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ISLANDS, NEW GUINEA

JARED M. DIAMOND AND MARY LECROY

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## ABSTRACT

We analyze the avifaunas of Karkar and Bagabag, two Quaternary volcanic islands off the northeast coast of New Guinea. Our discussion is based on collections and observations of birds, and incidental collections of mammals, made on these islands in 1969. The first part of our discussion considers general features of interest in the avifaunas, and the second part consists of individual species accounts.

Most bats and nonvolant mammals of Karkar and Bagabag occur in the adjacent New Guinea lowlands and on other nearby islands. However, the bat *Pteropus tonganus* is otherwise absent from the New Guinea and Bismarck regions, though widespread on more remote Pacific archipelagoes from the New Hebrides eastward.

As judged by distributions and subspecific affinities, most bird species have been derived from New Guinea, except for seven species (including four small-island specialists or "supertramps") derived from the Bismarck Archipelago. There are no endemic forms. Most of the bird species are superior overwater colonists shared with other nearby islands.

Altitudinal ranges are plotted for all resident species of Karkar. Species number decreases regularly with altitude. Altitudinal limits of different species show little tendency to coincide: i.e., there is little altitudinal zonation of the avifauna. Eight species on Karkar are confined to the mountains.

Comparison of the resident avifauna of Karkar in 1969 with that determined by Meek's collectors in 1914 yields a minimum turnover rate of 0.34 percent of Karkar's bird populations turning over (immigrating or going extinct) per year.

Karkar and Bagabag support only a fraction of the bird species found in similar habitats on New Guinea. Total population densities on Karkar and Bagabag are considerably below those on New Guinea. Due to this reduction in interspecific competition, half of the species on Karkar undergo niche shifts—i.e., occupy broader altitudinal, habitat, or vertical ranges or live at higher densities than do the source populations on New Guinea.

Study of primary molt and gonad condition of collected specimens and nest records permit tentative conclusions about reproductive cycles for most species. Few species breed in the dry season except for frugivores. Some species, especially wide-ranging colonizers, increase their reproductive potential by molt-breeding overlap, adventitious breeding, or both.

Our accounts of individual species report measurements and weights of collected specimens, color of soft parts, local names, breeding and molt data, stomach contents, taxonomic conclusions, and voice and other field observations.

## INTRODUCTION

Off the northeast coast of New Guinea lie two volcanic islands, Karkar (formerly called Dampier) and Bagabag (formerly Rich). In 1969 one of us (Jared Diamond) made collections and ecological studies of birds on these islands. The collected specimens were subsequently studied by Mary LeCroy. A collection of Karkar birds had been obtained in 1914 for the Tring Museum by associates of Albert Meek (Rothschild and Hartert, 1915a), but no previous studies of birds had been made on Bagabag. In the present report we summarize available information about the birds of these two islands.

The avifaunas of Karkar and Bagabag are of interest for several reasons. Although the main source of colonists was New Guinea, some

came from the Bismarck Archipelago, so that Karkar and Bagabag form part of a zoogeographically interesting mixing zone. These islands have been colonized by a very nonrandom sample of the New Guinea and Bismarck avifaunas, and therefore afford an opportunity to obtain insight into the general problem of species differences in colonizing ability. Because Karkar and Bagabag habitats lack most of the species that occur in similar habitats on New Guinea, the successful colonists have undergone striking ecological changes or niche shifts, including changes in abundance, altitudinal range, habitat, vertical foraging range, and diet. Karkar is high enough to support a distinct montane avifauna. The prior survey by Meek's collectors permits tentative estimates of



species turnover rates on Karkar by comparison of Meek's and Diamond's species lists. Gonad and molt condition of the specimens permits some tentative conclusions about reproductive cycles, a little studied aspect of avian ecology in New Guinea.

Our report begins with a brief description of Karkar and Bagabag: their geography, geology, climate, vegetation, and mammal fauna. After an account of the senior author's fieldwork, we discuss general features of interest in the avifaunas as outlined in the preceding paragraph. Finally, we give species accounts that summarize collected specimens, taxonomic affinities, ecology, and behavior for each species that he recorded.

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### DESCRIPTION OF KARKAR AND BAGABAG

**GEOGRAPHY:** Karkar is 142 sq. mi. in area and 6007 ft. in elevation; Bagabag, 14.4 sq. mi. and 1968 ft. Karkar lies 10 miles from the coast of New Guinea, Bagabag 27, and Karkar and Bagabag are 13 miles from each other. The nearest island of the Bismarck Archipelago, Crown Island, lies 50 miles east of Bagabag and 68 miles east of Karkar. Figure 1 depicts the location of these islands.

**GEOLOGY:** Karkar and Bagabag belong to a chain of recent (Quaternary) volcanic islands that constitute the western part of the Bismarck Volcanic Arc and lie along the north coast of New Guinea. From west to east these islands are: the Schouten group consisting of Vokeo, Viai, Blupblup, Kadovar, and Bam; Boisa; Manam; Karkar; Bagabag; Crown; Long; Tolokiwa; Umboi (formerly called Rooke); Sakar; and Ritter. Ten of these islands, including Karkar but not Bagabag, are still active volcanically. Other, submarine volcanoes also belong to this chain, which continues to a chain of volcanoes on New Britain's north coast (e.g., Langila, Talawe, Tangi, Dakataua caldera, Lake Hargy caldera, Ulawun, Rabaul caldera) and volcanic islands off New Britain's

north coast (the Witu islands, Lolobau, and Vuatom). There are further islands along New Guinea's north coast west of the Schouten group (Kairiru, Mushu, Walis, and Tarawai), but these are not Quaternary volcanoes. Within this island chain it is convenient to consider those from Crown eastward as belonging to the Bismarck Archipelago, since their avifaunas have been derived mainly from New Britain and other Bismarck islands, whereas the avifaunas of Bagabag and Karkar have been derived mainly from New Guinea.

Karkar is a stratovolcano with a central caldera 3.5 mi. in diameter, breached and drained to the northwest. Sunk into the center of this caldera is a magnificent circular crater 2 mi. in diameter and 500 ft. deep, with nearly vertical walls, a flat floor at an altitude of 3500 ft., and a rim at 4000 ft. In the center of this crater is a cone named Bagiai, 1000 ft. high and with thermal activity in two small craters near its top (fig. 2). The highest point on Karkar, Mt. Kanagiioi (6007 ft.), is a cone on the south rim of the caldera.

There are historical accounts of eruptions on Karkar in 1895, 1885, 1700, and 1643. Car-

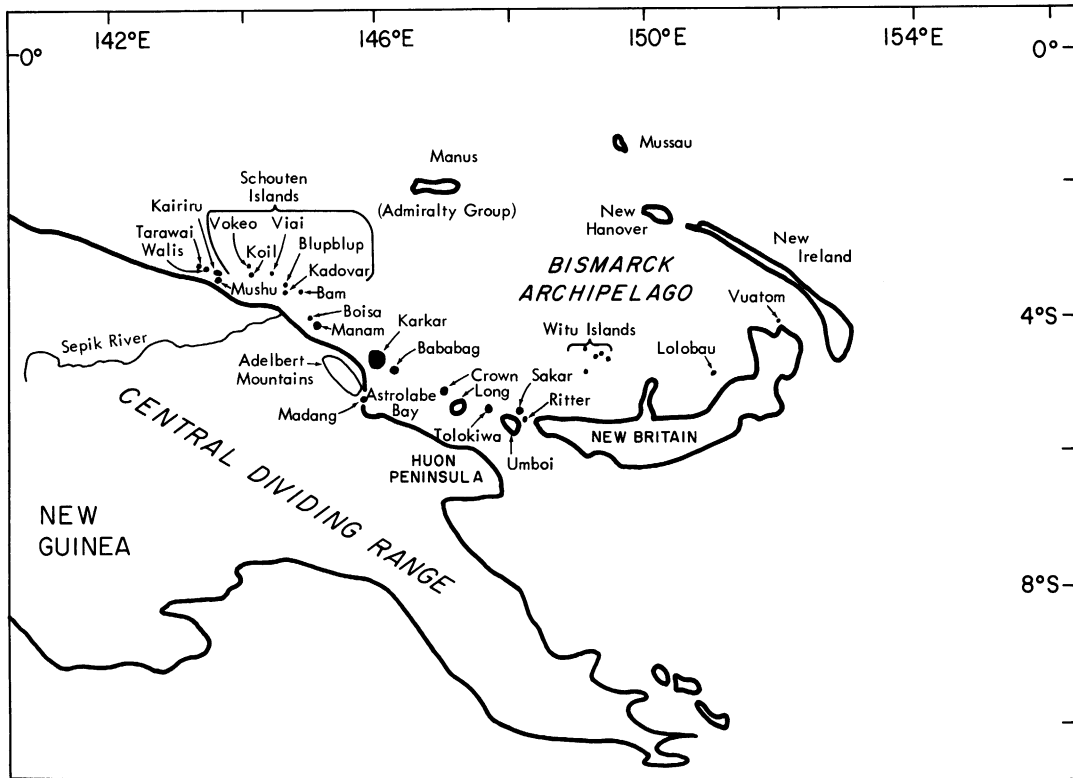


FIG. 1. Karkar and Bagabag belong to a chain of volcanic islands along the northeast coast of New Guinea and north New Britain, extending from the Schouten Islands in the west to Vuatom in the east.

bon-14 dates on carbonized wood in pyroclastic deposits on Karkar indicate further eruptions around 870 B.C. and in A.D. 520, 1130, and 1220. The age of Karkar's present fauna and flora is unknown, but the oral history of Karkar's human population implies that Karkar has not been defaunated within at least the past few centuries. The sole current volcanic activity on Karkar consists of the hot fields on Bagiai cone, and perhaps a recent small explosion at a low cinder cone (Ulumam) within the crater.<sup>1</sup>

Bagabag is an extinct volcano, probably an old stratovolcano. The central crater has a rim at 1400–1968 ft., with the highest point of 1968 ft. being on the western rim. The crater has been breached by the sea to the southeast at New Year Bay. From the crater rim, steep knife-edge ridges lead to the coast.

<sup>1</sup>There was an eruption on Karkar in March 1979.

Karkar is surrounded by water more than 200 m. deep, Bagabag by water more than 1000 m. deep. Hence neither island was connected to New Guinea or to each other during late-Pleistocene times when sea level was about 100 m. lower than at present.

Further geological details of Karkar and Bagabag, and the volcanic chain to which they belong, are given by Johnson, Taylor, and Davies (1972).

**CLIMATE:** Rainfall records are available for five stations on Karkar, all in the coastal lowlands (Brookfield and Hart, 1966; McAlpine, Keig, and Short, 1975). At all five stations annual rainfall averages between 136 and 160 inches, with the months June through September relatively drier and December through March relatively wetter. Although total annual rainfall varies little among these stations, the degree of seasonality does: northwest Karkar is



FIG. 2. Aerial photograph of Karkar caldera, showing the crater floor, crater outer wall, Bagiai cone, and vent near the top of the cone.

more seasonal (dry months drier, wet months wetter) than the rest of Karkar. The explanation may be a rainshadow effect from the central peak of Karkar in the path of the southeast trade winds. If a similar pattern of a more severe dry season on the northwest coast applies to neighboring islands for which rainfall records are unavailable, this may explain why several of these islands (Bagabag, Tolokiwa, Umboi, Crown) have extensive grassland confined to the northwest coast.

Rainfall data are unavailable for Bagabag and for inland locations on Karkar. We presume that rainfall increases with elevation as is true elsewhere in the tropical southwest Pacific and as suggested by abundant moss at high elevations on Karkar.

**HABITATS:** The dominant vegetation of both Karkar and Bagabag is rainforest, interspersed

in the lowlands with gardens and coconut plantations. The highest gardens on Karkar are at about 2000 ft. Human settlements on both islands are coastal (human population *ca.* 13,000 on Karkar, 500 on Bagabag, as of the 1960 census). Bagabag has an extensive grassland near Matiu II village on the north coast, and a small mangrove swamp at New Year Bay on the southeast coast. Karkar has several meandering rivers in the lowlands, numerous streams on the caldera, a small lowland swamp on the northeast coast, and a highland swamp at 5000 ft.

As one ascends Karkar, tree ferns and mossing appear around 2000 ft. At about 3500 ft. one is in forest up to 130 ft. tall, with an open canopy, heavy mossing on the trees, and many ferns in the understory. The most striking features of this forest are the abundance of tree



pandanus, limbun palms, and especially of climbing pandanus, which covers the tree trunks. On the crater rim at 4000 ft. the forest becomes distinctly two-storied: a middle story of tree pandanus and limbun palms at 20-40 ft., and buttressed canopy trees covered with climbing pandanus up to 130 ft. Tree pandanus disappears around 4500 ft. By 5000 ft. the forest is only 50 ft. tall, heavily mossed, and still with many limbun palms and much climbing pandanus. There is a swamp on the caldera rim at this elevation at the base of Mt. Kanagioi. The last 500 ft. below the summit of Mt. Kanagioi are covered with dense subalpine-like shrubbery 6-10 ft. tall, including *Rhododendron* sp., many ferns (*Gleichenia* sp.), and lycopodium.

The crater floor of Karkar is perhaps the most difficult terrain we have encountered anywhere: a "broken-bottle" field of sharp and brittle lava thrown into fissures and ridges up to 30 ft. deep or high. On this moonscape grows a pandanus forest with canopy at 20-40 ft., emergent trees over the canopy, understory shrubs 2-4 ft. tall, and a virtually empty middle story between the shrub layer and the pandanus crowns.

The forest at higher elevations (1500-1968 ft.) on the steep ridges of Bagabag is similar to that at about 1000 ft. higher on Karkar. Trees are up to 100 ft. tall and support climbing pandanus, though less than on Karkar. There are only a few tree ferns, tree pandanus, and limbun palms. At the summit itself trees are 30 ft. tall and heavily mossed, and there are many ferns (*Gleichenia* sp.) and much ginger.

**MAMMALS:** On Karkar and Bagabag, Diamond made small collections of mammals by mist-net, shotgun, and purchase of skulls from residents. In Diamond's collection the following species were recorded for Karkar (K) and/or Bagabag (B): the bandicoot *Echymipera kalubu* (K, B), phalangiers *Phalanger orientalis vulpecula* (the New Guinea race, not the Bismarck race *P. o. ducatoris*) (K, B) and *Petaurus breviceps* (B), wallaby *Thylogale bruijni* (B), rat *Rattus praetor* (K), megachiropteran bats *Rousettus amplexicaudatus stresemanni* (the New Guinea race, not the very distinct Bismarck race *R. a. brachyotis*) (B), *Pteropus hypomelanus* (K, B), *P. tonganus*

(K), *P. neohibernicus* (K), *Dobsonia moluccensis magna* (the New Guinea race) (K) and *D. m. anderseni* (the Bismarck race) (B), *D. minor* (B), *Macroglossus lagochilus* (K), *Syconycteris australis papuana* (the New Guinea race, not the Bismarck race *S. a. finschi*) (B), *Nyctimene major lullulae* (the race of Woodlark and probably Kiriwina, not the race *N. a. geminus* of east New Guinea and the Louisiades nor the race *N. m. major* of the Bismarcks) (K, B), and *N. albiventer* (B), and microchiropteran bat *Hipposideros galeritus*. There are surely more mammal species to be recorded from both islands.

All of these species have been recorded from the lowlands of northeast New Guinea opposite Karkar and Bagabag, except for *Pteropus tonganus* and *Nyctimene major*. The former is a supertramp bat species, comparable in its distribution to the four supertramp bird species that have colonized Karkar and Bagabag (p. 478). On species-poor Pacific archipelagoes distant from New Guinea *Pteropus tonganus* occurs on large as well as small islands (Samoa, Tonga, New Caledonia, New Hebrides). In the Solomons, however, it is confined to a single outlying island, Rennell; it is unknown from the Bismarcks; and in the New Guinea region it is known only from Karkar. *Nyctimene major* is presently known on the mainland of New Guinea from one dubious record from south of the Huon Peninsula, but not from the lowlands of northeast New Guinea opposite Karkar and Bagabag.

All these mammal species have also been recorded from New Britain, New Ireland, or nearby islands in the Bismarck Archipelago, except for *Dobsonia minor* (only New Guinea and Bagabag) and *Pteropus tonganus*. Evidently, certain mammal as well as bird species are disproportionately successful at crossing water gaps: if they reach Karkar and Bagabag, they are also likely to reach other islands.

The bat species of Karkar and Bagabag surely arrived by flying. The nonvolant mammal species may have also arrived unassisted by humans, by rafting on floating vegetation washed to sea from the Sepik River; or they may have been introduced by humans, accidentally as stowaways in canoes or as escaped pets, or intentionally.

## ACCOUNT OF FIELDWORK

Diamond's fieldwork on Karkar and Bagabag came as part of a five-month expedition during which he also made ornithological studies at Astrolabe Bay and Mt. Albert-Edward on New Guinea, on Cape Gloucester of west New Britain, and on the islands of Espiritu Santo (New Hebrides), Viti Levu and Ovalau (Fiji), and Upolu (Samoa). On May 17, 1969 Diamond made a reconnaissance flight from Madang (New Guinea) to Karkar and Bagabag in a small aircraft. The field party consisted initially of Diamond and four men from the New Guinea Highlands who had worked with Diamond on several previous expeditions and were expert in identification of New Guinea birds: Paran Aneyabu and Esa Tapani of Okapa, and Homuai Tom and Kariniga Male of Karimui. On May 26 the party flew to Karkar with supplies and equipment, went by tractor to Mom village at 800 ft. on the northwest flank of the caldera, and walked with carriers to a forest camp at 3400 ft. near the caldera's main drainage channel on the northwest flank. From this camp a trail led to the crater rim 540 ft. higher.

Between May 26 and June 3 the party, augmented by six Karkar men from Mom village, collected birds daily between 1925 ft. and an elevation of 4700 ft. on the crater rim. Collection of specimens was by mist-nets and shotguns. Diamond began by staking off the trail with an altimeter into zones each spanning an altitude range of a few hundred feet, so that the other expedition members could attribute their bird observations to these zones. Diamond constantly carried an altimeter with him. In this way the altitudinal ranges of montane bird species were worked out in detail. On May 30 the party climbed to the summit of Mt. Kanagioi. On June 1 they descended to the floor of the crater by an extremely steep path made by wild pigs, collected in the crater, and climbed the hot central cone Bagiai.

Assisted again by carriers, the party moved back down to Mom village on June 3 and made its base there until June 12. Each day Diamond

and his 10 associates set out by truck around the coastal road that makes the circuit of Karkar, and groups spent the day at different localities to observe and collect in the lowlands and on the lower flanks of the caldera. Sites to which particular attention was devoted included Duc, Bulu, areas of grassland, a swamp in the lowlands on the east, Miak and Mom in the lowlands of the northwest, Kol and Dor on the east flank of the caldera, and Kavailo on the south flank of the caldera up to 3500 ft. On June 9 botanists Jo van der Bergh and Elizabeth Mann from Lae Herbarium joined the party to make plant collections. On June 10 Diamond climbed again to the crater rim from Mom and up to 5000 ft. at the base of Mt. Kanagioi. Mist-nets were operated in the lowlands near Duc and Bulu throughout the period June 3-11.

On June 12 Diamond, his four Highlands associates, plus four of the Karkar men from Mom, transferred by ship to Bagabag, followed a day later by the two botanists. Base camp on Bagabag was on the south coast at Badilu village. Between June 12 and 18 observations and collections by mist-nets and shotguns were made on Bagabag. Diamond climbed to 1100 ft. on the south flank of Bagabag crater on June 14, climbed to one of the three summits (Mt. Tapati) on the west crater rim on June 15, and made a complete circuit of Bagabag on foot in the coastal lowlands on June 16. Collectors repeatedly visited the grassland at the northwest end of Bagabag. On June 18 the party departed Bagabag by ship, briefly touched at Karkar to leave the field helpers from Mom, and reached Madang late that day.

The total number of birds collected, including mist-netted specimens weighed and released alive, was 624 on Karkar and 209 on Bagabag. The number of mist-nets simultaneously in operation varied between 46 and 66. Mammals were also collected, mainly by mist-net (for bats) and purchase of trophy skulls from Karkar and Bagabag residents, occasionally by shotgun. All bird and mammal specimens collected

have been deposited in the American Museum of Natural History.

Diamond devoted all his time in the field to observations, while his associates collected and prepared specimens and also made observations. Diamond weighed each specimen and

recorded gonad condition and stomach contents. In the evening Diamond spent much time quizzing Karkar and Bagabag residents about their knowledge of birds, so that the bird surveys would be as complete as possible.

## ZOOGEOGRAPHIC ORIGIN OF THE AVIFAUNA

From the proximity of Karkar and Bagabag to the mainland of New Guinea one would expect the affinities of the avifauna to be with New Guinea. This usually proves to be the case. However, as the following summary shows, several populations were derived from the more distant Bismarck Archipelago. In a few cases where the colonization has been from New Guinea, it has been possible to determine which part of the adjacent mainland supplied the colonists. The details on which these statements are based are discussed below.

The following seven headings cover all the birds of Karkar and Bagabag except one species: *Megapodius freycinet affinis* x *eremita*. In this case, as discussed more fully in the species account, apparently both the New Guinea and the Bismarck Archipelago subspecies reached Karkar and Bagabag and hybridized.

