecies *G. albertisii* (New Guinea), no vocalization was ever heard from *G. solomonensis.*

Eos cardinalis. Cardinal Lory. Abundant in small flocks, up to about 830 m. The call is very shrill and grating. The four lowland lories form a size sequence, each weighing approximately double the next: *Eos cardinalis* (170–205 g) > *Trichoglossus haematodus* (75–105 g) > *Vini margarethae* (45–60 g) > *V. placentis* (25–35 g).

Vini meeki. Meek's Lorikeet. The high-altitude equivalent of the similar-sized *V. placentis.* A few were seen on Mt. Balbi up to 1800 m.

Vini margarethae. Duchess Lorikeet. This lorikeet is common in small flocks of up to 10 birds, both in coconut plantations and in forest, from the coast up to at least 1350 m. The call note, rapidly repeated 2–8 times, has a peculiarly squeaky quality, unlike the shrill notes of most other lories.

Micropsitta finschii. Finsch's Pygmy Parrot. This inconspicuous and tiny parrot is nuthatch-like in behavior, gleaning from bark while going vertically up tree trunks or upside-down along the undersides of branches. It is said to nest in arboreal ants' nests. I failed to observe *M. bruijnii,* which replaces *M. finschii* at higher elevations on Bougainville and several other high islands of Northern Melanesia.

Geoffroyus heteroclitus. Song Parrot. This uncommon parrot of the lowlands includes unripe bananas in its diet. In voice, it is more similar to *G. simplex* (New Guinea) than to *G. geoffroyi* (New Guinea).

Cacatua ducorpsi. Solomon White Cockatoo. Common from the coast up to at least 1800 m.

Cacomantis variolosus. Brush Cuckoo. Shy, yet common and noisy, from sea level up to at least 1200 m. Whereas on New Guinea *C. variolosus* is excluded from forest by *C. castaneiventris* and lives in clearings, on Bougainville (where *C. castaneiventris* is absent) *C. variolosus* is most common in forest. Compared to the shrill song on New Guinea and New Britain (Diamond 1972a:166), the Bou-

gainville song is even shriller and is also quite different in pattern (fig. 2) and in that some of the notes are slightly trilled. Descriptions of the song on Guadalcanal, San Cristobal, and Ulawa (Cain and Galbraith 1956) and on New Georgia (Sibley 1951) suggest differences between the songs on Bougainville and on these other Solomon islands.

Chrysococcyx lucidus. Shining Bronze Cuckoo. Single individuals of this winter visitor from New Zealand were fairly common in the crowns of trees up to at least 760 m and were perhaps more common at the forest edge than in forest. Sometimes they joined multispecies insectivorous flocks of resident passerines. I never heard this species call on Bougainville.

Ninox jacquinoti. Solomon Boobook Owl. Said to feed on insects and frogs. On 2 successive days, one was discovered roosting in a hollow beneath an overhanging branch of a large tree, 15 m above the ground, in forest at 1100 m. The call is a monosyllabic, somewhat throaty and hoarse, unmusical note, not loud, repeated at prolonged intervals. The races of Guadalcanal and San Cristobal, which are rather different from the Bougainville race morphologically, also appear to differ in call, as described by Cain and Galbraith (1956:132: "a high plaintive 'oh . . . oh . . .'"). In my experience, *N. theomacha* (New Guinea), *N. novaeseelandiae* (New Zealand), and *N. connivens* (New Guinea) have disyllabic calls repeated at prolonged intervals, as also described for *N. rufa* and *N. strenua* in Australia (Slater 1970), while the call of *N. odiosa* (New Britain) is a rapidly repeated monosyllable.

Nesasio solomonensis. Fearful Owl. Not observed. Several informants stated independently that the diet consists mainly of phalangers, and that the call is a single, drawn-out note rising in pitch at the end, with a ghostly, mournful, human quality.

Hemiprocne mystacea. Mustached Swift. This striking lowlands species is more common on Bougainville than on New Guinea, and occurs in groups of one to three, flying out from perches in the crowns of tall trees. The call of the Bougainville race (*woodfordiana*) is a fairly loud, fairly high-pitched, nasal downslur, similar to the call of the nominate race of New Guinea.