1. Marine species  
*Fregata* sp.  
*Sterna bergii cristatus*
2. Migrant winter visitors from Australia  
*Chrysococcyx lucidus plagosus*  
*Halcyon s. sancta*  
*Merops ornatus*  
*Eurystomus orientalis pacificus*  
*Hirundo n. nigricans*  
*Coracina novaehollandiae* subsp.  
*Myiagra cyanoleuca*

Among these visitors, it is worth noting that *Eurystomus orientalis pacificus* is commoner in north New Guinea than in south New Guinea, and that *Myiagra cyanoleuca* may be commoner on islands off the northeast New Guinea coast than on the northeast New Guinea mainland.

3. Migrant winter visitors from the Palearctic region

- Pluvialis dominica* subsp.  
*Tringa hypoleucos*<sup>1</sup>  
*Cuculus saturatus horsfieldi*<sup>1</sup>  
*Motacilla cinerea caspica*<sup>1</sup>
4. Widespread race (or species, if monotypic), occurring both on New Guinea and the Bismarck Archipelago  
*Egretta s. sacra*  
*Accipiter meyerianus*  
*Gymnocrex p. plumbeiventris*<sup>1</sup>  
*Ptilinopus s. superbus*  
*Chalcophaps s. stephani*  
*Gallinula j. jobiensis*  
*Caloenas n. nicobarica*<sup>1</sup>  
*Scythrops novae-hollandiae*<sup>2</sup>  
*Caprimulgus macrurus yorki*  
*Aplonis cantoroides*  
*Erythrura trichroa sigillifera*
  5. New Guinea species which do not extend to the Bismarck Archipelago  
*Falco berigora novaeguineae*<sup>3</sup>  
*Ptilinopus magnificus puella* x *poliura*  
*Ducula pinon jobiensis*  
*Ducula zoeae*  
*Reinwardtoena reinwardtii*  
*Chalcophaps indica chrysochlora*  
*Loriculus aurantiifrons* subsp.  
*Chrysococcyx malayanus poecilurus*<sup>1</sup>  
*Tyto alba meeki*<sup>3</sup>  
*Ninox connivens assimilis*  
*Collocalia h. hirundinacea*  
*Ceyx azureus ochrogaster*  
*Tanyptera galatea meyeri*  
*Pitta sordida novae-guineae*<sup>3</sup>  
*Gerygone magnirostris affinis*

<sup>1</sup>Species recorded by Meek but not by Diamond.

<sup>2</sup>Probably only a migrant winter visitor from Australia.

<sup>3</sup>Reaches Long Island in the Bismarck Archipelago.



- Dicaeum pectorale rubrocoronatum*  
*Lonchura tristissima calaminoros*
6. Bismarck Archipelago species which do not extend to New Guinea  
*Macropygia mackinlayi arossi*  
*Vini rubrigularis*  
*Myzomela sclateri*
7. Species with different races on New Guinea and the Bismarck Archipelago
- 7a. In which the affinities of Karkar and/or Bagabag birds are with New Guinea  
*Aviceda subcristata megala*  
*Rallina tricolor tricolor*<sup>1</sup>  
*Amaurornis olivaceus moluccanus*  
*Ptilinopus rivoli bellus*  
*Ducula s. spilorrhoea*  
*Trichoglossus haematodus microp-  
 teryx* (Bagabag)  
*Micropsitta pusio beccarii*  
*Cacomantis variolosus oreophilus*  
*Eudynamis scolopacea rufiventer*  
*Collocalia e. esculenta*  
*Ceyx lepidus solitarius*  
*Eurystomus orientalis waigiouensis*  
*Hirundo tahitica frontalis*  
*Coracina tenuirostris muelleri*  
*Turdus poliocephalus keysseri*  
*Cisticola exilis diminuta*  
*Phylloscopus trivirgatus giulianetti*  
*Aplonis m. metallica*  
*Nectarinia s. sericea*  
*Nectarinia jugularis frenata*
- 7b. In which the affinities of Karkar and/or Bagabag birds are with the Bismarck Archipelago  
*Ducula pistrinaria rhodinolaema*<sup>1</sup>  
*Gallinolumba beccarii johannae*  
*Trichoglossus haematodus massena*  
*Monarcha cinerascens impediens*

Of the three species and four subspecies which have their affinities with the Bismarck Archipelago, four (*Myzomela sclateri*, *Monarcha cinerascens*, *Ducula pistrinaria*, and *Macropygia mackinlayi*) are supertramps (Diamond, 1974 and 1975a): i.e., species that have colonized many small islands but are competitively excluded as residents from large, spe-

cies-rich islands such as New Guinea and New Britain. *Myzomela sclateri* occurs on many small islands off New Britain and between New Britain and New Guinea without morphological differences and without having invaded either large island. If the subspecies *Monarcha cinerascens nigrirostris* proves invalid (see species account), then the Bismarck subspecies *impediens* will in fact occur occasionally on the New Guinea mainland. The area from Tarawai to the Huon Gulf is one of the few areas on the mainland where the species has been found. It also occurs on the north coast of the Vogelkop, and in that case the subspecies is the same (*inornatus*) as that occurring on the Aru Islands, Misol and Waigeu. Thus it seems that colonization of the mainland is from the offshore islands. There are a few occurrences of the species in southeastern New Guinea (New Guinea Bird Society Newsletter no. 60, Mt. Lawes and Takoa; and I. Weston, *in litt.*, netted at Kuriva), but the subspecific identity is not known. It has not been reported from the mainland of New Britain.

Three of the species with Bismarck affinities are pigeons. The fruit pigeon *Ducula pistrinaria* favors small islands. It is the subspecies *D. p. rhodinolaema* of the Admiralty Islands, rather than *D. p. vanwyckii* of islets near New Britain and New Ireland, that has colonized Karkar. *Ducula p. postrema* occurs on the islands off southeastern New Guinea, and there is a recorded sighting at Brown River (B. Coates, New Guinea Bird Society Newsletter no. 59).

The occurrence of the cuckoo-doves *Macropygia mackinlayi* and *M. nigrirostris* together on Karkar provides the first record of these two species occurring together as residents on an island (see Species Account under *nigrirostris*). It may be that the arrival of *nigrirostris* is recent as it was not obtained by Meek.

The ground doves *Gallinolumba beccarii* and *G. jobiensis* are sympatric over much of their range. However, the New Guinea subspecies *G. b. beccarii* is largely confined to the mountains, and it is the island race *G. b. johannae* from the Bismarck Archipelago that reached Karkar.

Two parrots, *Trichoglossus haematodus*

<sup>1</sup>Species recorded by Meek but not by Diamond.

and *Vini rubrigularis*, have also reached Karkar from the Bismarcks. The colonization of Karkar and Bagabag by different races of *Trichoglossus haematodus* is discussed fully in the Species Account, and provides the sole instance of subspecific differences between the Karkar and Bagabag populations of a species. *Vini rubrigularis* is part of the small mountain avifauna present on Karkar, and it is of interest that one of these few montane species should have affinities with the more distant Bismarck Archipelago.

When the source of colonization has been New Guinea, the actual area from which the colonists came can be pinpointed in a few cases.

*Ptilinopus magnificus puella* x *poliura*. Huon Peninsula birds are pure *poliura*; Astrolabe Bay birds are intermediate between *puella* and *poliura*. Apparently colonization was from Astrolabe Bay.

*Trichoglossus haematodus micropteryx*. It was the Huon Peninsula subspecies that colonized Bagabag, not *T. h. intermedius* of Astrolabe Bay and the Sepik Basin.

*Cacomantis variolosus oreophilus*. The subspecies *infaustus* only occurs as far eastward as the Sepik River in the north; *oreophilus* occurs from Astrolabe Bay eastward to southeastern New Guinea.

*Ceyx azureus ochrogaster*. The subspecies *ochrogaster* occurs in the north of New Guinea between the Mamberamo River and

Astrolabe Bay; *lessonii* occurs in the rest of New Guinea.

*Tanysiptera galatea meyeri*. The subspecies *meyeri* occurs between the Mamberamo River and Astrolabe Bay; the species is virtually absent between Astrolabe Bay and the Kumusi River; *minor* occurs east of the Kumusi River.

*Turdus poliocephalus keysseri*. This is the Huon Peninsula subspecies, not *T. p. erebus* of the Central Range. The species does not occur in the Astrolabe Bay area.

Rothschild and Hartert (1915a) considered the Karkar populations of *Vini* (= *Charmosyna*) *rubrigularis* and *Macropygia mackinlayi* (= *rufa*) to have differentiated to subspecific level. With the more extensive material available to us, we have found these endemic subspecies not to be valid. These cases are discussed in the respective species accounts.

In summary, the vast majority of the birds of Karkar and Bagabag are derived from New Guinea. They have come both from the Huon Peninsula and from Astrolabe Bay in the few cases where it is possible to tell. There is, however, a significant proportion of the avifauna (13%) derived from the Bismarck Archipelago, mostly species known to favor small islands and have great powers of dispersal. *Vini rubrigularis* is an exception; it is part of the small mountain avifauna of Karkar. We did not find an endemic element in the avifauna.

## SPECIES COMPOSITION OF THE LOWLAND AVIFAUNA

Table 1 lists those nonmarine bird species that breed in the New Guinea region or in the Bismarck Archipelago and were recorded on Karkar (by Diamond, Meek, or both) and/or on Bagabag (by Diamond). The occurrence of these species on eight other islands or island groups off New Guinea's north coast is also noted in the table.

A total of 60 resident species has been re-

corded from Karkar, Bagabag, or both. The main colonization source for these islands, New Guinea, has about 513 resident species. What prevented the missing 453 species from establishing themselves on at least the larger island, Karkar? Were the 60 successful colonists selected at random from the New Guinea species pool?

An obvious explanation for the absence of

TABLE 1  
**Distribution of Karkar and Bagabag Resident Bird Species on Other Islands off New Guinea's Northeast Coast**

	Karkar	Bagabag	New Britain	New Ireland	Long. Toloktiwa	Manam	Kairuru, Mushu	Madang islets	Schouten	Walis, Tarawai
<i>Egretta sacra</i>	+	+	+	+	+	—	+	—	—	+
<i>Aviceda subcristata</i>	+I	—	+	+	—	—	+	—	—	+
<i>Haliastur indus</i>	+I	+	+	+	+	+	+	—	+	+
<i>Accipiter meyerianus</i>	+I	+	+	—	—	—	+	—	—	+
<i>Haliaeetus leucogaster</i>	+I	+	+	+	+	—	+?	—	+	+
<i>Falco berigora</i>	+	—	—	—	+	+	+?	—	+?	+
<i>Megapodius freycinet</i>	+	+	+	+	+	—	+	+	+	—
<i>Rallina tricolor</i>	+E	—	—	+	—	—	—	—	—	—
<i>Gymnocrex plumbeiventris</i>	+E	—	—	+	—	—	—	—	—	—
<i>Amaurornis olivaceus</i>	+I	—	+	+	+	—	+?	+	—	—
<i>Ptilinopus superbus</i>	+I	+	+	+	+	+	+	+	+	—
<i>Ptilinopus iozonus</i>	+I	—	[+]	[+]	[+]	—	+	—	—	+
<i>Ptilinopus rivoli</i>	+I	—	—	—	[+]	—	—	—	—	—
<i>Ptilinopus magnificus</i>	+	+	—	—	—	+	+	—	—	—
<i>Ducula pistrinaria</i>	+E	—	+	+	+	+	+	+	+	+
<i>Ducula spilorrhoa</i>	+E	+	[+]	[+]	—	+	+	+	+	—
<i>Ducula pinon</i>	+E	+	—	—	—	—	—	—	—	—
<i>Ducula zoeae</i>	+I	—	—	—	—	—	—	—	—	—
<i>Macropygia nigrirostris</i>	+I	—	+	+	—	(+)	(+)	—	(+)	—
<i>Macropygia mackinlayi</i>	+I	—	+	—	+	—	—	—	—	—
<i>Reinwardtoena reinwardtii</i>	+I	—	[+]	[+]	—	—	—	—	—	—
<i>Chalcophaps indica</i>	—	+	—	—	—	+	—	+	—	—
<i>Chalcophaps stephani</i>	+	+	+	+	+	—	+	+	+	+
<i>Gallinolumba beccarii</i>	+	—	+	+	—	—	+	—	—	—
<i>Gallinolumba jobiensis</i>	+	+	+	+	—	+	+	+	—	—
<i>Caloenas nicobarica</i>	+E	—	+	+	+	—	+	+	+	—
<i>Trichoglossus haematodus</i>	+	+	+	+	+	+	+	+	+	—
<i>Vini rubrigularis</i>	+	—	+	+	(+)	—	+	—	—	—
<i>Micropsitta pusio</i>	+	+	+	+	+	+	+	—	+	—
<i>Loriculus aurantiifrons</i>	+I	—	[+]	[+]	—	—	—	—	—	—
<i>Cacomantis variolosus</i>	+	+	+	+	+	+	+?	+	+	+
<i>Chrysococcyx malayanus</i>	+E	—	—	—	—	+	+?	+	+?	+
<i>Eudynamis scolopacea</i>	+	+	—	+	+	+	+?	—	+	+
<i>Tyto alba</i>	+	—	—	—	+	+	—	—	—	—
<i>Ninox connivens</i>	+	+?	—	—	—	+	—	—	—	—
<i>Caprimulgus macrurus</i>	+	—	+	+	—	—	—	—	—	—
<i>Collocalia esculenta</i>	+	+	+	+	+	—	+	+	+	+
<i>Collocalia hirundinacea</i>	+	—	(+)	(+)	(+)	—	—	—	—	—
<i>Ceyx azureus</i>	+	—	[+]	[+]	—	—	+	—	—	—
<i>Ceyx lepidus</i>	+	—	+	+	—	—	+	—	—	—
<i>Tanyptera galatea</i>	+	+	(+)	—	—	+	—	—	—	+
<i>Eurystomus orientalis</i>	+	+	(+)	+	+	—	—	—	—	+



many of these species is the absence of suitable habitats for them on Karkar. Karkar lacks lakes, savannas, and elevations above 6000 ft., and has only two small swamps, a few small rivers, and a modest area of montane forest at 2000-6000 ft. New Guinea has a rich variety of birds restricted to each of these habitats. Karkar thus has no species characteristic of any of these habitat types except a few montane species.

However, habitat differences account for only part of the avifaunal differences between Karkar and New Guinea. On the portion of the New Guinea mainland (Astrolabe Bay) opposite Karkar and only 10 miles away, about 228 bird species have been recorded in lowland forest and open habitats apparently similar to those on Karkar. This list excludes species of lakes, savannas, swamps, and rivers. Only about 46 of these 228 species occur on Karkar. Some of the missing 182 species may perhaps have subtle habitat requirements not satisfied on Karkar, but many of them occupy a sufficiently broad range of habitats on New Guinea that habitat considerations surely cannot explain their absence on Karkar. A similar question is posed by the avifaunas of the other islands along New Guinea's north coast. As summarized in table 1, all these islands have far fewer species (25-127) than occur at Astrolabe Bay on New Guinea. The number of species increases with the area of the island. The actual numbers of lowland bird species resident on Karkar and Bagabag in 1969, 44 and 29 respectively, agree well with the values of 45 and 27 predicted for these islands from their areas of 142 and 14.4 square miles and the species/area relation for New Guinea oceanic islands generally. This relation is:  $S = 15.1 A^{0.22}$ , where S is the number of lowland resident bird species and A is island area in square miles (Diamond, 1972b). However, even the largest and highest one of these north-coast islands, New Britain, has less than half the number of bird species occurring in an equivalent area around Astrolabe Bay (the 228 forest and open-country species, plus water, swamp, and montane species).

Table 1 also indicates, for each of these north-coast islands, how many of its bird species are actually shared with Karkar, and how

many would be shared if its species and Karkar's species were randomly drawn from the 228 forest and open-country species that constitute the potential colonist pool at Astrolabe Bay. For example, of Bagabag's 29 species, 27 are actually shared with Karkar and its 58 species, but only seven would be expected to be shared if colonists for each island had been selected at random ( $(58/228) \times 29 = 7$ ). Corresponding figures for Manam are 35 species present, 29 actually shared with Karkar, nine expected to be shared if colonization were random ( $(58/228) \times 35 = 9$ ). Evidently, some species in the colonist pool are consistently good colonists, whereas others are consistently poor colonists. These unexpectedly high proportions of shared species have arisen mainly because certain species independently colonize islands from New Guinea again and again, and not merely because of colonization from one island to another. Certainly, Bagabag is twice as close to Karkar as to New Guinea and may have received more colonists from Karkar, despite New Guinea's far greater size. However, each of the other islands listed in table 1 is nearer to New Guinea than to the other eight islands. In some cases subspecific affinities of the island populations prove that the islands were colonized independently of each other (cf. taxonomic discussion of *Trichoglossus haematodus* populations on Karkar and Bagabag in Species Accounts).

Examination of species lists for these islands immediately shows which species are the most successful colonists. At the one extreme, the best colonists are *Megapodius freycinet*, *Cacomantis variolosus*, *Eudynamis scolopacea*, and *Nectarinia jugularis*, present on all 10 islands or island groups. Nearly as good colonists are *Egretta sacra*, *Haliastur indus*, *Haliaeetus leucogaster*, *Ptilinopus superbus*, *P. iozonus*, *Ducula spilorrhoea*, *Chalcophaps stephani*, *Trichoglossus haematodus*, *Micropsitta pusio*, *Collocalia esculenta*, *Hirundo tahitica*, *Monarcha cinerascens*, *Myiagra alecto*, *Aplonis metallica*, and *Nectarinia sericea*, present on all but one or two of the islands. At the opposite extreme are the numerous New Guinea species that have failed to colonize any of these nine islands. In fact, 134 of New Guinea's 325

lowland bird species not only have failed to reach these 10 islands, but also have failed to reach any of the hundreds of other oceanic islands (islands lacking Pleistocene land bridges to New Guinea) that surround New Guinea—even small islands within a mile of New Guinea and large islands within 5-10 miles of New Guinea. These 134 species include many common, widespread species of the New Guinea lowlands, such as *Melidora macrorrhina*, *Eupetes caerulescens*, *Crateroscelis murina*, *Pitohui kirhocephalus*, *Meliphaga aruensis*, and *Melanocharis nigra*. There are no taxonomic patterns to colonizing success: for many good colonists one can cite congeners or close relatives that have never colonized an island overwater from New Guinea, despite being abundant on New Guinea. Examples of these surprising contrasts, citing the good colonist first and the universally unsuccessful colonist second in each case, are: *Megapodius freycinet* vs. the *Talegalla* superspecies; *Ptilinopus iozonus* and *P. superbus* vs. *P. pulchellus*; *Ducula pinon*, *D. zoeae*, and *D. spilorrhoea* vs. *D. rufigaster*; *Gallicolumba jobiensis* and *G. beccarii* vs. *G. rufigula*; *Trichoglossus haematodus* vs. *Pseudeos fuscata* and the *Chalcopsitta* superspecies; *Coracina tenuirostris* vs. *C. melaena*; *Gerygone magnirostris* vs. *G. chrysogaster* and *G. palpebrosa*; and *Monarcha cinerascens* vs. *M. frater*, *M. telescopthalmus*, and *M. manadensis*. In some of these cases the species listed as a poor colonist does occur on some islands with Pleistocene land bridges to New Guinea (e.g., Aru, Japen,

Batanta, Salawati, Misol, Waigeu), but these colonizations probably occurred over the former land bridge rather than overwater. To prevent confusion, we note explicitly: it is *not* the case that these unsuccessful colonists occasionally reach islands and fail to establish breeding populations. Instead, they have never even been recorded from a single oceanic island off New Guinea.

Thus, part of the reason why Karkar has fewer species than New Guinea, why the north-coast islands share far more species than one would expect as a random selection of the colonist pool, and why species differ consistently in colonizing success, is that species differ enormously in dispersal ability (Diamond, Gilpin, and Mayr, 1976). Some species refuse to cross water gaps of a fraction of a mile, whereas others regularly cross gaps of dozens of miles. These differences in dispersal ability arise only in part because some species are stronger fliers than others: the reasons are partly behavioral, since many species that never cross water gaps are strong fliers overland (*Harpyopsis novaeguineae*, *Pseudeos fuscata*, *Chalcopsitta* superspecies: see Diamond, 1972b, 1976, for further discussion). Differences in dispersal ability in turn provide only part of the explanation for differences in colonizing ability, as species may differ in probability of colonizing success for reasons that become important only after colonists have reached an island (e.g., reproductive potential, philopatry, ecological amplitude, and ability to shift into a new habitat).

## MONTANE AVIFAUNA OF KARKAR

Figure 3 depicts altitudinal ranges of all 52 species resident on Karkar in 1969, plus three of the commonest migrants. This figure has been used to construct figure 4, which depicts number of species as a function of altitude from sea-level to the summit.

Figure 4 shows that species number decreases fairly regularly with altitude, from 46 species at sea level to three species at the summit. Similar results have been obtained for bird distributions on mountains elsewhere in the

humid tropics, such as New Guinea (Diamond, 1972a) and Peru (Terborgh, 1971). Probably the two main reasons for the decrease in species number with altitude are that: (a) bird species diversity generally is highest in complexly structured habitats (MacArthur, Recher, and Cody, 1966), and habitat structural complexity as measured by foliage height diversity and forest height decreases with altitude; (b) area of available habitat decreases with altitude.