Collocalia spodiopygia. White-rumped Swiftlet. Common in the lowlands, sometimes in mixed flocks with *C. vanikorensis.* This swiftlet was first reported for Bougainville by Filewood (1969). *C. esculenta,* which flies more slowly and closer to vegetation, was common up to at least 1950 m.

Halcyon leucopygia. Ultramarine Kingfisher. Uncommon in lowland forest, perching motionless for many minutes in the crowns of tall trees, like its New Britain relative *H. albonotata.* I observed it singly or in pairs. The four resident forest kingfishers form a size series: *H. bougainvillei* (ca. 200 g) > *H. chloris* (80 g) > *H. leucopygia* (45 g) > *Ceyx lepidus* (20 g).

Coracina holopolia. Black-bellied Graybird. Fairly common in crowns of lowland forest up to 760 m. This graybird was sometimes accompanied by *C. tenuirostris* and was often seen in mixed insectivorous flocks. It appears to be mainly insectivorous. *C. holopolia* is unusual within genus *Coracina,* not only in being the smallest species but also in taking much of its insect prey by sallying or by hovering.

Coracina lineata, Barred Cuckoo-Shrike and *Coracina papuensis,* Papuan Cuckoo-Shrike. Whereas the New Guinea population of *C. lineata* lives in hill forest and is absent at sea level, the Bougainville population and the New Britain population occur at sea level and are often seen in the crowns of isolated trees. *C. papuensis* and *C. lineata* are of similar sizes and occur in similar habitats up to about 1100 m, but *C. lineata* appears from published reports and from my experience to take more fruit than insects, *C. papuensis* vice versa. The call of *C. papuensis* is a disyllabic note similar to that of the New Guinea population. The call of *C. lineata* is a loud, nasal, whistled downslur.

Coracina novaehollandiae. Black-faced Cuckoo-Shrike. This winter visitor from Australia was seen occasionally in flocks in open country near the coast.

Acrocephalus stentoreus. Great Reed Warbler. Several were heard singing near Kieta Harbor in tall reeds that I visited once. This warbler was previously reported for Bougainville by Beecher (1945), Virtue (1947), and Filewood (1969).

Phylloscopus trivirgatus. Leaf Warbler. Solitary individuals were common from about 970 to at least 1950 m, generally in the middle or upper stories of the forest. The song is a short, high, formless warble like the song of the New Guinea, New Britain, and Karkar races, despite the marked subspecific plumage differences among these populations.

Rhipidura rufifrons. Rufous-fronted Fantail. Common in forest from sea level to about 830 m, where it is replaced by *R. drownei.* It occurs singly or in pairs in the lower and middle stories, usually in mixed insectivorous flocks.

Rhipidura drownei. Solomon Mountain Fantail. Common in all strata of the forest from 830 m to at least 1600 m, singly or in groups of two or three. The faint, high-pitched song has a tinkling quality like the songs of the closely related *R. nebulosa* (Samoa) and *R. fuliginosa* (New Hebrides, Australia; the song of the New Zealand race seems to me squeakier and less tinkling).

Rhipidura cockerelli. Cockerell's Fantail. Common in forest from sea level to about 950 m. This flycatcher was found singly or in pairs, mainly in the middle story, often in mixed insectivorous flocks. Whereas most small species of *Rhipidura*, including *R. drownei*, are nervous, in constant motion, frequently fan the tail, and hold the body nearly horizontal, *R. cockerelli* remains stationary for relatively long times between moves, perches upright, fans its tail infrequently, and sallies like a flycatcher of genus *Microeca* or *Myiagra* rather than a *Rhipidura.* In behavior the related *R. rufiventris* (New Guinea, New Britain) deviates from most *Rhipidura* species in the same ways as does *R. cockerelli* but not to such an extreme degree. The white wing patch is conspicuous in the field.

Monarcha castaneiventris. Chestnut-bellied Monarch. Very common in forest from sea level to at least 850 m (possibly much higher), in the middle story and canopy but not close to the ground. The noisy, varied, and frequently given calls include rapidly repeated, scolding rasps; plaintive, downslurred whistles repeated about once every 2 sec, each note crescendoing; and a series of more rapidly repeated and louder whistled notes, each note crescendoing, and each note either upslurred, downslurred, or at constant pitch. The calls of the related *M. frater* (New Guinea) and *M. cinerascens* (small islets) similarly consist of repeated whistled or rasped notes. *M. castaneiventris* regularly occurs in two's and three's in mixed insectivorous flocks, where its abundance and noisiness may give it the role of a nuclear species.

Monarcha barbata. Solomon Pied Monarch. In mixed flocks in forest from sea level to about 760 m, but less numerous than *M. castaneiventris.*

Myiagra ferrocyanea. Solomon Broad-billed Flycatcher. This flycatcher is common from sea level to about 850 m, not only in forest but also at the forest edge and in isolated trees. It is regularly found farther from forest than all other flycatchers of Bougainville except *Rhipidura leucophrys.* Usually it is seen in male-female pairs in the crowns, occasionally in the middle story, but never close to the ground. It catches insects by sallying or hovering and remains motionless on its perch between sallies except for quivering its tail. The common song is a series of two to six identical, upslurred or downslurred whistled notes, similar to songs of *Chrysococcyx lucidus* (New Zealand), and differing from calls of *Monarcha castaneiventris* in the higher pitch and absence of crescendoes. Other calls include repeated weak rasps or unvoiced notes "wh-zz."

Petroica multicolor. Scarlet Robin. Single individuals and occasionally pairs were fairly common in forest from 1200 to at least 1950 m, generally more than 2 m above the ground. The call is a high-pitched, tinkling note monotonously repeated every half-second.

Pachycephala pectoralis. Golden Whistler. Among different islands and even within the same island, populations of this species differ in altitude and distribution. Some populations are confined to the mountains, while others extend from the mountains down to sea level, and still others live on low, flat islands. In the Kieta-Rotokas area I found the Golden Whistler only between 600 and 900 m; the Whitney Expedition (Mayr 1932a), and Danis's (1938) collector Poncelet, similarly found it absent from the Buin plains of south Bougainville; and in west New Britain I found it only above 300 m. However, at Cape Torokina on west Bougainville, Baker (1948) collected one in the lowlands, and it is common at sea level on San Cristobal, Guadalcanal, Umboi, Espiritu Santo, and many other islands. The song on Bougainville is typical of other populations of *P. pectoralis* and even other *Pachycephala* species in that it consists of separate, whistled notes ending in a louder, crescendoing slur. In the five-note patern illustrated in figure 2, the first two notes are tinkling in quality, the next two are louder and more mellow, and the last is an explosive upslur.

Pachycephala implicata. Solomon Mountain Whistler. Replaces *P. pectoralis* at higher elevations up to at least 1750 m. The few that I saw were quiet, solitary, and stayed out of sight in dense understory.

Aplonis grandis. Brown-winged Starling. Fairly common in forest or isolated trees from sea level to about 670 m. It lives mainly in the crowns, descending to within 2 m of the ground at the forest edge, and is often seen in figs and other fruit trees, which it shares with *Mino dumontii* and *Ptilinopus viridis.* Unlike *Aplonis metallicus* and *A. cantoroides*, this starling is always met singly or in pairs, never in flocks. The nest is a very large structure in a treetop. The wingbeat is loud, and

the calls are very high-pitched whistles, but this species is much less noisy and conspicuous than the other two *Aplonis* species. The common species of Sturnidae on Bougainville are all mainly frugivorous and come in three sizes: large (*Mino dumontii*, ca. 180–215 g), medium (*Aplonis grandis*, 110–150 g), and small (*Aplonis cantoroides*, 50–60 g, and *A. metallica*, 50-65 g).

Mino dumontii. Papuan Myna. Common and noisy from sea level to 600 m in the crowns of the forest and isolated trees, in groups of up to four. This species is often seen in fruit trees with *Ptilinopus* and *Ducula* pigeons and *Aplonis* starlings. On morphological grounds the Solomon and Bismarck populations have been joined in a race *kreffti*, distinct from the nominate race on New Guinea. The calls of Bougainville birds resemble those of other *kreffti* populations that I have heard (New Britain, Umboi) in consisting of loud whistles, rather than the totally unmusical, bullfrog-like calls of New Guinea birds.

Corvus woodfordi. Solomon Crow. Common in groups of up to three from sea level to at least 1600 m, in forest, gardens, and coconut plantations. The call is a typical corvid "cah" that has a tense quality and often drops in pitch. The Guadalcanal population, sometimes separated as a distinct allospecies, differs ecologically in that it is absent from the lowlands (Cain and Galbraith 1956).