If ceilings and floors of species' altitudinal



### BIRD ALTITUDINAL RANGES ON KARKAR

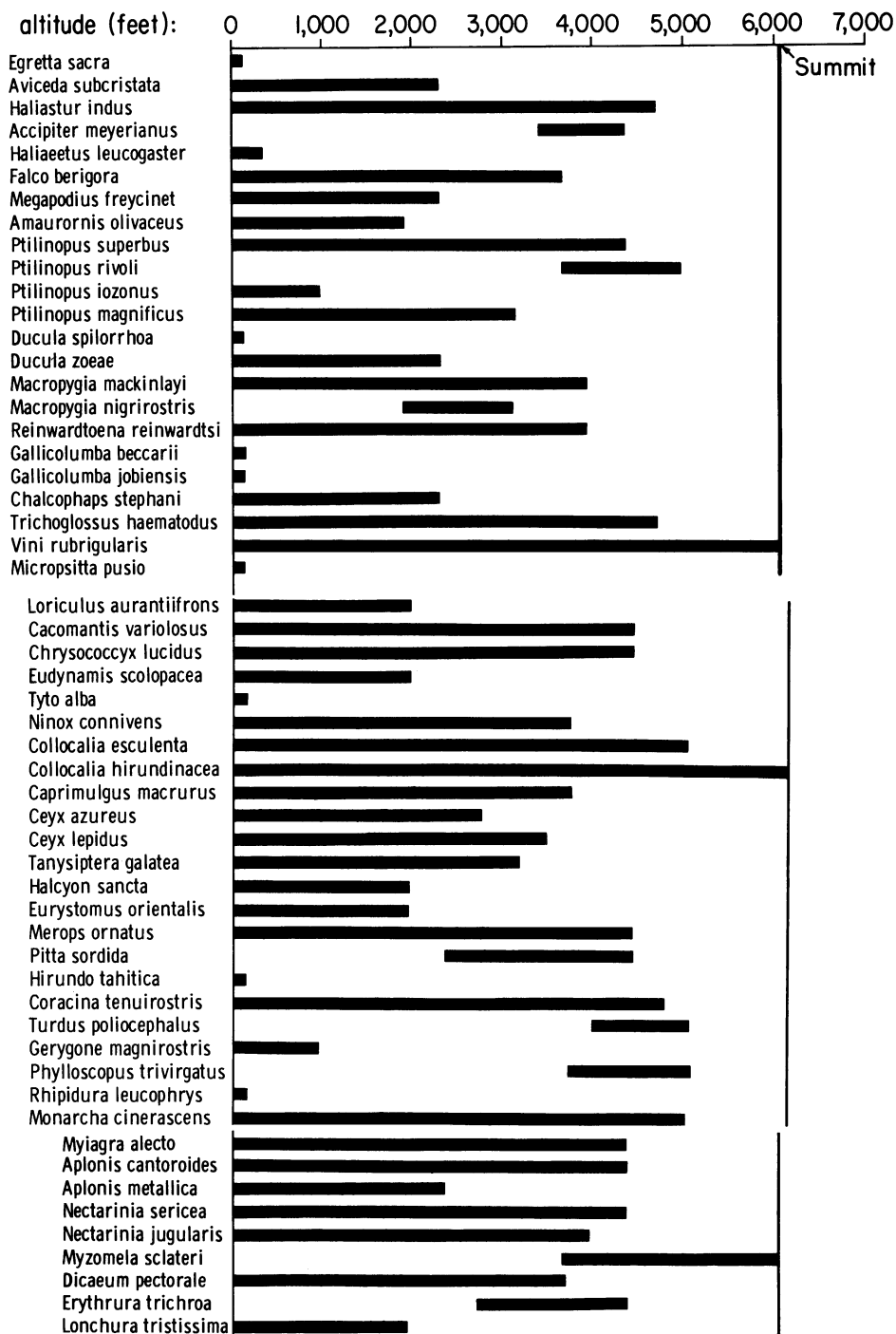


FIG. 3. Altitudinal ranges of the 52 species resident on Karkar in 1969, plus the three commonest migrants (*Chrysococcyx lucidus*, *Halcyon sancta*, *Merops ornatus*). The figure is based on observations by Diamond and his field associates along an altitudinal transect from sea level to Karkar's summit. Observations were recorded

ranges tended to clump at certain altitudes, it would be convenient to recognize altitudinal zones for bird distribution. Examination of figures 3 and 4 shows that zones are not well marked on Karkar: species' altitudinal limits are distributed over the whole altitudinal gradient, with perhaps four weak suggestions of clumping. These are as follows: 1. There is a slight accumulation of ceilings in the lowlands, associated with coastal species (*Egretta sacra*, *Haliaeetus leucogaster*, *Ducula spilorrhoa*, *Hirundo tahitica*, *Rhipidura leucophrys*) that do not reach the lowest inland station surveyed

(940 ft.). For this reason the drop in species number between sea level and 940 ft. is perhaps slightly steeper than between 940 and 4000 ft. 2. There is another accumulation of species ceilings around 2300 ft., corresponding to the lower limit of unbroken forest and hence the upper limit for open-country species (*Aviceda subcristata*, *Amaurornis olivaceus*, *Loriculus aurantiifrons*, *Halcyon sancta*, *Eurystomus orientalis*, *Aplonis metallica*, *Lonchura tristissima*). 3. There is a slight accumulation of species floors around 3500 ft., where *Ptilinopus rivoli*, *Phylloscopus tri-*

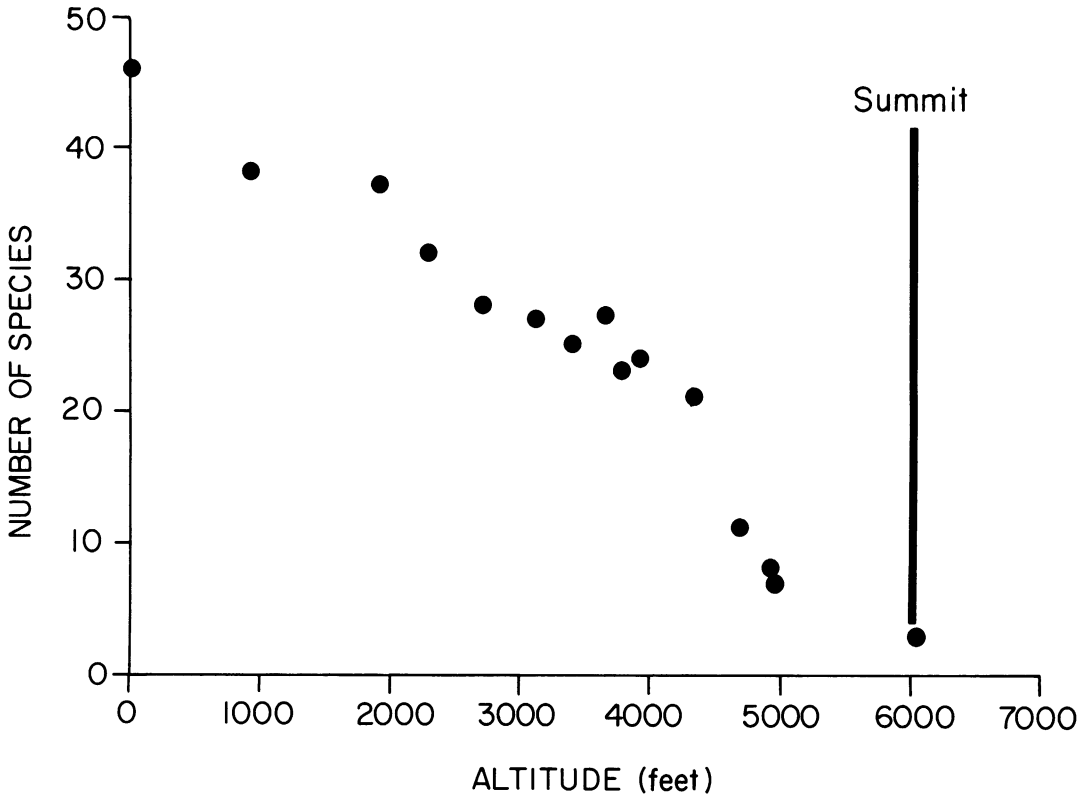


FIG. 4. Number of bird species as a function of altitude on Karkar. This figure is based on the species altitudinal ranges depicted in figure 2.

by altitudinal zones 120-420 vertical feet in extent above 1925 ft., and by three broader altitudinal zones at lower elevations. In constructing this figure, we assumed that species altitudinal ranges are continuous: if a species was recorded above and below but not at a certain elevation, it was assumed to be present at that elevation but to have been overlooked. For the purposes of this figure we have ignored several observations of a single individual of a species far beyond the altitudinal limit for other observations of that species.

*virgatus*, and *Myzomela sclateri* reach their lower limits. 4. There are no species floors above 3800 ft., where *Turdus poliocephalus* reaches its lower limit. Presumably the reason is that the area at high elevations on Karkar is sufficiently small so that a montane species could not maintain a large enough population to ensure continued existence if its floor lay much above 3500 ft.

Karkar has a small montane avifauna of eight species that are confined to the mountains and fail to reach sea level: *Accipiter meyerianus*, *Erythrura trichroa*, *Myzomela sclateri*, *Ptilinopus rivoli*, *Collocalia hirundinacea*, *Pitta sordida*, *Turdus poliocephalus*, and *Phylloscopus trivirgatus*. As discussed in the preceding section on zoogeographic origins of the avifauna, the first two of these species could have arrived either from New Guinea or from the Bismarcks, *Myzomela sclateri* must have arrived from the Bismarcks, and the other five species must have arrived from New Guinea. For southwest Pacific islands generally, the number of montane populations is found to equal 2.7 percent of the species number at sea level, multiplied by the island elevation in feet and divided by 1000 (Diamond, 1972b). For Karkar this formula predicts seven montane populations ( $0.027 \times 44 \times 6007 \div 1000 = 7$ ), in good agreement with the observed eight.

How did these eight species reach the mountains of Karkar? Of the four mechanisms distinguished by Mayr and Diamond (1976) for the origin of montane bird populations, two account for all the montane populations of Karkar. Six of the eight montane populations (all except *Pitta sordida* and *Myzomela sclateri*) "jumped" directly into the mountains of Karkar from the mountains of New Guinea or New Britain. That is, they are derived from montane populations on these two source islands by direct overwater colonization flights into the mountains of Karkar. *Myzomela sclateri*

reached the mountains of Karkar by a "push-pull shift." That is, it is derived from a lowland population on islets off north New Britain; it was pushed into the mountains of Karkar by competition from the sunbirds *Nectarinia sericea* and *N. jugularis* in the lowlands, and it was pulled into the mountains by the availability of nectar and insect resources exploited by few bird species at high elevations on Karkar. *Pitta sordida* is similarly derived from a lowland population on New Guinea, but it is difficult to discern any competition-based reasons for its absence from the lowlands of Karkar.

One other colonist of Karkar that jumped in directly from a source montane population is *Vini rubrigularis*, otherwise confined to the mountains of three large Bismarck islands (New Britain, New Ireland, New Hanover) by competition from the very similar *V. placentis* in the lowlands of these islands. *V. placentis* is absent from Karkar, so that *V. rubrigularis* descends to the lowlands of Karkar.

Thus, there are seven montane species that colonized Karkar directly. This contrasts with the situation for southwest Pacific ants, as emphasized by Wilson (1961) in his classic paper on taxon cycles. According to Wilson, montane ant populations in the Pacific are generally endemic forms derived from coastal lowland ancestors. Evidently, montane birds are better colonists than montane ants, though worse colonists than lowland birds.

In addition to these eight montane populations on Karkar, many of the bird individuals encountered in montane forest on Karkar belong to species also present in lowland forest on Karkar (cf. altitudinal ranges of *Cacomantis variolosus*, *Coracina tenuirostris*, and *Monarcha cinerascens*), although the New Guinea populations of these species are absent from montane forest. These species will be discussed further in the section on niche shifts.

Bagabag is too low to have any bird population confined to higher elevations.

## SPECIES TURNOVER ON KARKAR

Within the past decade there has been increasing recognition of the fact that biotas are not static but turn over as local populations

fluctuate out of existence and are founded by immigrants, Species turnover is expected even in old, stable environments. Considerations of

how immigration rates and extinction rates of species may vary with island area and distance have been invoked by MacArthur and Wilson (1967), in their well-known equilibrium theory of island biogeography, to interpret why the number of species on an island increases with island area and proximity to the colonization source.

Several authors have estimated species turnover rates for island bird communities by comparing thorough species surveys in different years (Diamond, 1969b and 1971; Terborgh and Faaborg, 1973; Jones and Diamond, 1976; Diamond and May, 1977). Diamond (1971) previously estimated species turnover in this way for Karkar by comparing his 1969 survey with Meek's in 1914. In this section we provide an updated discussion of turnover on Karkar. The 1914-vs.-1969 comparison provides only a minimum estimate of turnover on Karkar, as annual surveys have revealed that island bird surveys at an interval of several decades underestimate turnover rates by about an order of magnitude, due to the same species repeatedly immigrating and becoming locally extinct over the course of several decades (Jones and Diamond, 1976; Diamond and May, 1977).

How complete were the 1914 and 1969 surveys? If they were incomplete, differences between their species lists might not reflect true turnover but merely the chance of which species happened to be recorded in which year though present in both years.

The 1969 survey party consisted of 11 members, six of them residents of Karkar, and all of them thoroughly familiar with New Guinea birds. In addition to recording species by sight and call, we collected with two shotguns and 46 to 66 mist-nets daily. We repeatedly visited all major habitat types on Karkar from sea level to the summit, including the small areas of swamp, grassland, and riverine habitat. As it turned out, no species on Karkar was restricted to a small, specialized habitat. Most species had a widespread distribution in forested or open habitats or both, except for the five coastal species. Even the montane species had altitudinal ranges spanning at least 1000 vertical feet, usually more. Availability of motorized transport let us examine all sides of Karkar. Many residents of Karkar gave extensive ac-

counts of bird species that they had observed on Karkar. We eventually succeeded in observing ourselves all species they reported except for the Barn Owl *Tyto alba*, which was described by numerous Karkar residents and which had already been collected on Karkar in 1914. Of the remaining 51 species recorded in 1969, we observed or collected all repeatedly. Hence the 1969 survey was probably virtually complete.

The completeness of the 1914 survey must be assessed indirectly, as Meek's party collected specimens but provided no field notes. Meek was the most experienced collector of his generation in the New Guinea area and spent several decades obtaining birds and butterflies for the Rothschild Museum at Tring, England. He did not visit Karkar himself but sent his boat, collectors, and crew, who spent about three months on Karkar. The 1969 party found five species virtually confined on Karkar to elevations above 3000 ft.: *Accipiter meyerianus*, *Turdus poliocephalus*, *Ptilinopus rivoli*, *Phylloscopus trivirgatus*, and *Myzomela sclateri*, of which the last three were common or abundant. Of these five, Meek's collectors obtained only *Myzomela sclateri*, which may undertake seasonal altitudinal movements like many other nectarivorous species. Hence it is safe to assume that the 1914 party did not ascend over 3000 ft. However, it must have reached lower elevations in the hills, as it collected all three montane species (*Collocalia hirundinacea*, *Pitta sordida*, *Erythrura trichroa*) whose floors the 1969 party found to lie between 940 and 2200 ft. Undoubtedly, there would have been some lowland species that the 1914 party would have observed without being able to collect. We conclude that the 1914 collection represents a fairly adequate sample of the lowland and hill avifauna but not of the high-elevation avifauna.

Let us therefore compare the list of 43 species obtained in 1914 with the list of 48 (omitting the four high-altitude species) obtained in 1969. As indicated in table 1, six species were recorded in 1914 but not 1969: *Rallina tricolor*, *Gymnocrex plumbeiventris*, *Ducula pistrinaria*, *D. pinon*, *Caloenas nicobarica*, and *Chrysococcyx malayanus*. Eleven species (ignoring the high-altitude species *Accipiter meyerianus*, *Ptilinopus rivoli*, *Turdus pol-*

*iocephalus*, and *Phylloscopus trivirgatus*) were recorded in 1969 but not 1914: *Aviceda subcristata*, *Haliastur indus*, *Haliaeetus leucogaster*, *Amaurornis olivaceus*, *Ptilinopus iozonus*, *Ducula zoeae*, *Macropygia nigrirostris*, *Reinwardtoena reinwardtii*, *Loriculus aurantiifrons*, *Coracina tenuirostris*, and *Rhipidura leucophrys*. *Prima facie*, this comparison suggests six extinctions and eleven immigrations between 1914 and 1969. Are these changes real, or are they merely artifacts from species having been overlooked by one of the two surveys?

Of the six species recorded in 1914 but not 1969, three could scarcely have been missed if present in 1969: the pigeons *Ducula pinon*, *D. pistrinaria*, and *Caloenas nicobarica*. These are among the best known and most conspicuous species of the New Guinea region. The first two call loudly and frequently. Many Karkar residents were familiar with these species from other islands and stated that they did not presently occur on Karkar. The rails *Rallina tricolor* and *Gymnocrex plumbeiventris* are much more inconspicuous but are sufficiently distinctive to be familiar to New Guinea villagers in regions where they occur. Karkar villagers told us correctly that we would instead find a third, equally shy rail on Karkar, *Amaurornis olivaceus*. The cuckoo *Chrysococcyx malayanus* is also inconspicuous but must have formerly been fairly common on Karkar, as the 1914 party took three specimens, all on different dates. Thus, of these six species, at least three, probably more, and possibly all represent real local extinctions.

Of the 11 lower elevation species recorded in 1969 but not 1914, some were probably present in 1914 but escaped collection, as suggested by the excess of apparent immigrations (11) over apparent extinctions (6). In particular, the eagle *Haliaeetus leucogaster* can be difficult to collect. At the opposite extreme, the small hawk *Aviceda subcristata*, the pigeon *Reinwardtoena reinwardtii*, the Cicada Bird *Coracina tenuirostris*, and the Willie Wagtail *Rhipidura leucophrys* are conspicuous, noisy, easily collected species unlikely to have escaped the 1914 party if present then. The patchy distributions of *Ptilinopus iozonus*, *Ducula zoeae*, and *Macropygia nigrirostris* in 1969 suggest that they

may have reached Karkar recently and not yet occupied all available habitat. Thus, of these 11 species, probably some but not all represent real immigrations.

Could these changes be due to habitat alteration or effects of man? Karkar has been populated by humans since the time of the earliest written records, so that there were already gardens and open habitats in 1914, but large areas of forest remained in 1969. There was no volcanic activity on Karkar between 1914 and 1969 outside the thermal fields on Bagioi cone. The species changes do not represent gains by one habitat and losses by another. Instead, two fruit pigeons of the forest canopy disappeared (*Ducula pinon* and *D. pistrinaria*) and were replaced by two others (*D. zoeae* and *Ptilinopus insolitus*); two ground-dwelling rails disappeared (*Rallina tricolor* and *Gymnocrex plumbeiventris*) and were replaced by another (*Amaurornis olivaceus*). The possibility that human activities and habitat changes played a role can never be excluded, but the species changes fail to provide support for this possibility.

Could the changes have involved nonbreeding vagrants rather than breeding populations? This question cannot be answered with certainty, as the 1914 and 1969 parties obtained firm proof of breeding for few species. These include one of the putative immigrants (*Reinwardtoena reinwardtii*) and one of the putative extinct species (*Gymnocrex plumbeiventris*), both collected at the nest. Of the other 10 putative immigrants, seven were singing, one was collected with enlarged gonads, five were common and widespread over Karkar, and four were observed at several widely scattered sites. Karkar villagers were familiar with most of these birds as resident species of Karkar. Only in the case of the eagle *Haliaeetus leucogaster*, of which we observed individuals on several occasions, does the question of a nonbreeding individual not seem implausible.

The faunal turnover rate (the percentage of island species turning over per year) may be calculated as  $100(I + E)/t(S_1 + S_2)$ , where  $S_1$  and  $S_2$  are the total number of species recorded in the earlier and later censuses, respectively,  $t$  is the number of years between surveys, and  $I$

and E are the number of apparent immigrations and extinctions based on comparing the species lists for the two years. For the 1914 and 1969 surveys of Karkar,  $I = 11$ ,  $E = 6$ ,  $S_1 = 43$ ,  $S_2 = 48$ ,  $t = 55$  years. This yields an apparent turnover rate of  $100(11 + 6)/55(43 + 48) = 0.34\%/year$ . That is, on the average apparently 0.34% of Karkar's bird populations fluctuate out of existence each year and are replaced by a corresponding number of immigrant species—or, one species replacement every seven years. The immigration rate may also be expressed relative to the available New Guinea pool of colonists: the 228 lowland bird species of Astrolabe Bay, of which 33 were actually present on Karkar in 1914. The percentage of this available pool that immigrated to Karkar in the period 1914-1969 was  $(100)(11)/(228-33)(55) = 0.1\%/year$ .