Nectarinia jugularis. Yellow-breasted Sunbird. Fairly common outside of forest (especially in plantations and coconut trees) from sea level to 600 m, and up to at least 16 km inland. The niche breadth of this species is markedly subject to competition from myzomelid honeyeaters (Diamond 1970a). Where there are no myzomelids, the sunbird occurs within forest as well as outside forest (Karkar lowlands, Bagabag); in the presence of one myzomelid species, as on Bougainville and Umboi, it is common outside of forest but absent in forest; and on islands with two myzomelid species, the sunbird is rare or confined to a coastal strip (New Britain, Long), or is entirely absent (Tolokiwa, San Cristobal). (See also Ripley 1959 and Cain and Galbraith 1956.)

Myzomela lafargei. Bougainville Myzomela. Fairly common from sea level to at least 1800 m, in forest and also in coconut plantations. Since I did not come upon flowering trees that would have attracted large numbers, I only saw single individuals or groups of two or three. These were always in the crowns and frequently hovered like a sunbird, to feed at flowers. The call is a high-pitched, sweet, sunbird-like "tsip-tsip."

"Stresemannia" bougainvillei. Bougainville Honeyeater. At 1950 m I twice glimpsed single individuals gleaning nervously in inner parts of tree crowns. The records of the Whitney Expedition show broad altitudinal overlap with the smaller honeyeater *Myzomela lafargei*, which appears to weigh one-half to one-third as much (no weights are available for *"Stresemannia"*). I agree with Mayr (1932b, 1955) that this undistinctive species, whose taxonomic position has been variously guessed as in or near the genera *Lichmera* (Mayr 1932b), *Meliphaga* (Mayr 1955), *Melilestes* (Salomonsen 1967), or *Vosea* = *Melidectes* (Mayr 1971), surely does not deserve to be placed in a monotypic genus. I reluctantly use *"Stresemannia"* only because of my ignorance as to the affinities of the species.

Dicaeum aeneum. Solomon Midget. Single individuals or pairs were very common in forest as well as open habitats with trees, from sea level to at least 1300 m. There are two call notes, both very weak: a spitted note, sometimes rapidly repeated, and a sibilant note very similar to the call of *Ceyx lepidus*.

Zosterops metcalfei. Solomon Yellow-throated White-eye. Common in forest and open habitats with trees from sea level to 900 m. More often it is seen in the middle story and canopy than in the understory. It lives in small flocks, occasionally joining multi-species insectivorous flocks. The call is a bright, fairly loud, single note with a sharp attack, like the call of *Z. lateralis* (New Zealand, New Hebrides, Fiji).

Zosterops ugiensis. Solomon Gray-throated White-eye. The most abundant bird of the Bougainville mountains from 900 to at least 1950 m, replacing *Z. metcalfei* at these elevations. It is generally met in small flocks in the middle story and canopy. Both the call-note and song are loud, mellow, not hoarse, and without a sharp attack. Especially in mellowness, the vocal quality of *Z. ugiensis* is unlike that of *Z. metcalfei* or of most other Pacific *Zosterops* species I have encountered. The call-note is downslurred, while the song, a mellow phrase reminiscent of New World orioles (*Icterus*), is the main component of dawn choruses in the mountains.

Erythrura trichroa. Blue-faced Parrot-Finch. Common in forest from 1130 to at least 1950 m. This finch was first reported for Bougainville by Filewood (1969), who found it in the lowlands and at 800 m. Its call (Diamond 1972a:407) can easily go unnoticed if one is not familiar with it. Moreover, its green

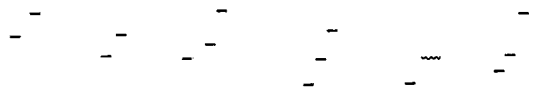

FIGURE 3. Song of an unidentified montane bird species of Bougainville, as discussed on p. 21.

plumage blends with forest vegetation. Even on islands where it is abundant in forest, it is far less often seen than heard or mist-netted. The absence of earlier records could reflect this inconspicuousness, or else there may have been a recent increase in abundance, associated either with seeding of bamboo or else with growth of thickets due to the recent cyclone damage to forest.

The other species that I observed on Bougainville were: *Sterna bergii*, *Anas superciliosa*, *Haliastur indus*, *Tringa hypoleucos*, *Pluvialis dominica*, *Numenius phaeopus*, *Ptilinopus superbus*, *Ducula rubricera*, *Macropygia mackinlayi*, *Trichoglossus haematodus*, *Vini placentis*, *Eclectus roratus*, *Eudynamis scolopacea*, *Collocalia vanikorensis*, *Collocalia esculenta*, *Alcedo atthis*, *Ceyx lepidus*, *Halcyon chloris*, *Halcyon sancta*, *Eurystomus orientalis*, *Aceros plicatus*, *Hirundo tahitica*, *Coracina tenuirostris*, *Rhipidura leucophrys*, *Aplonis cantoroides*, and *Aplonis metallica*.

One additional unidentified bird song of the Bougainville mountains is so remarkable as to warrant description, in the hope of alerting some future observer to the problem of its identification. The song was heard only on Mt. Balbi between 1140 and 1340 m. Its author was said by local informants to be confined to the mountains and is called "kópipi" in the native language used at Rotokas, "ódedi" in the language of the mountain people inland of Kieta. The most striking features of the song are the beauty and human quality of its pure, whistled tones. The thrush-like pattern (fig. 3) consists of two-note or three-note rising phrases at time intervals of a few seconds. The pitch is high, and occasional notes are slightly trilled. In pattern and in quality the song suggests that of the Hermit Thrush of North America (*Catharus guttatus*). I heard the song during the dawn chorus and later during rainy mornings, sometimes from several individuals simultaneously in different directions. I have no good clues to the identity of the singer, other than that it is apparently montane, shy, not uncommon, and possibly solitary and territorial.

SUMMARY

Some general features of the avifauna of Bougainville (Solomon Islands) are briefly reviewed. There are 16 montane species, close to the number predicted by inserting Bougainville's elevation and lowland species number into an empirical equation describing the montane avifaunas of southwest Pacific islands. Members of six pairs of congeners have mutually exclusive altitudinal ranges, and altitudinal expansion of one member in the absence of the other (apparently due to relief from competition) has been demonstrated in most of these pairs. Five groups exhibit "size sequences" of up to four species, which differ from each other in weight by approximately a factor of 2. Multi-species insectivorous foraging flocks have been recorded. Observations on distributional ecology, habits, "niche shifts," and geographical variation in songs and calls are presented for 51 species, especially for endemic forms of Northern Melanesia.

ACKNOWLEDGMENTS

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LITERATURE CITED

BAKER, R. H. 1948. Report on collections of birds made by United States Naval Medical Research Unit no. 2 in the Pacific war area. Smithsonian Misc. Coll. 107, no. 15.

BEECHER, W. J. 1945. A bird collection from the Solomon Islands. Fieldiana (Zoology) 31:31–37.

BROOKFIELD, H. C., AND D. HART. 1966. Rainfall in the tropical southwest Pacific. Australian National University, Canberra. 25 p.

CAIN, A. J., AND I. C. J. GALBRAITH. 1956. Field notes on birds of the eastern Solomon Islands. Ibis 98:100–134, 262–295.

DANIS, V. 1937a. Étude d'une collection d'oiseaux de l'ile Bougainville. Bull. Mus. Hist. Nat. Paris 9:119–123.

DANIS, V. 1937b. Étude d'une nouvelle collection d'oiseaux de l'ile Bougainville. Bull. Mus. Hist. Nat. Paris 9:362–365.

DANIS, V. 1938. Étude d'une nouvelle collection d'oiseaux de l'ile Bougainville. Bull. Mus. Hist. Nat. Paris 10:43–47.

DIAMOND, J. M. 1969. Preliminary results of an ornithological exploration of the North Coastal Range, New Guinea. Amer. Mus. Novitates 2362:1–57.

DIAMOND, J. M. 1970a. Ecological consequences of island colonization by southwest Pacific birds. I. Types of niche shifts. Proc. Natl. Acad. Sci. U.S.A. 67:529–536.

DIAMOND, J. M. 1970b. Ecological consequences of island colonization by southwest Pacific birds. II. The effect of species diversity on total population density. Proc. Natl. Acad. Sci. U.S.A. 67: 1715–1721.

DIAMOND, J. M. 1972a. Avifauna of the Eastern Highlands of New Guinea. Nuttall Ornithological Club, Cambridge, Mass. Publ. No. 12. 438 p.