As mentioned before, annual censuses of other islands suggest that the true values of the turnover rate and immigration rate are probably

an order of magnitude higher, because comparisons of surveys 55 years apart do not show immigrations reversed by extinctions (and vice versa) between the censuses (Jones and Diamond, 1976; Diamond and May, 1977). Turnover rates of temperate-zone islands surveyed at 1-year intervals are mostly 2-20%/year, comparable to what the Karkar value would be if the estimate of 0.34%/year were an underestimate by an order of magnitude. Values similar to the Karkar turnover estimate have been obtained for three other tropical islands similarly surveyed at intervals of several decades: Mona, 0.23%/year (Terborgh and Faaborg, 1973); Long, 0.18%/year (Diamond, 1974); Vuatom, 0.40%/year (Diamond, 1975a).

Obviously, our analysis gives only the grossest estimate of turnover on Karkar. Repeated surveys of tropical islands at one-year intervals are needed to assess how turnover on tropical and temperate islands differs.

## NICHE SHIFTS

Karkar and Bagabag support only a fraction of the bird species that occur in similar habitats on New Guinea or New Britain. Those species that did succeed in establishing themselves on Karkar or Bagabag face many fewer competing species than they encounter in the source region. Freed of these competitors, more than half of the successful colonists have expanded their populations, by utilizing resources that would otherwise have gone to the missing competitors. As a result, many of the species occurring in lowland forest and in montane forest on Karkar are ones confined to other habitats on New Guinea.

For example, the interior of lowland rainforest supports about 90 species at Astrolabe Bay on the New Guinea mainland but only 27 species on Karkar. Of those 27 species, only 16 occur in lowland forest on New Guinea (or on New Britain, in the case of species derived from New Britain). The other 11 species are derived from other habitats on the source island: two from montane forest (*Gallicolumba beccarii* and *Vini rubrigularis*), two from off-

shore islets (*Macropygia mackinlayi* and *Monarcha cinerascens*), and seven from open habitats, second growth, and forest edge (*Cacomantis variolosus*, *Ninox connivens*, *Coracina tenuirostris*, *Myiagra alecto*, *Aplonis metallica*, *Nectarinia jugularis*, and *N. sericea*).

Similarly, montane forest at 4000 ft. supports about 90 species on New Guinea's Central Dividing Range but only 23 species on Karkar. Only six of these 23 species are montane on the source island, the other 17 being confined to the lowlands there. At 5000 ft. Karkar is even more impoverished: about 65 species on New Guinea's Central Range, eight species on Karkar, three of these eight species being ones that are confined to the lowlands on New Guinea or New Britain.

For each species on Karkar, table 2 summarizes whether and how it has expanded its niche, compared to the niche it occupies on New Guinea or New Britain. The results of this table may be described in more detail as follows:

Fourteen species have expanded their range



TABLE 2  
Types of Niche Shifts in Karkar Bird Species

	Altitude	Habitat	Vertical	Diet	Abundance	No shifts detected
<i>Egretta sacra</i>	—	—	—	—	—	+
<i>Aviceda subcristata</i>	—	—	—	—	+	—
<i>Haliastur indus</i>	—	—	—	—	—	+
<i>Accipiter meyerianus</i>	—	—	—	—	—	+
<i>Haliaeetus leucogaster</i>	—	—	—	—	—	+
<i>Falco berigora</i>	—	—	—	—	—	+
<i>Megapodius freycinet</i>	—	—	—	—	—	+
<i>Amaurornis olivaceus</i>	—	—	—	—	—	+
<i>Ptilinopus superbus</i>	—	—	↓	—	+	—
<i>Ptilinopus rivoli</i>	—	—	—	—	+	—
<i>Ptilinopus iozonus</i>	—	—	—	—	—	+
<i>Ptilinopus magnificus</i>	—	—	↓	—	—	—
<i>Ducula spilorrhoea</i>	—	—	—	—	—	+
<i>Ducula zoeae</i>	—	—	—	—	—	+
<i>Macropygia mackinlayi</i>	↑	→ inland	—	—	—	—
<i>Macropygia nigrirostris</i>	—	—	—	—	—	+
<i>Reinwardtoena reinwardtii</i>	—	—	—	—	+	—
<i>Gallicolumba beccarii</i>	↓	—	—	—	—	—
<i>Gallicolumba jobiensis</i>	—	—	—	—	—	+
<i>Chalcophaps stephani</i>	—	→ coast	—	—	—	—
<i>Trichoglossus haematodus</i>	—	—	—	—	+	—
<i>Vini rubrigularis</i>	↓	—	—	—	—	—
<i>Micropsitta pusio</i>	—	—	—	—	—	+
<i>Loriculus aurantifrons</i>	—	—	—	—	+	—
<i>Cacomantis variolosus</i>	—	→ forest	—	—	—	—
<i>Eudynamis scolopacea</i>	—	—	—	—	+	—
<i>Tyto alba</i>	—	—	—	—	—	+
<i>Ninox connivens</i>	—	→ forest	—	—	—	—
<i>Collocalia esculenta</i>	—	→ forest	—	—	—	—
<i>Collocalia hirundinacea</i>	↓	—	—	—	—	—
<i>Caprimulgus macrurus</i>	—	—	—	—	—	+
<i>Ceyx azureus</i>	—	—	—	—	—	+
<i>Ceyx lepidus</i>	—	—	—	—	—	+
<i>Tanyptera galatea</i>	↑	—	—	—	+	—
<i>Eurystomus orientalis</i>	—	—	—	—	—	+
<i>Pitta sordida</i>	↑	—	—	—	—	—
<i>Hirundo tahitica</i>	—	—	—	—	—	+
<i>Coracina tenuirostris</i>	↑	→ forest	—	—	+	—
<i>Turdus poliocephalus</i>	↓	—	—	—	—	—
<i>Gerygone magnirostris</i>	—	→ forest edge	—	—	—	—
<i>Phylloscopus trivirgatus</i>	—	—	—	—	—	+
<i>Rhipidura leucophrys</i>	—	—	—	—	—	+
<i>Monarcha cinerascens</i>	↑	→ inland	—	—	—	—
<i>Myiagra alecto</i>	↑	→ forest	↑	—	+	—
<i>Aplonis cantoroides</i>	↑	→ forest	—	—	—	—
<i>Aplonis metallica</i>	—	→ forest	↓	—	—	—
<i>Nectarinia sericea</i>	↑	→ forest	—	—	+	—
<i>Nectarinia jugularis</i>	↑	→ forest	—	—	—	—
<i>Myzomela sclateri</i>	↑	→ inland	—	—	—	—

TABLE 2 — (Continued)

	Altitude	Habitat	Vertical	Diet	Abundance	No shifts detected
<i>Dicaeum pectorale</i>	—	—	—	—	—	+
<i>Erythrura trichroa</i>	—	—	—	—	—	+
<i>Lonchura tristissima</i>	—	—	—	+	—	—
Total	14 (10†, 4‡)	14	4 (1†, 3‡)	1	11	23

For each resident bird population on Karkar, the table shows in what respect, if any, the niche is altered with respect to the niche of the source population on New Guinea or New Britain. Karkar populations may have an expanded altitudinal range († = higher ceiling, ‡ = lower floor), wider habitat range (expanded from coastal to inland habitats or vice versa, from open habitats and second-growth to forest, or from waterside habitats to forest edge), expanded vertical foraging range († = higher toward canopy, ‡ = lower toward ground), wider diet, or else higher abundance in the same habitat as occupied on the source island. The last line gives the total number of species in each category.

of habitats occupied. Three of these are species that have expanded from coastal islets into forest (*Macropygia mackinlayi*, *Monarcha cinerascens*, *Myzomela sclateri*); nine, from edge and open habitats into forest (the seven species named in the second paragraph of this section as having expanded into lowland forest, plus *Collocalia esculenta* and *Aplonis cantoroides*, which have expanded into montane forest). *Gerygone magnirostris* lives mainly in waterside vegetation on New Guinea but occurs at the forest edge far from water on Karkar. An interesting niche difference between Karkar and Bagabag involves ground doves. On New Guinea the dove *Chalcophaps indica* is in coastal habitats, *C. stephani* further inland. Both doves occur on Bagabag and occupy these same habitats there. Only *C. stephani* is on Karkar, where it occurs on the coast as well as inland.

Fourteen species have expanded their altitudinal range, four to lower elevations, 10 to higher elevations. The details of many of these cases are of interest. The lorikeet *Vini rubrigularis* is replaced below 1500 ft. on New Britain by its close relative *V. placentis*, but descends to sea level on Karkar in the absence of *V. placentis*. The swiftlet *Collocalia hirundinacea* is largely replaced by the very similar *C. vanikorensis* below about 4000 ft. on New Guinea, but descends to 900 ft. on Karkar in the absence of its congener. The thrush *Turdus poliocephalus* is confined to elevations above

9000 ft. on New Guinea but descends to 3800 ft. on Karkar. The dove *Gallicolumba beccarii*, confined above 4000 ft. on New Guinea, reaches sea level on Karkar and New Britain. The upward expansions are equally remarkable. *Pitta sordida* and *Myzomela sclateri*, confined to low elevations on New Guinea and on New Britain coastal islets respectively, have entirely transferred their niches into the mountains on Karkar: they are absent from the Karkar lowlands. *Macropygia mackinlayi*, *Monarcha cinerascens*, *Nectarinia jugularis*, and *N. sericea* are virtually confined to sea level on New Guinea or New Britain but occur from sea level to 4000 or 5000 ft. on Karkar.

Expansions in vertical foraging range affect four species. On New Guinea *Ptilinopus superbus*, *P. magnificus*, and *Aplonis metallica* are canopy species rarely caught in mist nets. *Ptilinopus magnificus* was caught once in understory nets on Karkar, the other two species repeatedly. Conversely, *Myiagra alecto* lives in the understory and middle story on New Guinea but forages up to 80 ft. in the canopy on Karkar.

Eleven species are clearly more abundant on Karkar than in the same habitat on New Guinea, regardless of whether they also occupy a wider range of habitats on Karkar. In nine cases this statement is made on the basis of qualitative impressions, but in two cases it was confirmed quantitatively: *Tanyiptera galatea* and *Myiagra alecto* were netted twice as often

on Karkar (individuals caught per net per day) than under comparable conditions on New Guinea.

In no instance was there a visible difference in foraging technique between a Karkar population and New Guinea conspecifics. In only two instances was a shift in diet established: the finch *Lonchura tristissima* is virtually the sole bird species in Karkar grassland, just as the warbler *Cisticola exilis* lives virtually alone in Bagabag grassland, and each takes both seeds and insects. In New Guinea grasslands, where several finch species coexist with several warbler species, the former take mainly or exclusively seeds, the latter insects.

Thus, on Karkar as on other Pacific islands (Diamond, 1970a, 1970b, and 1976; Diamond and Marshall, 1977), avian niche shifts affect mainly spatial niche parameters (altitude, habitat, and vertical foraging range) and abundance, rarely foraging technique or diet.

Of Karkar's 52 species, 29 were observed to undergo one or more types of niche expansions. Some of the remaining 23 species may really have inflexible niches, whereas others may undergo subtle niche shifts that would require quantitative field observations to detect. Thirteen of Karkar's 52 species live on New Guinea (or New Britain) without congeners, while 39 live with congeners. Twenty-four of the latter 39 (62%) expand their niches on Karkar, whereas only five of the former 13 (38%)

do. If the comparison is confined to passerines, the difference is more striking: only one of the four passerines (25%) lacking congeners on New Guinea expands its niche on Karkar, compared to 11 of the 13 (85%) with congeners on New Guinea. This suggests that species are most likely to have their niche limits compressed by competition from congeners. Species lacking New Guinea congeners may occupy on New Guinea as wide a niche as their physiological adaptations permit, and therefore cannot undergo any further niche expansion on Karkar.

One would expect that species which expand their habitat range on Karkar are less efficient in these new habitats than the species which exclude them from these habitats on New Guinea. This may be one reason why, despite all these niche shifts, bird population densities are much lower on Karkar and Bagabag than in comparable New Guinea habitats: many species in the island forests are ill-adapted to these forests, compared with New Guinea's lowland and montane forest specialists. Bird population densities in lowland forest, as estimated by mist-net yields, are 63 percent lower on Karkar, and 77 percent lower on Bagabag, than in New Guinea. This discrepancy is even greater in montane forest: population densities 89 percent lower on Karkar than New Guinea (Diamond, 1970b).

## MOLT AND BREEDING

Reproductive cycles of New Guinea birds have been so little studied (Archbold and Rand, 1935; Rand, 1942a and 1942b; Ripley, 1964; Schodde and Hitchcock, 1968; Diamond, 1972a) that it seems important to attempt a preliminary assessment for Karkar and Bagabag, despite our limited data base. Obviously, our conclusions about molt and breeding must be tentative: they are based on only one or two seasons, on few nests, and often on few specimens per species. Specimens collected by Diamond in 1969 and by Meek in 1914 were examined for primary molt, to try to determine the length of the molting period. In addition,

gonad condition was known for the 1969 but not the 1914 specimens, and some nests were found in 1969, permitting some conclusions about breeding seasons. Recall that December through March are relatively wet, June through September relatively dry, on Karkar and presumably Bagabag. Meek's collectors were on Karkar from January to March 1914, Diamond on Karkar and Bagabag in May and June 1969. We consider in turn the following problems: season of molt; correlation of molt with gonadal enlargement; comparisons of congeners; and breeding seasons.

SEASON OF MOLT: In the following analysis,

primaries are numbered, beginning proximally with number 1. Species fall into four categories with respect to molt:

1. No molt in either collecting period: *Ducula pinon*, *Pitta sordida*, *Hirundo tahitica*, *Nectarinia jugularis*, *Dicaeum pectorale*.

2. Molting January-March, no molt May and June: *Egretta sacra*, *Ptilinopus superbus*, *Gallicolumba jobiensis*, *Eudynamis scolopacea*, *Ninox connivens*, *Caprimulgus macrurus* (one March specimen had outer primaries growing), *Collocalia esculenta*, *Ceyx azureus* (molt beginning January-March), *Aplonis cantoroides* (molt being completed January-March), *Aplonis metallica* (molt being completed January-March), *Lonchura tristissima*.

3. No molt January-March, molting May and June: *Chalcophaps stephani*, *Gallicolumba beccarii*, *Halcyon sancta*, *Tanyptera galatea*, *Nectarinia sericea*, *Myzomela sclateri*, *Erythrura trichroa*.

4. Molting both in January-March and May and June:

*Megapodius freycinet*. Three of four individuals were completing molt in January-March, but in May and June one bird had the central primaries growing.

*Ptilinopus magnificus*. In both periods some individuals were completing molt.

*Ducula spilorrhoea*. There was some molt in both periods, but there were few specimens available.

*Macropygia mackinlayi*. Individuals collected in January-March had inner primaries in molt; over half of those collected in May and June had outer primaries in molt with the rest in fresh plumage. No immatures were collected in May and June and gonad size did not indicate breeding, but molt is apparently almost complete by that time.

*Trichoglossus haematodus*. Molt seems to have just begun in the population in January-March; some individuals collected in May and June were just beginning molt, others were completing it. Molt apparently does not differ in the two subspecies (recall that the Karkar and Bagabag populations differ subspecifically), and there was no indication of breeding.

*Vini rubrigularis*. In January-March only one of seven specimens had begun molt. By

May and June all but one of the nine specimens had begun molt. This one individual may be an immature.

*Micropsitta pusio*. Molt is present during both periods but apparently has no regular pattern, and the two wings are often out of phase.

*Cacomantis variolosus*. In January-March one of eight individuals was completing molt; in May and June two of three individuals had the central primaries growing.

*Ceyx lepidus*. Some individuals were in molt during both periods.

*Eurystomus orientalis*. In the winter visitor *E. o. pacificus*, one female was completing molt in June. In the resident race *E. o. waigiouensis*, two females had the center primaries growing in January-March. Data are insufficient to determine whether there is a difference in time of molt between the two subspecies.

*Gerygone magnirostris*. Some individuals are molting in both periods.

*Monarcha cinerascens*. Some individuals are completing molt in both periods.

*Myiagra alecto*. A few individuals are in molt in January-March; most have completed molt by May and June.

**CORRELATION OF MOLT WITH GONADAL ENLARGEMENT:** An analysis of primary molt versus gonadal enlargement was carried out for the specimens Diamond collected to try to determine whether there is molt-breeding overlap in any Karkar species. Our results are as follows.

Twenty-three species showed no primary molt. Of these, specimens of four species had no gonad information, and they were presumably not breeding (*Aviceda subcristata*, *Ducula pinon*, *Gallicolumba jobiensis*, *Loriculus aurantiifrons*). Eight species had gonads noted as not enlarged or slightly enlarged and were probably not breeding (*Egretta sacra*, *Amaurornis olivaceus*, *Eudynamis scolopacea*, *Ninox connivens*, *Caprimulgus macrurus*, *Ceyx azureus*, *Hirundo tahitica*, *Turdus poliocephalus*). At least some of the individuals of the remaining 11 species had enlarged gonads. These are discussed more fully.

*Ptilinopus superbus*. All 13 males had enlarged testes, and three females contained a

large egg. These specimens were in fresh plumage with no primary molt. One nest containing an egg was found. Breeding was probably underway, judging by the relatively few females collected.

*Ducula zoeae*. The male had testes slightly enlarged; two females had the ovary enlarged. The species was perhaps breeding or ready to breed.

*Chalcophaps indica*. Two males had gonads enlarged, and one female was ready to lay. The species was perhaps breeding or ready to breed.

*Collocalia esculenta*. One of two females was collected on a nest.

*Pitta sordida*. One nest with a nestling was found.

*Phylloscopus trivirgatus*. Gonads were enlarged in all five males.

*Aplonis metallica*. Most males had somewhat enlarged gonads, and two of 16 females were nearly ready to lay. Numerous immatures were seen and collected. It was probably the end of the breeding season in this species. Molt was being completed in January-March (see above).

*Aplonis cantoroides*. Testes were considerably enlarged in one male, slightly enlarged in the other.

*Nectarinia jugularis*. Virtually all 13 males had somewhat enlarged gonads; none of six females had enlarged gonads. Molt was apparently completed by March (see above).

*Dicaeum pectorale*. All of three males and none of three females had enlarged gonads.

*Lonchura tristissima*. One male had enlarged gonads; one female did not.

Twenty-eight species showed some primary molt. Of these, 17 species had no or only slight gonad enlargement, or we had no information on gonad condition, and they were presumably not breeding: *Accipiter meyerianus* (copulation witnessed), *Ducula spilorrhhoa*, *Macropygia nigrirostris*, *Gallinula beccarii*, *Trichoglossus haematodus*, *Vini rubrigularis*, *Micropsitta pusio*, *Cacomantis variolosus*, *Chrysococcyx lucidus* (migrant winter visitor), *Ceyx lepidus*, *Halcyon sancta* (migrant winter visitor), *Tanyptera galatea*, *Merops ornatus* (migrant winter visitor), *Eurystomus orientalis*, *Coracina tenuirostris*, *Cisticola exilis*, *Erythrura trichroa*.

At least some individuals of the remaining 11 species had some gonad enlargement and are discussed more fully below.

*Megapodius freycinet*. The male had gonads not enlarged; one of three females contained a large egg. Primary number five was growing in the male.

*Ptilinopus rivoli*. Thirteen of 19 males and two of six females had gonads enlarged. The large proportion of males to females collected may indicate that females were incubating. Specimens were nearing the end of primary molt.

*Ptilinopus magnificus*. Seven of eight males had the gonads slightly enlarged to enlarged, and one of six females contained a large egg. These May and June birds were completing molt, but so were some birds in January-March (see above). The female with a large egg had two centers of active molt, and two males with enlarged gonads were completing primary molt.

*Reinwardtoena reinwardtii*. Three of four males had gonads somewhat enlarged; none of four females showed gonadal enlargement. One of the males was collected on a nest containing one egg. Wing molt was present in three specimens, one of these a male with enlarged gonads.

*Macropygia mackinlayi*. Numerous males had somewhat but not greatly enlarged gonads. No females had enlarged gonads. Fourteen specimens showed some degree of wing molt. Apparently the population was nearing completion of the molt before breeding began.

*Chalcophaps stephani*. One of four males and none of five females had enlarged gonads. Six of nine specimens were completing molt, and one immature with primaries in sheath was collected.

*Gerygone magnirostris*. Two of the three males had gonads enlarged; one of these had primary number three in molt. The other two males were not in molt.

*Monarcha cinerascens*. At high altitudes on Karkar almost all males had enlarged testes, and one female was nearly ready to lay. All individuals collected on the lower island of Bagabag, and all except one in the lowlands of Karkar, had small gonads. Primary molt was being completed in most individuals, as it was in some individuals in the January-March pe-

riod (see above). These facts, along with the presence of many immatures, may indicate an extended breeding season and overlap with molt in the population, and clearly show that breeding season varies with altitude.

*Myiagra alecto*. More than half the males show some enlargement of gonads, but none of eight females do. Only one of 21 individuals shows primary molt and in that case primaries eight and nine are growing in.

*Nectarinia sericea*. Most of 22 males had gonads enlarged, but none of five females did. A number of individuals were completing primary molt, but these did not include any of the males with enlarged gonads. Many fewer females than males were collected, and one immature with primaries still in sheath was collected. Breeding may have been in progress.

*Myzomela sclateri*. Almost all of 15 males had enlarged gonads, but none of four females did. Only one female had the inner primaries in molt; primary molt was being completed in the other specimens although many males showed heavy head molt. This head molt may be pre-breeding as four males with enlarged gonads showed the condition and wing molt was essentially finished. That many more males than females were collected may indicate that breeding was in progress, but the large number of immatures implies an extended breeding season and overlap of breeding and molt in the population.

COMPARISON OF CONGENERS: The following chart compares species in the same genus with respect to molt and gonad enlargement.

	Jan.-Mar. molt	May & June molt	May & June gonads enlarged
<i>Ptilinopus superbis</i>	yes	no	yes
<i>Ptilinopus rivoli</i>	—	yes	yes
<i>Ptilinopus magnificus</i>	yes	yes	yes
<i>Ducula spilorrhoa</i>	yes	yes	no
<i>Ducula pinon</i>	no	no	no
<i>Ducula zoeae</i>	—	no	yes

<i>Macropygia nigrirostris</i>	—	yes	no
<i>Macropygia mackinlayi</i>	yes	yes	no
<i>Chalcophaps indica</i>	—	no	yes
<i>Chalcophaps stephani</i>	no	yes	yes
<i>Gallicolumba beccarii</i>	no	yes	no
<i>Gallicolumba jobiensis</i>	yes	no	no
<i>Ceyx azureus</i>	yes	no	no
<i>Ceyx lepidus</i>	yes	yes	no
<i>Aplonis metallica</i>	yes	no	yes
<i>Aplonis cantoroides</i>	yes	no	yes
<i>Nectarinia sericea</i>	no	no	yes
<i>Nectarinia jugularis</i>	no	no	yes

These data suggest that *Ducula zoeae* may breed at a different time from the other two *Ducula* species, at least in 1969. Indications are that the molt period differs in *Ptilinopus superbis* from the other two *Ptilinopus* species, in *Ducula spilorrhoa* from the other two *Ducula* species, between the two *Chalcophaps* species, between the two *Gallicolumba* species, and between the two *Ceyx* species.

BREEDING SEASONS: Even with gonad information, it is often not easy to decide which birds are actually breeding. There is considerable evidence of only partial regression of testes in males of some species (Miller, 1962; Stresemann and Stresemann, 1966; Payne, 1969; Foster, 1975), and we had the impression that such was the case in many species from Karkar where the numbers of males and females collected were approximately equal but males showed testis enlargement and females showed no ovary enlargement. We have not used the condition of male gonads alone to decide on whether or not a species was breeding. In cases where many more males than females were collected and there was evidence of gonad enlargement in either sex, we believe that this may be an indication of breeding activity, as females are more likely to be inconspicuously incubating than are males.

There is little indication of molt and gonad



enlargement occurring together in the same individual, but when it occurs, the individual is usually a male. However, as noted above, gonad enlargement does not necessarily imply breeding capability, and concurrent molt and breeding in an individual may be rare indeed, at least during the dry season.

Twenty-eight resident species were not breeding in May and June and six others were probably not. Thus, 34 of 49 resident species analyzed were not breeding during the dry season, which is probably the "lean" season for insectivores at least (see Fogden, 1972). Of the remaining 15 species, seven are pigeons and are probably frugivorous. Fogden (1972) has pointed out that frugivorous species are less likely to be bound by the annual cycle of food availability in the timing of the breeding season than are insectivores, as fruiting trees are more likely to occur during the drier season, or on an irregular basis. Another factor that may allow pigeons to breed in the lean season is that their young are fed on "pigeon milk," thus a supply of insects may not be critical for raising the young. Four of these seven species of pigeon also had primary molt in progress. In two of these, *Ptilinopus rivoli* and *Chalcophaps stephani*, molt was just being completed and there is probably no overlap of molt and breeding. In *Ptilinopus magnificus* and *Reinwardtoena reinwardtii* there is indication of overlap of active molt and breeding in the population, and also in individuals.

Of the eight nonpigeon species, the data are insufficient for interpretation for three, *Megapodius freycinet*, *Collocalia esculenta*, and *Pitta sordida*. *Aplonis metallica* is a colonially nesting frugivore and may nest adventitiously when fruit is abundant, but there is apparently no overlap of molt and breeding. *Monarcha cinerascens*, *Nectarinia sericea*, *Nectarinia jugularis*, and *Myzomela sclateri* are discussed more fully below.

We have no data as to which species may be breeding in the wet season, nor do our data with one exception (*Monarcha cinerascens*) indicate a correlation of breeding season with altitude. There were no differences noted between Karkar and Bagabag birds.

From the 36 species collected by both Meek

and Diamond we can get some idea of when the birds molt. There were 20 species which showed no molt in either collecting period or for which we have insufficient data to assign a molt period. Three species were completing molt in January-March (*Caprimulgus macrurus*, *Aplonis cantoroides*, *A. metallica*). Three species showed no molt in January-March but both molt and breeding in May and June: *Chalcophaps stephani* may be an adventitious breeder (see above) and, if so, its breeding and molt cycles may not have been at the same time in 1914 and 1969; *Nectarinia sericea* and *Myzomela sclateri* are discussed below. *Gallicolumba beccarii*, *Halcyon sancta*, *Tanysiptera galatea* and *Erythrura trichroa* were molting in May and June but we have no further data on their molt cycle. The remaining six species had molt in both periods. Two were finishing molt by May and June: *Macropygia mackinlayi* may be an adventitious breeder, but *Myiagra alecto* would probably not breed until after the dry season. *Vini rubrigularis* had only begun molt in January-March, but by May and June most individuals were molting. As a nectar and flower feeder, it may be an adventitious breeder.

Four species mentioned above deserve somewhat more detailed commentary.

*Monarcha cinerascens* is a supertramp (Diamond, 1974) which has managed to colonize far-flung islands in the southwest Pacific; one would therefore expect its breeding cycle to be adaptable. From the data presented above one may conclude that the breeding season is extended, that there is overlap of breeding and molt in the populations, and that there is variation in breeding season with altitude. As this species is insectivorous, adventitious breeding is probably precluded (Fogden, 1972) but molt-breeding overlap on the population level may serve to extend the period during which there are at least some individuals breeding and thus allow the species to adapt to a wide range of environments.

As for the sunbirds *Nectarinia jugularis* and *N. sericea*, molt was apparently completed by March in *N. jugularis* and by June in *N. sericea*. It is possible that breeding was underway in both species as larger numbers of males than

females were collected in both and immatures of *N. sericea* were collected. That this is the case indicates that both species may be adventitious breeders, even though they are partially insectivorous. Both species have spread widely and may also compete with certain widespread myzomelids. Either adventitious breeding or the ability to breed during the lean season by exploiting both insects and fruit (Fogden, 1972) would provide an advantage for a colonizing bird species.

*Myzomela sclateri* is another supertramp. That primary molt was just being completed and breeding was apparently already in progress, with many immatures collected, all seems to indicate an overlap of molt and breeding in this species.

CONCLUSIONS: Although the above data are preliminary they do seem to agree with Fogden (1972) in that few species are breeding in the dry (= lean) season and most of these are

probably frugivores, mixed frugivores-insectivores or nectivores. A few species do apparently show molt-breeding overlap in individuals (Foster, 1975) as a means of extending the breeding season and perhaps increasing productivity by repeated nestings. Two of these are pigeons (*Ptilinopus magnificus* and *Reinwardtoena reinwardtii*), determinate layers, and thus limited in adjustments they can make to productivity. Several of the adventitious breeders are also pigeons, indicating that both these methods of increasing productivity are open to birds with a constant clutch size.

The four species that are supertramps or wide-ranging colonizers also show breeding modifications either of adventitious breeding or molt-breeding overlap on the population level. This high reproductive potential probably contributes to their success in colonizing new areas.

## SPECIES ACCOUNTS

INTRODUCTION: In the following accounts measurements of adults are given in millimeters of the flattened wing, of the tail from insertion of the central feathers to tip of the longest feather, and of culmen from base, unless otherwise noted. Weights are in grams. Primary molt only is analyzed and primaries are numbered proximally to distally. The number of specimens examined includes numerous individuals taken in mist nets and released alive, or brought to camp by local residents but not made into skins. However, weights and other information were taken from such individuals. Following the Latin and English names of each species we give its name, where known, in the language spoken on Bagabag or at Mom village on Karkar.

*Fregata* sp.  
Frigatebirds  
Del (Karkar)

DISCUSSION: Small groups of unidentified frigatebirds (*F. ariel* or *F. minor*) were twice seen soaring offshore near Karkar and once over Bagabag.

*Egretta sacra sacra*  
Reef Heron

Katámam (Bagabag)

SPECIMENS EXAMINED: Bagabag: 1 ♂.

MEASUREMENTS: Wing: 297. Tail: 103. Culmen: 94. Tarsus: 82. Weight: 520.

PERISHABLE COLORS: Iris: yellow. Bill: dull yellow. Legs: yellow-green.

BREEDING AND MOLT: The gonads of the specimen were small. There was no molt.

STOMACH CONTENTS: Fish remains.

TAXONOMY: We follow Bock (1956, p. 39) in placing this species in genus *Egretta* and in not recognizing the monotypic genus *Demi-gretta*.

DISCUSSION: This heron occurred in low numbers along the coasts of both Bagabag and Karkar, either as solitary individuals or in groups of up to three. It foraged in shallow water and on offshore reefs, and also perched in trees overlooking the ocean. All birds seen and the one collected were in the gray phase, as was Meek's sole Karkar specimen, but Bagabag residents reported the white phase also to occur.

*Aviceda subcristata megala*

## Crested Hawk

SPECIMENS EXAMINED: Karkar: 2 ♀, 1 imm. ♀.

MEASUREMENTS: Wing: ♀ 317, 331; imm. ♀ 314. Tail: ♀ 204, 212; imm. ♀ 216. Culmen from cere: ♀ 21.0, 21.5; imm. ♀ 21.0. Tarsus: ♀ 35.0, 35.5; imm. ♀ 37.5. Weight: ♀ 350, 360; imm. ♀ 290.

PERISHABLE COLORS: Iris: yellow. Bill: black. Legs: whitish.

BREEDING AND MOLT: There was no molt apparent.

STOMACH CONTENTS: Insects.

TAXONOMY: Karkar specimens agree in color and size with *megala*, the race of east New Guinea, rather than with *stenozona*, the smaller race of west New Guinea. Measurements of seven females of each race are: *megala*, wing 314-331 (av. 320), tail 203-214 (210); *stenozona*, wing 295-313 (303), tail 180-208 (195). The race *bismarckii* of New Britain is quite different in plumage, while *coultasi* of Manus is close to *megala* in appearance but has a shorter tail (one female: wing 317, tail 189).

DISCUSSION: The Crested Hawk occurred on Karkar from sea level to about 2300 ft. and was considerably commoner than on the New Guinea mainland. Alone or in groups of two or three, it perched in the forest crown or soared high. This species was not collected by Meek.

*Haliastur indus girrenera*

## Red-backed Kite

Sengsik (Karkar). Kob (Bagabag)

SPECIMENS EXAMINED: Karkar: 1 ♀, 1 ?sex. Bagabag: 1 ♂.

MEASUREMENTS: Weight: ♂ 490; ♀ 590; ?sex 445.

PERISHABLE COLORS: Iris: brown. Bill: very pale greenish. Legs: whitish.

BREEDING AND MOLT: Gonads of the male were small.

STOMACH CONTENTS: Grasshoppers.

DISCUSSION: This kite was common from the coast to the summit of Bagabag and from the coast to about 4700 ft. on Karkar. It was usually seen soaring, occasionally perched within the shade of a tree crown at the forest edge or overlooking the ocean. A pair repeatedly attacked a soaring eagle *Haliaeetus leucogaster*

and was in turn attacked by the swallow *Hirundo tahitica*.

VOICE: A weak nasal downslur, as in New Guinea.

*Accipiter meyerianus*

## Meyer's Goshawk

SPECIMENS EXAMINED: Karkar: 1 ♂.

MEASUREMENTS: Weight: 530. Other measurements are given in table 3, together with those of all other specimens in the American Museum of Natural History, as this species is so uncommon in collections.

PERISHABLE COLORS: Iris: brown(?). Bill: black with a pale gray base. Cere: pale gray. Legs: dull lemon.

BREEDING AND MOLT: Primaries 5 and 9 were growing in each wing.

STOMACH CONTENTS: Feathers.

TAXONOMY: One other specimen of a male in comparable plumage was available for comparison. This bird was taken on Ceramlaut by H. Kühn on December 17, 1899 and is very similar to the Karkar bird except that the latter has the tail obscurely barred and has white bars on some of the upper tail coverts; whereas, the former is entirely blackish above and has a longer tarsus.

DISCUSSION: A pair of this rare goshawk frequented Karkar crater. A calling individual perched in a dead tree on the crater's rim was answered from a distance by another individual, which flew up, briefly mounted the perched bird, and flew off. One individual was seen in leisurely flight at 3100 ft. The sole record on Bagabag was of a calling individual flying over the summit. Meek did not collect this species.

VOICE: A fairly high, slightly hoarse, up-slurred screech "ka-ah," repeated at 1½-5 times per second.

*Haliaeetus leucogaster*

## White-bellied Sea Eagle

Bok, kogeneg (Bagabag)

DISCUSSION: On several occasions we saw a single individual soaring over the lowlands and foothills of Karkar, and often saw a group of three soaring high over Bagabag.

*Falco berigora novaeguineae*

DISCUSSION: We saw an individual in slow

TABLE 3  
Measurements of *Accipiter meyerianus*

Locality	Sex	Wing	Tail	Culmen from cere	Tarsus	Phase	Iris
Karkar	♂	296+	201	23	72	normal	brown
Ceramlaut	♂	307	201	26	79	normal	"chromeous"
Kulambangra	♀	320	227	28	75	normal	reddish brown
New Britain	♀	340	244	28	86	black	dark red
Umboi	♀	335	236	26	79	normal	orange-brown
South Halmahera	♀	298	215	22	71	immature	—

flight or perched in a tree twice at Karkar airport and once in Karkar crater. Meek took a specimen.

*Megapodius freycinet affinis x eremita*

Common Scrub Fowl

Malang (Karkar). Mailau (Bagabag)

SPECIMENS EXAMINED: Karkar: 1 ♂, 2 ♀. Bagabag: 1 ♀.

MEASUREMENTS: Wing: ♂ 229; ♀ 215, 225, 232. Tail: ♂ 73; ♀ 68, 72. Bill: ♂ 28; ♀ 27, 27, 28. Tarsus: ♂ 65; ♀ 61, 62, 63. Weight: ♂ 750; ♀ 580, 700, 780.

BREEDING AND MOLT: One female contained a large egg. The male had primary number five growing in each wing; no molt was apparent in the females.

STOMACH CONTENTS: Insects in one specimen, a large centipede in another, and only pebbles or sand in the other two.

TAXONOMY: Mayr (1938c, pp. 10-14) discussed the differences between *eremita*, the race of the Solomons and Bismarcks, and *affinis*, the race of north New Guinea. He concluded that characters of the populations on the islands along New Guinea's north coast changed from west to east, from pure *affinis* on Japen, Tarawai, and Manam, to *affinis x eremita* hybrids on Karkar as judged from Meek's 1914 specimens, to *eremita* with slight tendencies toward *affinis* on Long and Umboi, to pure *affinis* on New Britain. The 1969 Karkar and Bagabag specimens fit this scheme; however, they are closer to *eremita* than are Meek's specimens, not only in their darker color (possibly an artifact of greater fading in the 1914 specimens), but also in the medium to short crest, bare forehead (except for one Kar-

kar female that has a feathered forehead), dark olivaceous mantle, and little brown on the flanks. The wings of the 1969 specimens are quite blackish and do not appear to have much gray. The marked sexual dimorphism of the 1914 specimens (females nearer *affinis*, males nearer *eremita*) is not apparent in the 1969 series, except perhaps in that the sole 1969 specimen with a feathered crest (an *affinis* trait) is female. Thus, the proportion of *eremita* genes in the hybrid Karkar population may have increased over the past half-century.

DISCUSSION: Single individuals occurred in Karkar lowland forest in modest numbers, infrequently up to 2200 ft. but mainly near the coast. We found two incubation mounds. On Bagabag we saw only a few individuals and no mounds.

VOICE: An individual that was disturbed and flew up from the ground repeatedly called a high downslur "kee-ya" at about 1/sec. Karkar residents said that the species calls at night.

*Amaurornis olivaceus moluccanus*

Bush-hen

Kunil (Karkar)

SPECIMENS EXAMINED: Karkar: 1 ♂.

MEASUREMENTS: Wing: 142. Tail: 61. Bill from base of shield: 37. Tarsus: 58. Weight: 238.

PERISHABLE COLORS: Bill: greenish. Legs: dull yellow.

BREEDING AND MOLT: The gonads were small. There was no molt apparent.

STOMACH CONTENTS: Insects.

TAXONOMY: The single specimen from Karkar agrees with mainland New Guinea and Long Island birds in having the under tail cov-

erts a deep rich brown, not tawny as in *nigrifrons*, the New Britain form (Mayr, 1949, p. 20). Mayr has pointed out the extreme variation in size and coloration within populations of this species (1949, pp. 18-21; 1938a, p. 11), but the color of the under tail coverts seems to be a consistent difference between the two subspecies with which we are concerned.

DISCUSSION: This rail's call was heard at numerous locations on Karkar, in cultivated areas and adjacent forest, from the lowlands up to at least 1400 feet. Meek did not obtain this species on Karkar.

VOICE: A duet as on New Guinea (Diamond and Terborgh, 1968, p. 65), often given at night as well as during the day.

*Pluvialis dominica*  
Eastern Golden Plover

DISCUSSION: Our sole record was of a group on Karkar airstrip on May 17.

*Sterna bergii cristatus*  
Greater Crested Tern

DISCUSSION: We saw several groups diving for fish, or perched on reefs or floating logs, near Karkar and Bagabag.

*Ptilinopus superbus superbus*  
Superb Fruit Dove

SPECIMENS EXAMINED: Karkar: 10 ♂, 2 ♀. Bagabag: 7 ♂, 2 ♀.

MEASUREMENTS: Wing: ♂ 126-140 (130 ± 4, n = 13); ♀ 120, 120, 127. Tail: ♂ 70-75 (73 ± 2, n = 11); ♀ 65, 69, 71. Exposed culmen: ♂ 15-17 (15.8 ± 0.8, n = 12); ♀ 15, 15, 16. Tarsus: ♂ 19.5-23.0 (20.6 ± 0.9, n = 13); ♀ 20, 20, 20. Weight: ♂ 99-144 (120 ± 10, n = 13); ♀ 108-128 (115 ± 9, n = 7).

BREEDING AND MOLT: On June 15 on Bagabag an adult flew from a flimsy nest of sticks 15 feet above the ground, containing one white egg. Gonads of all males were enlarged, and three females were nearly ready to lay. The disproportionately small number of females collected may also indicate that breeding had begun. The specimens were in fresh plumage with no primary molt discernible. Three males had the crown in molt and one had the upper tail coverts in heavy molt.

STOMACH CONTENTS: Fruit, 7-26 mm. in diameter.

TAXONOMY: A widespread subspecies, occurring from the Moluccas to the Solomons and eastern Australia.

DISCUSSION: This dove was abundant in the forest canopy, where it was heard much more often than seen. On Bagabag it extended from the lowlands to the summit; on Karkar, from the lowlands commonly up to 3700 ft., above which altitude it was largely replaced by *P. rivoli*, but a few *P. superbus* individuals occurred up to 4000 ft. A displaying male puffed up his breast, spread his wings, and spread his tail to show the white band. This species has an emarginated outer primary that is probably responsible for the whirring sound that the bird makes in flight.

VOICE: As in New Guinea (Diamond, 1972a, p. 124).

*Ptilinopus iozonus* subsp.  
Orange-bellied Fruit Dove

DISCUSSION: On Karkar this dove was the least common of the three *Ptilinopus* species, but it nevertheless was found at four widely separated localities in the crowns of lowland second-growth forest and roadside trees up to about 1000 ft. Since Meek did not obtain this species and it is far commoner in similar habitats on New Guinea, it may be a recent invader of Karkar. It was more often heard than seen.

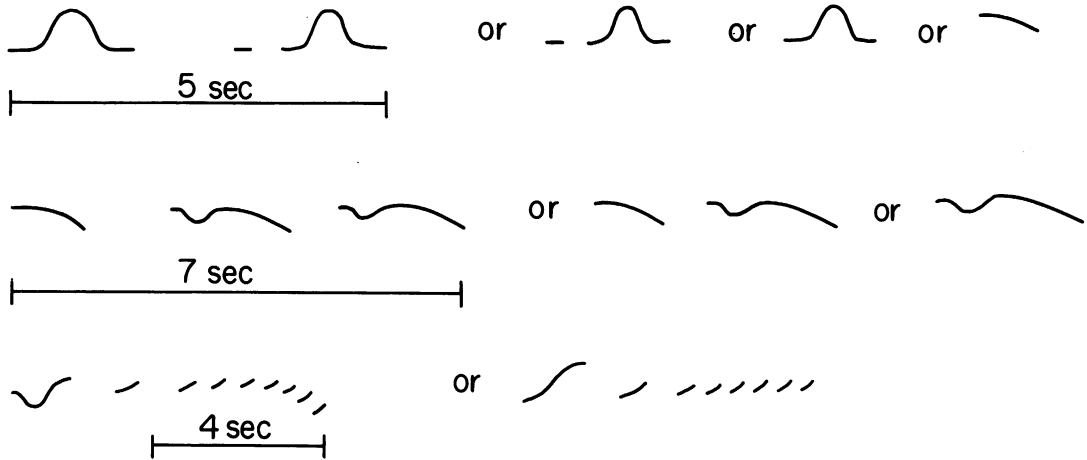
VOICE: Faint coo's, much softer than those of *P. superbus* or *P. rivoli*. The patterns, illustrated in figure 5, are either two very prolonged slurs, or else one such slur followed by a series of notes that accelerates and initially rises and then drops in pitch.