DIAMOND, J. M. 1972b. Biogeographic kinetics: estimation of relaxation times for avifaunas of southwest Pacific islands. Proc. Natl. Acad. Sci. U.S.A. 69:3199–3203.

DIAMOND, J. M. 1973. Distributional ecology of New Guinea birds. Science 179:759–769.

FILEWOOD, L. W. C. 1969. New avifaunal sight-recordings for Bougainville. Proc. Papua New Guinea Sci. Soc. 21:20–22.

FILEWOOD, L. W. C. 1972. Notes on the birds of Bougainville Island. Emu 72:32.

FOGDEN, M. P. L. 1972. The seasonality and population dynamics of equatorial forest birds in Sarawak. Ibis 114:308–343.

GALBRAITH, I. C. J., AND E. H. GALBRAITH. 1962. Land birds of Guadalcanal and the San Cristoval group, eastern Solomon Islands. Bull. Brit. Mus. (Nat. Hist.) Zool. 9:1–86.

MAYR, E. M. 1931. Birds collected during the Whitney South Sea Expedition. XVII. The birds of Malaita Island (British Solomon Islands). Amer. Mus. Novitates 504:1–26.

MAYR, E. M. 1932a. Birds collected during the Whitney South Sea Expedition. XX. Notes on thickheads (*Pachycephala*) from the Solomon Islands. Amer. Mus. Novitates 522:1–22.

MAYR, E. M. 1932b. Birds collected during the Whitney South Sea Expedition. XVIII. Notes on Meliphagidae from Polynesia and the Solomon Islands. Amer. Mus. Novitates 516:1–30.

MAYR, E. M. 1945. Birds of the southwest Pacific. Macmillan, New York, 316 p.

MAYR, E. M. 1955. Birds collected during the Whitney South Sea Expedition. LXIII. Notes on the birds of Northern Melanesia. 3. Passeres. Amer. Mus. Novitates 1707:1–46.

MAYR, E. M. 1957. Birds collected during the Whitney South Sea Expedition. LXIV. Notes on the Birds of Northern Melanesia. 4. The genus *Accipiter*. Amer. Mus. Novitates 1823:1–14.

MAYR, E. M. 1971. New species of birds described from 1956 to 1965. J. Ornithol. 112:302–316.

MAYR, E. M., AND H. M. VAN DEUSEN. 1956. Results of the Archbold Expeditions. No. 74. The birds of Goodenough Island, Papua. Amer. Mus. Novitates 1792:1–8.

RIPLEY, S. D. 1959. Competition between sunbird and honeyeater species in the Moluccan islands. Amer. Nat. 93:127–132.

ROTHSCHILD, W., AND E. HARTERT. 1905. Further contributions to our knowledge of the ornis of the Solomon Islands. Novitates Zool. 12:243–268.

SALOMONSEN, F. 1967. Meliphagidae, p. 338–450. *In* R. A. Paynter, Jr. [ed.] Check-list of birds of the world. Vol. 12. Mus. Comp. Zool., Cambridge, Mass. 495 p.

SIBLEY, C. G. 1951. Notes on the birds of New Georgia, central Solomon Islands. Condor 53: 81–92.

SLATER, P. 1970. A field guide to Australian birds. Non-passerines. Livingston, Wynnewood, Pa. 428 p.

TERBORGH, J. 1971. Distribution on environmental gradients: theory and a preliminary interpretation of distributional patterns in the avifauna of the Cordillera Vilcabamba, Peru. Ecology 52: 23–40.

VIRTUE, R. M. 1947. Birds observed at Torokina, Bougainville Island. Emu 46:324–331.

WHITE, C. M. N. 1938. [Notes on some Solomon Island birds]. Bull. Brit. Ornithol. Club 58:46–48.

APPENDIX

Common names (mainly from Mayr 1945).