*Ptilinopus rivoli bellus*  
White-breasted Fruit Dove

SPECIMENS EXAMINED: Karkar: 19 ♂, 6 ♀.

MEASUREMENTS: Wing: ♂ 131-145 (136 ± 4, n = 18); ♀ 127-136 (131 ± 4, n = 6). Tail: ♂ 75-85 (80 ± 3, n = 16); ♀ 72-76 (74 ± 1, n = 6). Exposed culmen: ♂ 16.0-19.0 (17.6 ± 0.7, n = 19); ♀ 16.5-18.0 (17.1 ± 0.6, n = 5). Tarsus: ♂ 22.0-25.0 (23.3 ± 0.9, n = 19); ♀ 22.0-23.5 (22.9 ± 0.5, n = 6). Weight: ♂ 122-168 (143 ± 11, n = 17); ♀ 106-145 (131 ± 12, n = 5).

BREEDING AND MOLT: The molt in this spe-

Ptilinopus iozonusFIG. 5. Voice of *Ptilinopus iozonus*.

cies agrees with that of *P. solomonensis* (Stresemann and Stresemann, 1966, pp. 129-130). In two specimens three feather generations were apparent. In the others primaries 5, 6, or 7 were growing and it was not possible to tell whether generations one and two or two and three were represented. However, in two other specimens only primaries 7 and 8 or 10 were growing and all of the more proximal feathers appeared to be of the same generation. This and the fact that all the specimens are in good plumage leads us to believe that the birds are nearing the end of wing molt. Most of the birds had enlarged gonads. None of the specimens were immatures, but the disproportionately small number of females collected may indicate that the breeding season had begun and that females were incubating.

**STOMACH CONTENTS:** Fruit 4-16 mm. in diameter, often identified as the fruit of the wild limbun palm.

**TAXONOMY:** These specimens have a yellow breast band bordered in white, a reddish violet spot on the lower breast, and a small amount of yellow tipping on the feathers of the abdomen and under tail coverts, characters distinguishing the mainland New Guinea race *bellus* from the Bismarck Archipelago race *rivoli* (white breast

patch, lavender to purple spot on lower breast, and bright yellow abdomen and under tail coverts).

**DISCUSSION:** This dove was abundant in Karkar montane forest at 3700-5000 ft., where it replaced *P. superbus* of lower elevations. The sole record of *P. rivoli* below 3500 ft. was an adult male at 2100 ft. A perched male seen to fan his wings repeatedly may have been displaying.

**VOICE:** An accelerating series of hoo's, as in New Guinea (Diamond, 1972a, p. 126).

*Ptilinopus magnificus puella* x *poliura*  
Wompoo Pigeon

Kuliak (Karkar). Ulaku (Bagabag)

**SPECIMENS EXAMINED:** Karkar: 8 ♂, 6 ♀. Bagabag: 2 ♂.

**MEASUREMENTS:** Wing: ♂ 160-167 (163 ± 3, n = 7); ♀ 155-161 (158 ± 2, n = 6). Tail: ♂ 132-147 (138 ± 5, n = 6); ♀ 117-137 (129 ± 7, n = 6). Exposed culmen: ♂ 18.0-22.0 (18.9 ± 0.7, n = 7); ♀ 18.0-20.0 (18.8 ± 0.7, n = 6). Tarsus: ♂ 22.0-23.0 (22.8 ± 0.4, n = 8); ♀ 23.0-23.5 (23.2 ± 0.3, n = 6). Weight: ♂ 154-209 (181 ± 14, n = 8); ♀ 137-183 (168 ± 13, n = 6).

**BREEDING AND MOLT:** On Karkar a flimsy



nest of sticks containing one white egg was found at a height of 15 ft. above the ground, overlooking a dry stream bed. A similar nest on Bagabag was at a height of 6 ft. Most males had the gonads slightly to moderately enlarged, and two of these were just completing molt. Two females were just completing molt, and two others had two centers of active molt in each wing: the fifth and tenth primaries were growing. One of these latter females contained a large egg, as did one other female not examined for molt.

STOMACH CONTENTS: Fruit, 13-20 mm. in diameter.

TAXONOMY: We follow Goodwin (1967) in considering this species congeneric with *Ptilinopus*. Rand (1942a) described the nest as atypical of that of *Ptilinopus*, but the nests described by Gilliard (Gilliard and LeCroy, 1966), and found by us are typical. We were unable to find other compelling reasons for retaining *Megaloprepia*. Goodwin's (1967, pp. 327-328) suggestion that the two species formerly comprising the genus are related to *P. subgularis* and *P. leclancheri* is supported by the black color and sometimes hairlike consistency of the feathers on the upper part of the maroon throat stripe of some individuals of *magnificus*. They appear very similar to feathers in the throat patch of *leclancheri*.

Rand and Gilliard (1967) recognized four similar subspecies of *magnificus*: *puella* from the western Papuan islands and the Vogelkop, *interposita* from the Wandammen Peninsula through south New Guinea from the Onin Peninsula to the Fly River area, *poliura* from the Merauke area through southeastern New Guinea to and including the Huon Peninsula, *septentrionalis* from northern New Guinea from Astrolabe Bay westward to the Mamberamo River and Japen island.

With over 200 specimens available, we have reexamined the characters used to separate the various subspecies and present our results in table 4 to facilitate comparison.

Birds of the subspecies *puella* from the Vogelkop and western islands have the yellow on abdomen and vent brightest, the under tail coverts greenest with narrowest yellow tips and

underside of the tail blackest. Birds from Wasior, Wandammen Peninsula (type of *interposita*) and southwestern New Guinea are very similar to *puella* and we follow Junge (1937) and Mees (1964) in considering *interposita* invalid.

The Fly River population appears to be intermediate between *puella* (i.e., *interposita*) and *poliura* of southeastern New Guinea, as might be suspected by the ranges as given by Rand and Gilliard.

Diamond (1972a) has considered his Karimui birds to be similar to Fly River birds in color. In addition, our analysis shows that these birds have the average longer tail of *poliura*. They should be considered as an intermediate population as well. Furthermore, the Karimui birds have the largest and most numerous yellow spots on the wings of any population.

The subspecies *poliura* is relatively distinctive and homogenous. The vent and lower abdomen are dull yellow to greenish yellow with greenish gray to gray under tail coverts broadly tipped dull yellow, and the undertail is less black than in *puella*, more grayish. The tail averages considerably longer than it does in other populations but the overlap is complete.

Greenway (1935) considered the birds taken at Upper Watut and Surprise Creeks to be intermediate between *septentrionalis* and *poliura* but gave no reasons.

Populations from northern New Guinea from Japen Island to Astrolabe Bay, including Karar, Bagabag and Manam, are variable and difficult to deal with. However, as none of them seems to have the longer tail of *poliura* and all populations seem to vary from dull to bright in color of the lower abdomen and vent and to be otherwise indistinguishable from the southern populations considered intermediate between *puella* and *poliura*, the most reasonable solution seems to be to consider these birds also intermediate, not recognizing *septentrionalis* as a separate subspecies.

There appear to us to be two ways to treat the populations taxonomically. One is to recognize *puella*, from the Western Papuan Islands and the Vogelkop eastward in the south through the Snow Mountains and including the Wan-

dammen Peninsula, and *poliura* from at least Redscar Bay in the west through southeastern New Guinea and the Huon Peninsula. The other series of birds that we have examined seem to vary randomly in the various characters separating *puella* and *poliura* and would need to be considered intermediates between them.

The other possibility is to recognize no subspecies and consider the variation clinal from east to west along both the northern and southern watersheds of New Guinea. However, it is not apparent that these intermediate populations do vary clinally in the characters discussed. There is some evidence of a degree of genetic isolation in some of these populations (i.e., the largest and most numerous yellow wing spots occur in birds from Karimui and these birds also have the average longer tail of *poliura*; the wing spots average whitest in the birds from Karkar, but equally white spots may be found in some mainland individuals; birds from Manam have on the average a quite yellowish vent).

At the present time it seems to us preferable to recognize the more uniform populations in the west and east, *puella* and *poliura*, and consider the other populations variable without recognizing them taxonomically. The effects of age on size (there appeared to be little size difference correlated with sex), and the effects of stage of wear of plumage on various color characters, should be examined more fully. Birds we examined that were obviously immature (dull plumage with the yellow and maroon tips of the feathers narrower allowing the greenish parts of the feathers to show, and sometimes with brownish under tail coverts; very small and whitish spots on the wings) usually had the shortest tails, but not always.

**DISCUSSION:** The Wompoo Pigeon was common in forest on Karkar from sea level to about 2900 ft., and observed regularly but not numerous on Bagabag. Like *Macropygia* species, this pigeon frequents the shaded lower portion of the forest crown at 15-50 ft. above the ground. It never takes an exposed perch in the top of a tree, as do other *Ptilinopus* species.

**VOICE:** A low-pitched call "hoo-wa-hoo," as in New Guinea (Diamond, 1972a, p. 130). The pitch varies significantly among individuals.

Occasionally one hears a soft, low-pitched growling note.

*Ducula spilorrhoea spilorrhoea*

Torres Strait Imperial Pigeon

Taraga (Karkar). Muluk (Bagabag)

**SPECIMENS EXAMINED:** Bagabag: 3 ♀.

**MEASUREMENTS:** Wing: 226, 233. Tail: 125, 130. Exposed culmen: 24. Tarsus: 28, 30. Weight: 520, 540, 580.

**BREEDING AND MOLT:** One individual had the fifth primary in one wing and the seventh primary in the other growing; no molt was seen in the second individual.

**STOMACH CONTENTS:** Fruit, including one 39 mm long.

**TAXONOMY:** The race *subflavescens* from the Bismarck Archipelago has a suffusion of yellowish on the white parts of the plumage, a wide black band on the outermost rectrices, wide black tips on the under tail coverts and a band of black on the flanks. Goodwin (1967, p. 421) apparently overlooked this subspecies in his treatment of the species. The nominate race from the New Guinea mainland has the white of the plumage mostly pure white (although some individuals show a trace of yellowish, mostly on the abdomen), the outer rectrix either without a black band or with a very narrow one, the tail coverts and flanks have a black band bordered by a white tip and there are scattered spots of black on the lower abdomen. The Bagabag birds agree in all these characters with the New Guinea birds.

**DISCUSSION:** We saw this species nearly daily on Bagabag but only three times on Karkar, in groups of up to six near the coast.

*Ducula pinon jobiensis*

Pinon Imperial Pigeon

**SPECIMENS EXAMINED:** Bagabag: 1 ♂.

**MEASUREMENTS:** Wing: 266. Tail: 137. Exposed culmen: 30. Tarsus: 42.

**BREEDING AND MOLT:** None.

**TAXONOMY:** This specimen agrees with *jobiensis* in having the wing coverts and upper tail coverts broadly scalloped with pale gray.

**DISCUSSION:** On Karkar Meek collected this species but we did not, although we observed it daily in small numbers from sea level up to about 1000 ft. on Bagabag. Many Karkar resi-

TABLE 4  
**Racial Characteristics of *Ptilinopus magnificus* Populations in New Guinea**

	Yellow of abdomen and vent	Under tail coverts	Spots on wings	Under tail	Wing	Tail	
<i>"septentrionalis"</i>	bright to dull	greenish gray to gray with broad yellow tips	medium large to large	less black	Bagabag, Karkar, Manam 151-171 (160±4, n=26) Sepik to Madang 151-175 (163±5, n=23) Torricelli Mountains 155-172 (163±5, n=13) Japan and north coast 154-172 (164±6, n=42)	126-147 (135±5, n=24) 125-149 (136±7, n=22) 125-149 (134±7, n=13) 126-154 (137±6, n=41)	
	<i>puella</i>	bright	bright green to grayish green with narrow yellow tips	small almost none to few	black	Misol, Batanta, Waigeu 156-172 (162±4, n=15) Vogelkop 159-169 (162±3, n=6)	126-153 (136±7, n=14) 129-144 (135±5, n=6)
		bright	gray-green to gray with narrow yellow tips	small to medium	black	Etma Bay to Snow Mountains 155-171 (163±5, n=12)	131-146 (138±5, n=12)
		bright to dull with more bright	gray-green to gray, yellow tips average broader	small to medium	less black	Fly River 151-173 (164±6, n=23)	121-147 (135±7, n=23)
		bright to dull, with more dull	gray-green to gray yellow tips average still broader	large numerous	less black	Karimui 160-175 (168±5, n=7)	139-152 (148±5, n=7)
	<i>poliura</i>	dull to greenish yellow	greenish gray to gray with broad yellow tips	small to medium	less black	Southeastern New Guinea 156-178 (168±4, n=42) Huon Peninsula 154-176 (173±2, n=8)	133-167 (146±8, n=41) 133-155 (149±2, n=8)
				few to many			

dents who had come to know this species well elsewhere said that it is now absent on Karkar. Because of its distinctive, far-carrying calls, it could hardly have been overlooked on Karkar if it had still occurred.

**VOICE:** A very deep and resonant call of three or four notes, as in New Guinea (Diamond, 1972a, pp. 130-132).

*Ducula zoeae*

Zoe Imperial Pigeon

Bidun (Karkar)

**SPECIMENS EXAMINED:** Karkar: 1 ♂, 2 ♀.

**MEASUREMENTS:** Wing: ♂ 233; ♀ 208, 224. Tail: ♂ 133; ♀ 119, 134. Exposed culmen: ♂ 25.0; ♀ 26.5, 27.0. Tarsus: ♂ 30.5; ♀ 29.0, 31.0. Weight: ♂ 600; ♀ 540, 560.

**BREEDING AND MOLT:** No molt apparent, wings unworn. The two females had enlarged gonads.

**DISCUSSION:** This species was not obtained by Meek. We found it uncommon and local on Karkar, in forest between sea level and 2700 ft.

**VOICE:** Broken hoo's as in New Guinea (Diamond, 1972a, pp. 132-133).

*Macropygia mackinlayi arossi*

Mackinlay's Cuckoo-dove

**SPECIMENS EXAMINED:** Karkar: 12 ♂, 5 ♀, 6 ? sex.

**MEASUREMENTS:** Exposed culmen: ♂ 12.0-13.0; ♀ 12.0-13.0. Tarsus: ♂ 19.5-21.0; ♀ 19.0-20.5. Weight: ♂ 85-100 ( $91 \pm 5$ ,  $n = 10$ ); ♀ 72-90 ( $81 \pm 7$ ,  $n = 5$ ). See table 5 for wing and tail. There was no indication of increase in size with altitude. The longest tail, 164 mm, was in a specimen of unknown sex.

**PERISHABLE COLORS:** Iris: yellow or red. Bill: black. Legs: carmine (males); carmine, dull carmine, dull purple, or dull brick-brown (females).

**BREEDING AND MOLT:** Fourteen specimens showed some degree of wing molt. Of these, 10 had primaries 9 or 10 in some stage of growth. Three others had primaries 7 or 8 growing in. One individual had both primaries 5 missing. Three specimens had testes slightly enlarged but the indications are that the population is nearing completion of the molt before breeding is begun. None of the individuals collected was immature.

**STOMACH CONTENTS:** Fruit, pebbles, or both.

**TAXONOMY:** Rothschild and Hartert (1915a, p. 28) described the subspecies *krakari*, from the series of skins collected on Karkar by Meek, on the basis of larger size, lighter color and presence of a delicate "bloom" on the underside. We do not find these characters to hold. Our measurements of the Meek specimens do not agree with those of Rothschild and Hartert and average smaller. Both wing and tail vary greatly in size between individuals and overlap broadly in measurements between populations.

The color is also extremely variable within the same population, and foxing apparently occurs, as our recently collected material averages darker than the material collected by Meek. The Meek material cannot be separated from specimens from other parts of the Bismarck Archipelago and Solomon Islands on the basis of color. We therefore consider *krakari* a synonym of *arossi*.

**DISCUSSION:** This cuckoo-dove was common on Karkar in lowland forest, in low numbers up to 3400 ft., and one or two records several hundred feet higher. It is surprising that this pigeon has spread hundreds of miles from its center of distribution in the Solomons and New Hebrides, through the Bismarcks, to Karkar (its western range limit), but is not on Bagabag near Karkar. It flies with a slow wing beat, is solitary, and frequents the middle story and lower canopy (mostly 15-40 ft., occasionally up to 90 ft. above the ground). Like *Ptilinopus magnificus* and unlike other *Ptilinopus* and *Ducula* species, it remains within the canopy and never occupies exposed treetop perches.

**VOICE:** A two-note call similar in quality to that of *M. amboinensis* and similar in pattern to the call of the European Cuckoo, *Cuculus canorus*: the first note is a third in pitch above the second note. This 2-note call is repeated at intervals of 1 or 2 seconds. Calls of this species that Diamond heard in the Bismarcks, Solomons, and New Hebrides were essentially the same.

*Macropygia nigrirostris nigrirostris*

Black-billed Cuckoo-dove

**SPECIES EXAMINED:** Karkar: 1 ♂, 2 ♀, 1 imm. ♂ (molting into adult plumage).

**MEASUREMENTS:** Wing: ♂ 143; ♀ 134, 143; imm. ♂ 134. Tail: ♂ 148; ♀ 144, 144. Ex-

TABLE 5  
Measurements of *Macropygia mackinlayi arossi*

	Males		Females	
	Wing	Tail	Wing	Tail
Karkar				
Diamond	141-152 (147±3, n=12)	146-158 (153±4, n=10)	136-148 (143, n=5)	131-150 (144, n=4)
Meek	143-149 (146, n=4)	152-155 (153, n=3)	142-146 (144, n=3)	150
Nissan	136-147 (143±3, n=7)	136-155 (148±7, n=7)	133-149 (140±5, n=7)	137-155 (147±8, n=6)
Witu	142-150 (145, n=4)	147-156 (150, n=3)	141, 144 (n=2)	147, 152 (n=2)
Umboi			144, 146 (n=2)	144, 155 (n=2)
Long			140	145
Talasea, New Britain			146	149
Bougainville	139-147 (143±3, n=12)	147-160 (153±4, n=9)	135-146 (141±3, n=9)	142-159 (149±6, n=8)

posed culmen: ♂ 15; ♀ 14, 14. Tarsus: ♂ 20.0; ♀ 19.5, 20.5; imm. ♂ 19.0. Weight: ♂ 86; ♀ 80, 92; imm. ♂ 70.

**PERISHABLE COLORS:** Bill: horn, gray, or black. Legs: dull dark brick, dull brown, or carmine.

**BREEDING AND MOLT:** The two females and the immature were in nearly identical stages of molt, with primaries 7 or 8 growing. The remaining primaries appeared unworn. Gonads were slightly enlarged in the adult male, small in the immature male and one female.

**STOMACH CONTENTS:** Fruit and pebbles.

**TAXONOMY:** Our specimens have the more robust bill of the New Guinea subspecies and differ in this respect from the Bismarck population *M. n. major* (Gilliard and LeCroy, 1967).

**DISCUSSION:** These four specimens, collected in forest at 1000-3000 ft. in two separate areas (Mom in northwest Karkar, Kavailo in south Karkar), were our sole records. Meek did not obtain this species. Its rareness on Karkar is probably due to the abundance of its ecologically similar close relative *M. mackinlayi*. These two species have almost mutually exclusive distributions: *M. mackinlayi* in the New Hebrides and Solomons, *M. nigrirostris* on New Guinea and several nearby large islands, and a checkerboard distributional pattern in the Bismarcks, where *M. nigrirostris* occupies mainly the larger central islands and *M. mackinlayi* the smaller or more remote islands (see Diamond, 1975a, p. 358). The sole islands other than Karkar from which both species have been reported are New Britain, where *M. nigrirostris* is established and *M. mackinlayi* vagrant or very local on the coast; and Vuatom, where *M. mackinlayi* is established and *M. nigrirostris* is a rare vagrant. Evidently, a resident population of one of these species makes it very difficult for the other to establish itself.

**VOICE:** We once heard the call, a soft rising and then descending series of coo's as in New Guinea (Diamond, 1972a, p. 136). The immature male specimen was collected when it came to our imitation of this call.

*Reinwardtoena reinwardtii griseotincta*  
Great Cuckoo-dove

**SPECIMENS EXAMINED:** Karkar: 5 ♂, 4 ♀.

**MEASUREMENTS:** Wing: ♂ 227, 234, 243, 245; ♀ 222, 225, 227, 237. Tail: ♂ 295, 306; ♀ 270, 274. Exposed culmen: ♀ 21.0, 21.5, 24.0; ♀ 21.0, 22.0, 22.5, 23.0. Tarsus: ♂ 26.5, 27.0, 27.0, 29.0; ♀ 26.0, 27.0, 27.0, 27.0. Weight: ♂ 257, 265, 280, 298, 305; ♀ 247, 265, 267, 289.