Anas superciliosa, Australian Black Duck.
Haliastur indus, Brahminy Kite.
Accipiter novaehollandiae, Rufous-breasted Hawk.
Accipiter albogularis, Pied Hawk.
Haliaeetus sanfordi, Sanford's Eagle.
Pandion haliaetus, Osprey.
Megapodius freycinet, Incubator Bird.
Porphyrio porphyrio, Purple Swamphen.
Pluvialis dominica, Eastern Golden Plover.
Numenius phaeopus, Whimbrel.
Tringa hypoleucos, Common Sandpiper.
Sterna bergii, Crested Tern.
Ptilinopus superbus, Superb Fruit Dove.
Ptilinopus solomonensis, Yellow-bibbed Fruit Dove.
Ptilinopus viridis, Red-throated Fruit Dove.
Ducula rubricera, Red-knobbed Pigeon.
Ducula pistrinaria, Gray Pigeon.
Gymnophaps solomonensis, Solomon Mountain Pigeon.
Columba vitiensis, White-throated Pigeon.
Columba pallidiceps, Yellow-legged Pigeon.
Macropygia mackinlayi, Rufous-brown Cuckoo Dove.
Reinwardtoena crassirostris, Solomon Crested Pigeon.
Eos cardinalis, Cardinal Lory.
Trichoglossus haematodus, Rainbow Lory.
Vini meeki, Meek's Lorikeet.
Vini placentis, Blue-eared Lorikeet.
Vini margarethae, Duchess Lorikeet.
Micropsitta finschii, Finsch's Pygmy Parrot.
Micropsitta bruijnii, Mountain Pygmy Parrot.
Geoffroyus heteroclitus, Song Parrot.
Eclectus roratus, Eclectus Parrot.
Cacatua ducorpsi, Solomon White Cockatoo.
Cacomantis variolosus, Brush Cuckoo.
Chrysococcyx lucidus, Shining Bronze Cuckoo.
Eudynamis scolopacea, Koel.
Ninox jacquinoti, Solomon Boobook Owl.
Nesasio solomonensis, Fearful Owl.
Hemiprocne mystacea, Mustached Swift.
Collocalia vanikorensis, Vanikoro Swiftlet.
Collocalia spodiopygia, White-rumped Swiftlet.
Collocalia esculenta, Glossy Swiftlet.
Alcedo atthis, River Kingfisher.
Ceyx lepidus, Dwarf Forest Kingfisher.
Halcyon chloris, White-collared Kingfisher.
Halcyon sancta, Sacred Kingfisher.
Halcyon leucopygia, Ultramarine Kingfisher.
Eurystomus orientalis, Dollar Bird.
Aceros plicatus, Papuan Hornbill.
Hirundo tahitica, Pacific Swallow.
Coracina holopolia, Black-bellied Graybird.
Coracina tenuirostris, Cicada Bird.
Coracina lineata, Barred Cuckoo-Shrike.
Coracina papuensis, Papuan Cuckoo-Shrike.
Coracina caledonica, Melanesian Cuckoo-Shrike.
Coracina novaehollandiae, Black-faced Cuckoo-Shrike.
Turdus poliocephalus, Island Thrush.
Acrocephalus stentoreus, Great Reed Warbler.
Phylloscopus trivirgatus, Leaf Warbler.
Rhipidura rufifrons, Rufous-fronted Fantail.
Rhipidura drownei, Solomon Mountain Fantail.
Rhipidura cockerelli, Cockerell's Fantail.
Rhipidura leucophrys, Willie Wagtail.
Monarcha castaneiventris, Chestnut-bellied Monarch.
Monarcha barbata, Solomon Pied Monarch.
Myiagra ferrocyanea, Solomon Broad-billed Flycatcher.
Petroica multicolor, Scarlet Robin.
Pachycephala pectoralis, Golden Whistler.
Pachycephala implicata, Solomon Mountain Whistler.
Aplonis cantoroides, Singing Starling.

Aplonis grandis, Brown-winged Starling.
Aplonis metallica, Metallic Starling.
Mino dumontii, Papuan Myna.
Corvus woodfordi, Solomon Crow.
Nectarinia jugularis, Yellow-breasted Sunbird.
Myzomela lafargei, Bougainville Myzomela.
"*Stresemannia*" *bougainvillei*, Bougainville Honeyeater.
Dicaeum aeneum, Solomon Midget.
Zosterops metcalfei, Solomon Yellow-throated White-eye.
Zosterops ugiensis, Solomon Gray-throated White-eye.
Erythrura trichroa, Blue-faced Parrot Finch.

This paper is dedicated (1974) with admiration and affection to Ernst Mayr, on his 70th birthday, and on the 45th anniversary of his field work on Bougainville.

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