**BREEDING AND MOLT:** Three specimens had the primaries in molt. One had the outer two primaries growing; the other two had the central primaries as well as the outer ones in molt. Three males had somewhat enlarged gonads. One male was collected from a nest of sticks about 15 ft. up, containing one white egg (measuring 40 × 25 mm.).

**STOMACH CONTENTS:** Fruit, once with pebbles.

**DISCUSSION:** On Karkar this cuckoo-dove was in forest from sea level to 3900 ft., but was uncommon at sea level and commonest at 2000-3600 ft., where it was more numerous than at any New Guinea location where we have met this species. Meek did not obtain this species.

We follow Mees (1964, p. 9) in amending the spelling of the species name from *reinwardtsi* to *reinwardtii*.

One individual was noted as having a red bill with a white tip. The bill of this species is usually noted in the literature as brown. A check of 35 specimens of this subspecies which had bill color noted showed that both bills noted as horn or brown and those noted as red with a light tip occurred in males and females and at all seasons. It seems more likely that bills noted as brown refer only to the swollen tip and that the area at the base is always red.

**VOICE:** Two distinct calls, as in New Guinea (Diamond 1972a, pp. 136-7): a series of disyllabic hoots, and a rapid descending series of notes resembling laughter. Calls were heard only in the hills, never in the lowlands.

*Chalcophaps indica chrysochlora*  
Green-winged Ground Dove

**SPECIMENS EXAMINED:** Bagabag: 2 ♂, 1 ♀.

**MEASUREMENTS:** Wing: ♂ 147, 150; ♀ 147. Tail: ♂ 92, 92; ♀ 88. Exposed culmen: ♂ 16.0, 17.5; ♀ 17.5. Tarsus: ♂ 25.5, 26.0; ♀ 25.5. Weight: ♂ 127, 129; ♀ 129.

**BREEDING AND MOLT:** The males had enlarged gonads; the female was ready to lay. There was no molt.

**STOMACH CONTENTS:** Twice pebbles only, once sand and ground-up fruit.

**DISCUSSION:** Neither Meek nor Diamond found this species on Karkar. Karkar and Bagabag each have three species of ground doves, of which two (*Chalcophaps stephani* and *Gallicolumba jobiensis*) are shared. The third is *G. beccarii* on Karkar and this species on Bagabag, where it is confined to open forest near the beach but heard regularly there.

**VOICE:** A series of up to seven coo's with a peculiar moaning quality repeated at one per second. Each note begins with an appoggiatura and then rises, and successive notes are slightly higher in pitch (fig. 6). Although this is a ground dove and one specimen was netted, several calling birds were in trees. One walked along a branch at the top of a tree as it called.

*Chalcophaps stephani stephani*

Stephan's Ground Dove

Gegekewagi (Karkar)

**SPECIES EXAMINED:** Karkar: 2 ♂, 4 ♀. Bagabag: 2 ♂, 1 ♀, 1 imm. ♀.

**MEASUREMENTS:** Wing: 136-148 ( $143 \pm 4$ ,  $n = 9$ ). Tail: 89-102 ( $94 \pm 4$ ,  $n = 9$ ). Exposed culmen: 17.5-21.0 ( $19.1 \pm 1.1$ ,  $n = 9$ ). Tarsus: 24.0-26.0 ( $24.6 \pm 0.6$ ,  $n = 9$ ). Weight: 102-115 ( $110 \pm 6$ ,  $n = 6$ ).

**BREEDING AND MOLT:** Molt is almost complete; the outer primaries are growing in six specimens. One male had the gonads enlarged.

**STOMACH CONTENTS:** In four individuals pebbles only, once seeds.

**DISCUSSION:** *Chalcophaps stephani* was fairly common in the lowlands of Karkar and Bagabag, once at 2300 ft.; and was more often heard than seen. We saw single individuals in forest, occasionally at the roadside, or in second growth or sago swamps, on the ground or at heights up to 15 ft. Most specimens were netted.

The immature female collected on June 13 weighed 112 grams. The feathers of the head, neck, and underparts are obscurely barred with black, and the glossy green on the wings is restricted to a band composed of the median coverts.

**VOICE:** As in New Guinea (Diamond, 1972a, p. 137), a faint, slightly rising series of notes lasting up to 15 seconds. The notes are repeated at three or four per second.

*Gallicolumba beccarii johannae*

Beccari's Ground Dove

**SPECIMENS EXAMINED:** Karkar: 2 ♂, 1 ♀.

**MEASUREMENTS:** Wing: ♂ 107, 112; ♀ 104. Tail: ♂ 69, 75; ♀ 63. Exposed culmen: ♂ 14.0, 14.5; ♀ 14.5. Tarsus: ♂ 26.0, 26.5; ♀ 24.0. Weight: ♂ 84, 85; ♀ 74.

**BREEDING AND MOLT:** One specimen has primary 10 growing. Gonads were slightly enlarged in one male, not enlarged in the other.

**STOMACH CONTENTS:** The stomachs of two birds contained only pebbles.

**TAXONOMY:** In this species it is the Bismarck Archipelago subspecies, *johannae*, which reaches Karkar. The Karkar population, as other Bismarck and Solomon populations, occurs in the lowlands, whereas the New Guinea race is virtually confined to the mountains above about 4000 ft.

**DISCUSSION:** Our sole records were of these three specimens, two of which were taken in nets, and all of which were taken near sea level.

*Gallicolumba jobiensis jobiensis*

White-breasted Ground Dove

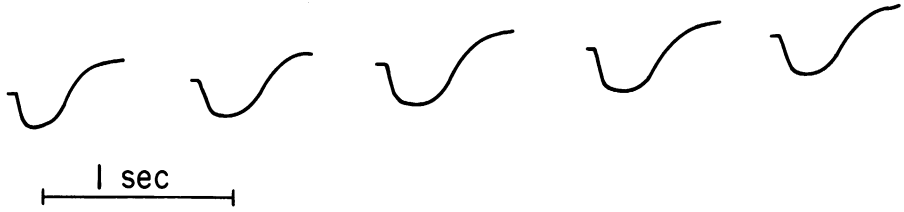
**SPECIMENS EXAMINED:** Karkar: 2 ♂. Bagabag: 1 ♀.

**MEASUREMENTS:** Wing: ♂ 144, 147; ♀ 135. Tail: ♂ 95, ♀ 83. Exposed culmen: ♂ 17.0, 17.5; ♀ 17.0. Tarsus: ♂ 25.5, 27.0; ♀ 26.0. Weight: ♂ 144, 150; ♀ 152.

**BREEDING AND MOLT:** Gonads were enlarged in one male. There was no molt.

**STOMACH CONTENTS:** Insects and a pebble in one stomach, a pebble in another.

**DISCUSSION:** Our female is very similar to the males in plumage. There are a few grayish tips to the feathers of the lower breast and abdomen, and the purple dorsal coloration is somewhat more restricted, but the sooty gray body color is similar and the throat and upper breast are white. There are a number of other females from various localities in the American Museum of Natural History collections which appear indistinguishable from males, and males

Chalcophaps indicaFIG. 6. Voice of *Chalcophaps indica*.

which appear indistinguishable from females in their grayer coloration and restricted purple. They seem to occur too frequently for all of these specimens to be mis-sexed, as Goodwin (1967, p. 272) supposed.

This species was listed under the name *Phlegoenas* [*sic*] *margarithae* by Rothschild and Hartert. It was collected by Meek.

Besides the three specimens collected, we saw six others on Karkar and Bagabag, all solitary and in the lowlands. They were in diverse habitats: forest, overgrown gardens, perched at 10 ft. in a dense patch of wild ginger, and on the ground in a coconut grove.

*Trichoglossus haematodus massena* and *T. h. micropteryx*

Rainbow Lory

Siril (Karkar). Sir (Bagabag)

SPECIMENS EXAMINED: Karkar: 11 ♂, 6 ♀, 2 ? sex. Bagabag: 4 ♂, 4 ♀, 3 ? sex.

MEASUREMENTS: See table 6.

PERISHABLE COLORS: Bill: yellow-orange. Legs: gray.

BREEDING AND MOLT: Stresemann and Stresemann (1966, p. 348) have described the molt in the Loriinae as regular, beginning with the sixth primary and moving from there in both directions. *Trichoglossus haematodus* follows this pattern. Eleven of 18 specimens were in some stage of molt. Five of these had the sixth primary missing, in five others molt had proceeded farther but apparently centered around primary number 6. On no occasion was more than one primary missing in a single wing, but the left and right wings of the same individual might be at slightly different stages of molt. The birds without traces of molt were

in fresh plumage and had apparently just completed molt.

There was one individual in which the molt differed from the normal pattern. This bird had the fifth primary worn in both wings, primary 4 was missing in the left wing and was worn in the right wing. The other primaries were not noticeably worn.

Gonads were slightly but not greatly enlarged in most males and in one female.

STOMACH CONTENTS: Vegetable matter containing some seeds; perhaps chewed-up flowers.

TAXONOMY: This species presents a complex picture in the Astrolabe Bay area. Cain (1955) considered Astrolabe Bay the dividing line between *T. h. intermedius* of north New Guinea and *micropteryx* of east New Guinea, with Karkar birds closest to the subspecies *massena* from the Bismarck Archipelago and eastward. Our Karkar birds are also definitely *massena* on the basis of their smaller size, particularly the much less heavy bill, and their paler red breast, compared to *intermedius* and *micropteryx*. They were also obviously smaller and paler than specimens from nearby Bagabag, all of which weighed more than any Karkar specimen. Measurements of AMNH specimens from the Sepik River, the Madang area, the Huon Peninsula and Manam Island are shown on the accompanying graph (fig. 7). Bagabag birds conform most closely in their measurements with birds from the Huon Peninsula (*micropteryx*). Birds from the Madang area and the Sepik River seem large, despite the small sample size; particularly are they heavy. Surprisingly, birds from Manam Island agree more closely with *micropteryx* in measurements (except for tail measurements of males), although



TABLE 6  
**Measurements of *Trichoglossus haematodus* on Karkar and Bagabag**

	Wing	Tail	Culmen from cere	Tarsus	Weight
Karkar	♂	100, 104, 106	20.0, 20.5, 21.0	16.5, 17.0, 17.5	92-114 (104±7, n=11)
	♀	94, 99	18.0, 18.5, 20.0	15.0, 16.5, 16.5	87-113 (98±10, n=6)
	? sex	99, 107	19.0, 20.0	16.0, 17.0	94, 114
Bagabag	♂	102-109 (105, n=4)	21.5-23.0, n=4)	18.0-19.0 (18.6, n=4)	127-142 (135, n=4)
	♀	102, 107, 107	21.0-23.5 (21.6, n=4)	18.0-19.0 (18.4, n=4)	125, 125, 126
	? sex	113, 115	22.0, 22.5	18.0, 18.5	115, 123, 141

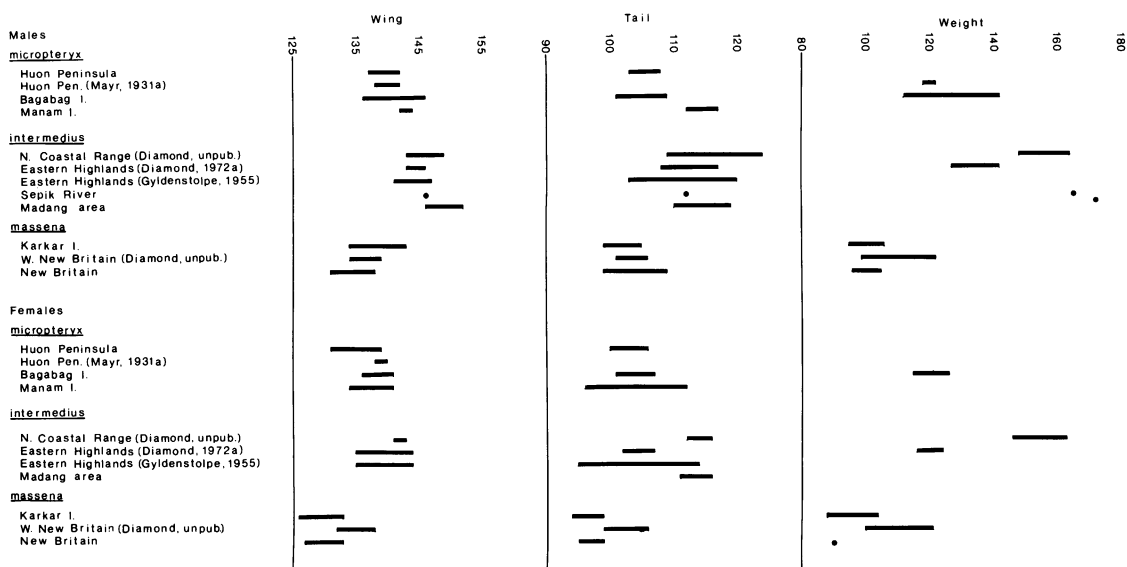


FIG. 7. Comparative measurements of *Trichoglossus haematodus*. The range of measurements is shown.

Manam is closer to Madang and the Sepik River than to the Huon Peninsula.

The picture becomes less clear when measurements of birds from the Eastern Highlands, identified as *intermedius*, are included. Published measurements by Gyldenstolpe (1955) and Diamond (1972a) are included in the graph (fig. 7). These measurements broadly overlap those of both *micropteryx* and *intermedius* and the weights are similar to those of our Bagabag birds. It may be that these two subspecies are not separable, but, until more material is available from the area between the Sepik River and Astrolabe Bay it seems preferable to consider the populations from Bagabag and Manam *micropteryx*, with *intermedius* confined to the mainland. In the case of these populations weights seem to be a useful character and more are badly needed.

There are two specimens from 1000 ft. on Bagabag that show the bronzing of the green parts which is so prevalent in *T. h. flavicans* (Cain, 1955, p. 440) from the northern Bismarck Archipelago, and comparison of our birds was made with specimens of *flavicans*. They have the breast more deeply marked with black and very slightly more salmon colored and lack the narrow pre-torqual band of reddish brown, as do *intermedius* and *micropteryx*.

Cain does not mention bronzing of the plumage in any subspecies other than *flavicans*, but there are in AMNH two specimens of *massena* from Witu Island which are bronzy, whereas six are of the normal color. Therefore, the bronzing is not restricted to *flavicans* and may in fact occur more frequently than collections indicate in populations of small islands.

**DISCUSSION:** This species was common on Karkar from sea level to up to 4500 ft., and on Bagabag at all elevations. At 3400-4000 ft. on the outer rim of Karkar crater this parrot was very noisy and abundant. Trees in this zone were full of displaying pairs opening and rapidly fluttering their wings at each other to show the colored bands in the underwing. Elsewhere on Karkar and Bagabag it concentrated in flowering trees.

#### *Vini rubrigularis*

##### Red-chinned Lory

**SPECIMENS EXAMINED:** Karkar: 14 ♂, 11 ♀, 3 ? sex.

**MEASUREMENTS:** Wing: ♂ 94, 95, 96; ♀ 92, 92, 94. Tail: ♂ 94; ♀ 92. Culmen from cere: ♂ 12.0, 12.0, 12.5; ♀ 12.5, 12.5, 13.0. Tarsus: ♂ 10.5, 11.0, 12.0; ♀ 11.0, 11.0, 11.0. Weight: ♂ 34-40 ( $37 \pm 2$ ,  $n = 13$ ); ♀ 33-40 ( $37 \pm 2$ ,  $n = 9$ ).

**BREEDING AND MOLT:** All except one of our nine specimens showed some wing molt, with primaries 5, 6, 7, or 8 actively growing. Two had the tails in molt as well. Stresemann and Stresemann (1966, p. 346) said that lorries renew the primaries in both directions from a focus which starts usually with the sixth primary. This would indicate that molt is just beginning in our birds. There was no sign of gonadal enlargement except in one female. The one bird not in molt is probably an immature as its measurements are small, especially the tail (83.5), and the red on the chin is quite restricted.

**STOMACH CONTENTS:** A white paste (nectar or chewed-up flowers?), sometimes with fragments of flowers.

**TAXONOMY:** Rothschild and Hartert (1915a, p. 3) described *krakari* as having a large red throat patch bordered by yellow. They had for comparison only a single skin from New Britain. The Ralum specimen that they saw is now in the American Museum of Natural History and appears to be an immature. The large series of New Britain skins that have been collected subsequent to the description of *krakari* has been used to make the following comparisons.

There is much variation in the amount of red on the throat and in the presence or absence of yellow in New Ireland, New Britain and Karkar birds, with the more restricted red apparently indicating immaturity. We can see no consistent differences between the populations.

Rothschild and Hartert also discuss the red on the "fourth outer primary." As there is no red on the primaries of any specimen, it is evident that they meant to say fourth outer rectrix. Hartert later (1924, p. 118) corrected this lapsus. The outer three rectrices do have red at the base; whether or not it is present on the fourth seems to vary individually in the Karkar, New Britain, and New Ireland birds and cannot be used as a subspecific character. Indeed, we found no color differences between the populations.

We have measured wing, tail, culmen from cere, and tarsus of all specimens in the American Museum of Natural History. Measurements of wing and tail are given in table 7. Culmen and tarsus measurements were very similar

TABLE 7  
Measurements of *Vini rubrigularis*

	Sex	Wing	Tail
Karkar	♂	94-96 (n=6)	94-100 (n=3)
	♀	91-95 (n=7)	91-96 (n=5)
New Britain			
Whiteman Mts.	♂	86-94 (n=7)	89-99 (n=6)
	♀	88-93 (n=5)	84-88 (n=4)
Baining Mts.	♂	86-94 (n=13)	86-94 (n=10)
	♀	86-92 (n=6)	86-92 (n=4)
Nakanai Mts.	♂	93 (n=3)	92, 95 (n=2)
	♀	90	78
New Ireland	♂	89 (n=2)	—
	♀	88-90 (n=3)	85, 91 (n=2)

(11.5-13.0 for bill and 10.5-12.0 for tarsus for males and females of all populations).

Additional specimens from New Ireland may show the size differences to be clinal with the birds averaging largest on Karkar and smallest on New Ireland. But sharp population differences in size do not occur and we suggest that the subspecies *krakari* to be placed in synonymy.

**DISCUSSION:** The Karkar population is the westernmost population of a species otherwise confined to three large islands of the Bismarck Archipelago. On Karkar it occurred at all elevations to the summit but was very uncommon below 2000 ft. In flocks of up to 10 it flew over the canopy, and fed in flowering trees together with *Trichoglossus haematodus*, *Nectarinia sericea*, and *Myzomela sclateri*.

**VOICE:** A high, shrill note, not as staccato or sharp as those of some other lorries.

*Micropsitta pusio beccarii*

Buffy-faced Pygmy Parrot

**SPECIMENS EXAMINED:** Bagabag: 2 ♂, 1 ♀, 3 ? sex.

**MEASUREMENTS:** Wing: 57-65 ( $61 \pm 3$ , n = 5). Tail (to tip of spike): 24-29 ( $26 \pm 2$ , n = 6). Culmen from cere: 8 (n = 4). Tarsus: 8.0-9.0 ( $8.3 \pm 0.4$ , n = 6). Weight: 13-15 ( $14 \pm 1$ , n = 6).

**BREEDING AND MOLT:** Five of our specimens showed some active molt. In two cases the wing apparently had a center of molt at primary 6, with only primary 6 having been replaced and primary 7 missing in one wing.

Otherwise we could see no regular pattern and the two wings were usually out of phase. Gonads were somewhat enlarged in one male.

**STOMACH CONTENTS:** Vegetable matter, apparently including seeds and flowers.

**TAXONOMY:** The subspecies differences cited in Rand and Gilliard (1967, p. 217) are confusing. In order to identify the Bagabag birds correctly, we looked carefully at a large series of specimens of all four currently recognized subspecies and found the following characters.

In adult males of *M. p. pusio* the lighter feathering of the forehead is broad; the forehead, eyestripe, sides of the nape and the face are reddish buff; the crown is on the average more royal blue than in the following subspecies. The females are similar but somewhat paler around the face and they average slightly more yellowish below.

In adult males of *M. p. beccarii* the light forehead is narrow, the forehead, eyestripe and sides of the nape are yellowish and the face is buffy; the crown averages more ultramarine blue. The females are similar.

Adult males of *harterti* are most similar to *pusio*, but more greenish below with a trace of an aqua breast band; the females are similar, but the two specimens available had no trace of the breast band.

Males of *stresemanni* are very similar to *pusio* but most individuals have a trace of an aqua breast band and they are larger; the females are similar.

Our specimens agree in all of these characters with *beccarii*.

**DISCUSSION:** On Bagabag this parrot was common in groups of 2 or 3 at all elevations, in forest, coconut trees, and feeding on bark. On Karkar we had only a few observations,

including a pair perched at 8-12 ft. on the trunk of a slender sapling in the forest understory.

**VOICE:** A faint, high-pitched, easily overlooked note call note "ts."

*Loriculus aurantiifrons* subsp.?

Bat Lorikeet

**SPECIMENS EXAMINED:** Karkar: 2 ♂, 1 ♀, 1 ? sex.

**MEASUREMENTS:** Wing: 68, 71, 71. Tail: 30.5, 31.0. Culmen from cere: 7, 7, 7. Tarsus: 8.5, 8.5, 9.0. Weight: 15, 15, 16, 16.

**BREEDING AND MOLT:** All specimens are in fresh plumage. Neither male had enlarged gonads.

**STOMACH CONTENTS:** Fruit; white paste, apparently flower sap.

**TAXONOMY:** All specimens of *L. a. batavorum* and *meeki* in the American Museum were measured. The measurements in table 8 show that *batavorum* averages smaller in wing length than *meeki*. The Karkar specimens are intermediate in size and until specimens are available from the adjacent New Guinea mainland the subspecies must remain in question. In fact, as there are no apparent differences in color, there may prove to be a cline of increasing size from west to east.

**DISCUSSION:** This species was not previously known from Karkar. It appears commoner on Karkar than on the New Guinea mainland. The specimens were collected in gardens at sea level and at 900-1900 ft. A pair flew across the road with a rapid, fluttering wing beat unusual for a parrot, to alight on a coconut leaf.

**VOICE:** A high-pitched call note.

*Cacomantis variolosus oreophilus*

Gray-breasted Brush Cuckoo

Kurugulumat (Karkar)

TABLE 8  
Measurements of *Loriculus aurantiifrons*

	Sex	Wing	Tail
<i>meeki</i>	♂	70, 72, 73, 73	31.0, 31.0, 32.0, 32.5
	♀	71, 71, 71, 72, 72, 74, 76	29.5, 30.0, 31.0, 31.0, 33.0, 33.0
Karkar	♂	68, 71	30.5, 31.0
	♀	71	—
<i>batavorum</i>	♂	67, 68, 68, 68, 69, 71, 71	30.0, 30.0, 30.0, 30.5, 30.5, 31.0, 31.0
	♀	68, 68, 68, 69	30.0, 30.0, 31.0, 31.0

SPECIMENS EXAMINED: Karkar: 1 ♂, 3 ♀.

MEASUREMENTS: See table 9. Weight: ♂ 36; ♀ 38, 41, 44.

BREEDING AND MOLT: Gonads were not enlarged. Two females were in active molt with primaries 8 and 5 growing in both wings in one individual and primary 5 growing in both wings of the other.

STOMACH CONTENTS: Insects.

TAXONOMY: Rothschild and Hartert (1914a, p. 4) named the subspecies *fortior* based on specimens from Fergusson and Goodenough Islands. Specimens from Umboi, Karkar, and Manam islands were subsequently referred to the same subspecies (Hartert, 1925, p. 168). Specimens of *fortior* were said by Hartert to be larger with broader, longer bills and longer wings than specimens of *infaustus* from the mainland of New Guinea.

The range of *C. v. infaustus* was considered at that time (1925) to include western New Guinea and some of the western Papuan islands and extend along the northern side of New Guinea to the Huon Peninsula and on the southern side to the Onin Peninsula; *oreophilus* occurred in eastern New Guinea from Collingwood Bay in the north to south of the Weyland Mountains in the south. Mayr (1931a, p. 697) ascribed a specimen from the Huon Peninsula to *infaustus* but said it could as well have been called *oreophilus*. Stresemann (1921, p. 37) named the long-tailed form, *C. v. macrocercus*, from New Britain.

With a very large series of birds at hand of

all of these nominal subspecies, it is apparent that color of plumage is too variable to be a useful character. Measurements are also very variable (see table 9). Specimens of *infaustus* do tend to have a more slender bill than specimens of *oreophilus*, but there is some overlap and apparently a cline of increasingly broader bill from west to east. However, the subspecies *infaustus* can be recognized on the basis of its usually slenderer bill, and it seems to occur no farther east than the Sepik River in the north and the Onin Peninsula in the south.

The overlap in measurements and width of bill between specimens of *oreophilus* and *fortior* from the coastal islands precludes the recognition of *fortior*. The Huon Peninsula birds also seem closer to *oreophilus*. Thus the range of *oreophilus* is from Astrolabe Bay, including the coastal islands, around southeastern New Guinea to south of the Weyland Mountains on the south coast.

The New Britain subspecies, *macrocercus*, has a much longer tail.

The plumage of adult females apparently falls into three morphs. One is very similar to the immature but with narrower dark bars on the feathers of the underparts, giving a lighter appearance, and broader buffy tips to the feathers of the underparts. A second form is like the male but with indistinct bars on the abdomen, and a third is indistinguishable from the male. There are breeding specimens of females in all three plumages.

Strikingly fewer females have been collected

TABLE 9  
Measurements of *Cacomantis variolosus*

	Wing	Tail	Bill from nostril
<b>Males</b>			
<i>infaustus</i>	111-123 (118±4, n=16)	99-118 (108±6, n=13)	13.0-15.0 (13.8±.6, n=17)
<i>oreophilus</i>	111-126 (120±4, n=46)	102-119 (109±4, n=39)	12.5-15.5 (14.3±.6, n=41)
<i>fortior</i>	119-131 (124±5, n=10)	110-126 (117±5, n=10)	14.0-16.0 (15.0±.5, n=9)
<i>macrocercus</i>	118-130 (125±3, n=13)	124-142 (133±7, n=11)	13.0-15.0 (13.8±.9, n=12)
<b>Females</b>			
<i>infaustus</i>	109-122 (116±4, n=9)	89-110 (102±6, n=8)	12.5-15.0 (13.9±.5, n=8)
<i>oreophilus</i>	112-125 (118±3, n=22)	98-109 (103±3, n=17)	12.5-15.0 (13.8±.5, n=19)
<i>fortior</i>	119-126 (121±3, n=8)	105-116 (107±4, n=6)	15.0-16.0 (15.3±.5, n=8)
<i>macrocercus</i>	122-128 (124±3, n=5)	119-134 (125±6, n=5)	12.5-15.0 (14.1±1.0, n=5)

than males. This perhaps indicates a behavioral difference between the sexes. For example, the song is loud and conspicuous and attracts collectors; perhaps only the male sings.

**DISCUSSION:** On Karkar this species was common and noisy from sea level to 4300 ft. It occurred regularly in the forest interior on Karkar as on the Solomon Islands, but it is excluded from forest on New Guinea (e.g., by its congener *C. castaneiventris*). On Bagabag, in contrast, it was uncommon, local, and confined to gardens at sea level. Perched individuals were seen at heights of 20-60 ft. A singer countersinging at another singer held its tail flared open.

**VOICE:** The unmistakable songs are like those heard on New Guinea (Diamond, 1972a, pp. 165-167) and unlike those heard on Bougainville (Diamond, 1975b, pp. 17-18). Songs were regularly heard at night as well as during the day.

*Chrysococcyx lucidus plagosus*

Golden Bronze Cuckoo

**SPECIMENS EXAMINED:** Karkar: 2 ♂, 1 ♀. Bagabag: 1 ♂.

**MEASUREMENTS:** Wing: ♂ 98, 100; ♀ 98. Tail: ♂ 65, 67; ♀ 66. Culmen from base: ♂ 18.0, 19.0; ♀ 19.5. Tarsus: ♂ 16.5, 17.0; ♀ 17.5. Weight: ♂ 24, 24, 25; ♀ 24.

**BREEDING AND MOLT:** Stresemann and Stresemann (1961, p. 330) reported on the molt in cuckoos. The genus *Chalcites* (= *Chrysococcyx*) is described as having an orderly transilient mode whereby there are two centers of molt each with its own ordered sequence of feather replacement. Our three specimens follow this pattern of molt, showing almost an alternation of fresh and worn primaries. Two of our specimens are in active molt. Gonads were very small in all specimens.

**STOMACH CONTENTS:** Insects.

**TAXONOMY:** These specimens have the dark iridescent bronze on the head and back that is characteristic of *plagosus*.

**DISCUSSION:** Apart from the specimens taken at sea level on Bagabag and in the mountains of Karkar at 500-4200 ft., our sole record of this winter visitor from Australia was an individual seen at sea level on Karkar.

*Eudynamis scolopacea rufiventer*

Indian Koel

**SPECIMENS EXAMINED:** Karkar: 1 ♂.

**MEASUREMENTS:** Wing: 188. Tail: 191. Bill: 30. Tarsus: 31. Weight: 197.

**BREEDING AND MOLT:** No molt; gonads not enlarged.

**STOMACH CONTENTS:** Fruit, 18 mm. in diameter.

**TAXONOMY:** Karkar birds are small like New Guinea mainland birds, compared to the larger Bismarck race *salvadorii*. Mayr (1937, p. 2) gave the measurements of 20 males of *rufiventer* as: wing 186-199 (av. 192); tail 164-198 (av. 186). Males of *salvadorii* from New Britain measure: wing 203, 205, 211; tail 201, 201, 201; weight 254, 300, 327.

**DISCUSSION:** On Karkar and Bagabag this noisy cuckoo was heard often and seen fairly often from the coast up to about 1000 ft.

**VOICE:** The loud song and calls resemble those of the New Guinea population (Diamond, 1972a, pp. 167 and 171).

*Scythrops novaehollandiae*

Channel-billed Cuckoo

**DISCUSSION:** Our sole record was of a single individual seen in flight at 1900 ft. on Karkar on June 6. Meek collected one specimen on March 10.

*Tyto alba*

Barn Owl

Sirar (Karkar)

**DISCUSSION:** Karkar residents described a large, white, nocturnal owl that eats rats and calls "ksh," surely a Barn Owl.

*Ninox connivens assimilis*

Barking Owl

Urguguk (Karkar)

**SPECIMENS EXAMINED:** Karkar: 1 ♂, 1 ♀.

**MEASUREMENTS:** Wing: 248, 269. Tail: 137, 146. Culmen from cere: 19. Tarsus: 34. Weight: ♂ 380, ♀ 430.

**PERISHABLE COLORS:** Iris: yellow. Bill: black. Feet: yellow.

**BREEDING AND MOLT:** No molt. Gonads were small.

**STOMACH CONTENTS:** Insects.

**DISCUSSION:** The female specimen was one

of a pair sleeping on a branch during the day. We heard the call every night while we were camped at 3400 ft. on Karkar. We obtained no records for Bagabag, but Bagabag residents described a nocturnal brown bird with large eyes and a call like that of *Ninox connivens*, and named "mukmuk," that may be this species.

VOICE: A disyllabic call like a dog barking, the first note at a higher pitch than the second, occasionally given as an antiphonal duet between two birds.

*Caprimulgus macrurus yorki*

Large-tailed Nightjar

Taratarong (Karkar)

SPECIMENS EXAMINED: Karkar: 1 ♂.

MEASUREMENTS: Wing: 182. Tail: 137. Bill: 22. Tarsus: 16. Weight: 69.

BREEDING AND MOLT: No molt apparent; gonads slightly enlarged. As Diamond walked along a dry, forest-shaded stream bed at sea level on Karkar during the day, five successive individuals of this nightjar flew up at intervals of several hundred yards. At three of the spots where these individuals had flown up, Diamond found a pair of eggs resting on the sand without any nest material. The eggs were coffee-colored with sparse, small, light gray-brown blotches and measured 30-34 mm. × 22-23 mm. One of the birds flopped on the ground with spread wings to distract attention from the eggs. Evidently this nightjar is a synchronized dry-season breeder, which prevents its eggs from being swept away in floods after rains.

STOMACH CONTENTS: Insects.

DISCUSSION: The call was heard each night while we were camped at 3400 ft. on Karkar. Our sole other records were of individuals disturbed while resting during the day on dry stream beds at sea level.

VOICE: A metallic "tuck-tuck-tuck", as on New Guinea (Diamond, 1972a, p. 179).

*Collocalia esculenta esculenta*

Glossy Swiftlet

SPECIMENS EXAMINED: Karkar: 3 ♂, 4 ♀, 2 ? sex.

MEASUREMENTS: Wing: ♀ 103, 108. Tail: ♀ 44, 46. Bill: ♀ 7.0, 7.5. Tarsus: ♀ 8.0, 8.5. Weight: ♂ 8.0, 9.0; ♀ 7.5, 8.0, 9.0.

BREEDING AND MOLT: There was no molt in

our four specimens. One of our females was collected on a nest which was one of two found under a boulder by a river. The nest was a crude cup of green and brown moss 3 inches deep and 4 inches in diameter. In the nest were two young. Diamond saw an individual fly back and forth along a deep-cut, narrow, forest-hung stream, hovering repeatedly at a moss-hung tree, flying off with moss trailing from its mouth and feet, and flying into a cavity in a shaded rock face down from which water was dripping. Possibly there was a nest in this cavity, though it was impossible to see inside to confirm.

STOMACH CONTENTS: Insects.

TAXONOMY: Rothschild and Hartert (1914b, p. 293) characterized the subspecies *stresemanni* as having the feathers of the "rump" with wide white borders all around, with the tip of the dark green spot on each feather frequently reaching the end of the feather. By "rump" feathers they probably meant flank and/or vent feathers as there are no white borders on the rump feathers. If this is true, then the character seems to be valid. Both *esculenta* and *stresemanni* have white in the outer three rectrices in varying amounts and this is not a valid character. On the basis of width of white border on flank and vent feathers Karkar birds are closest to *esculenta* with narrower tips.

DISCUSSION: *Collocalia esculenta* was common on Karkar and Bagabag at all altitudes. The two *Collocalia* species on Karkar segregate cleanly in foraging zone, *C. hirundinacea* foraging high above the treetops in the open, *C. esculenta* generally at a height below the treetops. *Collocalia esculenta* flew over rivers, in clearings, and even within the forest itself—for example, within 10 ft. of the ground inside montane forest 60 ft. high. The surprising presence of swiftlets in Karkar forest (surprising to someone who is familiar with these birds from New Guinea) may constitute a niche shift made possible by Karkar's lack of sallying insectivorous flycatchers, such as the species of *Rhipidura* and *Microeca* common in New Guinea. *Collocalia esculenta* on Karkar often skimmed close to foliage and even hovered at foliage like a hover-gleaning flycatcher, presumably to pick off insects or else nest material.

*Collocalia hirundinacea hirundinacea*  
Mountain Swiftlet

DISCUSSION: *Collocalia hirundinacea* was common in the mountains of Karkar, from about 800 ft. to the summit; not observed in the lowlands of Karkar, and absent from Bagabag. Unlike *C. esculenta*, this species foraged in the open well above the treetops. Both species of swiftlets flew in and out of a huge hole or vent in the volcanic cone in the center of Karkar crater.

*Ceyx azureus ochrogaster*  
Azure Kingfisher

SPECIMENS COLLECTED: Karkar: 1 ♂.

MEASUREMENTS: Wing: 74. Tail: 32. Culmen from base: 49. Tarsus: 10.5. Weight: 35.

PERISHABLE COLORS: Bill: black. Legs: orange.

BREEDING AND MOLT: Gonads not enlarged; no molt.

STOMACH CONTENTS: Insects.

TAXONOMY: Rothschild and Hartert originally ascribed Karkar birds to the subspecies *lessoni*, but Mayr (1941) included them in the subspecies *ochrogaster*, from northern New Guinea, which has paler underparts than *lessoni*. We agree; the present specimen also has the paler underparts.

DISCUSSION: On Karkar we saw single individuals on seven occasions, in forest, at small streams, and once in roadside second growth, always within 5 ft. of the ground. Most observations were in the lowlands, but the specimen was caught in a mist-net at 2500 ft.

*Ceyx lepidus solitarius*  
Dwarf Kingfisher

SPECIMENS EXAMINED: Karkar: 3 ♂, 3 ♀, 1 ? sex.

MEASUREMENTS: Wing: ♂ 56, 57; ♀ 56, 58, 58. Tail: ♂ 23.0; ♀ 22.0, 22.5. Bill: ♂ 37.0, 39.0; ♀ 38.0, 39.0, 39.5. Tarsus: ♂ 8.0, 9.0; ♀ 9.0, 9.0, 9.0. Weight: ♂ 14.0, 14.0, 21.0; ♀ 15.5, 17.0, 17.5; ? sex 19.0.

BREEDING AND MOLT: Two individuals were molting their fourth and fifth primaries, respectively. One of these was also in heavy body molt, as was another individual. None was in breeding condition.

STOMACH CONTENTS: Insects.

TAXONOMY: These specimens are of the small, black-billed, mainland race.

DISCUSSION: We found this species to be inconspicuous and uncommon in Karkar forest up to 3300 ft. Several sightings were at brooks or dry stream beds. Most of the specimens were taken in mist-nets, an indication of understory habits.

*Halcyon sancta sancta*  
Sacred Kingfisher

SPECIMENS EXAMINED: Karkar: 3 ♂, 6 ♀, 2 ? sex. Bagabag: 1 ♂, 6 ♀.

MEASUREMENTS: Wing: ♂ 91, 93; ♀ 90, 91, 93; ? sex 92. Tail: ♂ 57, 62; ♀ 60, 61; ? sex 60. Tarsus: ♂ 14.0, 14.0; ♀ 13.0, 13.0, 13.5; ? sex, 14.0. Culmen from base: ♂ 42, 49; ♀ 40, 43, 47; ? sex 47. Weight: ♂ 41, 43, 44, 44; ♀ 42-50 ( $46 \pm 3$ ,  $n = 11$ ).

MOLT AND BREEDING: Three individuals of eleven had about half finished primary molt and a fourth was replacing the tenth primary. None had enlarged gonads.

STOMACH CONTENTS: Insects (nine Karkar specimens), an orthopteran 8 cm. long (one from Bagabag), crabs (four from Bagabag). The difference between Karkar and Bagabag specimens is probably due to the fact that the Karkar specimens were taken inland, the Bagabag specimens on the coast.

DISCUSSION: The Sacred Kingfisher was common on Karkar up to 1900 ft., at the forest edge, along stream beds, and in open second growth, but not in forest, at heights up to 70 ft. On Bagabag it was very common along the coast and occasionally in forest, where two specimens were netted. One individual was seen to sally and catch an insect in midair.

*Tanysiptera galatea meyeri*  
Common Paradise Kingfisher

Belalarom (Karkar). Bilelo-agam (Bagabag)

SPECIMENS EXAMINED: Karkar: 9 ♂, 10 ♀, 1 imm. ♂, 5 imm. ♀. Bagabag: 2 ♂, 2 ♀, 1 imm. ♂.

MEASUREMENTS: Wing: ♂ 101-109 ( $105 \pm 3$ ,  $n = 7$ ); ♀ 103, 105, 106, 107; imm. ♂ 100, 104; imm. ♀ 98, 104. Tail without central tail feathers: ♂ 87, 100, 106, 109; ♀ 87-110 ( $96 \pm 9$ ,  $n = 5$ ); imm. ♂ 81, 81; imm. ♀ 84, 88, 117. Bill: ♂ 36.0-39.5 ( $38.0 \pm 1.3$ ,  $n = 7$ ); ♀ 35.0-40.5 ( $37.9 \pm 2.5$ ,  $n = 7$ ); imm. ♂ 36.5,



38.5; imm. ♀ 36, 37, 40. Tarsus: ♂ 16.5-18.5 (17.7 ± 0.7, n = 7); ♀ 17.5-19.0 (18.4 ± 0.6, n = 7); imm. ♂ 18.0, 18.5; imm. ♀ 17.5, 18.0, 19.0. Weight: ♂ 48-64 (54 ± 4, n = 11); ♀ 49-64 (57 ± 5, n = 12); imm. ♂ 59; imm. ♀ 49-59 (54 ± 4, n = 5).

**BREEDING AND MOLT:** Most adults were just completing primary molt, with primaries 9 and/or 10 growing. The immatures were not molting. No individual had enlarged gonads.

**STOMACH CONTENTS:** Insects.

**DISCUSSION:** On Karkar, this species was abundant in the lowlands, and in low numbers up to 2700 ft.; uncommon in Bagabag. This kingfisher is confined to the shaded forest interior, where it is heard far more often than seen. It lives mainly in the understory and is frequently caught in mist-nets. Occasionally it perches on the ground or as high as 30 ft. While perched, it sometimes raises and lowers its tail slowly.

**VOICE:** The song is a rising whistled trill that accelerates and is usually preceded by a slower, downslurred note (Diamond, 1972a, pp. 186 and 191). The call is a long, mournful, rising, whistled note. Several individuals may countersing simultaneously, as also true of the kingfisher *Dacelo gaudichaud*. In quality and pattern the song is very similar to that of the kingfishers *Melidora macrorhina*, *Halcyon torotoro*, and *H. megarhyncha*.

*Merops ornatus*

Ornate Bee-eater

Kurik-kurik (Karkar)

**SPECIMENS EXAMINED:** Karkar: 3 ♂, 6 ♀, 1 ? sex. Bagabag: 1 ♀.

**MEASUREMENTS:** Tail without central feathers: ♀ 76, 80. Bill: ♀ 37, 39. Tarsus: ♀ 10.5, 11.0. Weight: ♂ 28, 28, 30; ♀ 25-32 (28 ± 3, n = 6).

**BREEDING AND MOLT:** None of the specimens had enlarged gonads. All three specimens examined for molt had the seventh primary growing in. There is apparently one complete molt per year spread over about nine months. Specimens from Queensland were beginning molt in December and January. Wintering birds in New Guinea and New Britain were molting every month from February through August and

September, by which time the outermost primaries were growing.

**STOMACH CONTENTS:** Insects.

**DISCUSSION:** *Merops ornatus* was fairly common on Karkar at the forest edge up to at least 4100 ft., including in the crater. Just after dawn each morning while we were camped on the outer wall of the crater, we heard flocks flying overhead as if leaving communal night roosts. On Bagabag we saw only a few individuals in gardens. Meek did not collect this austral winter visitor.

*Eurystomus orientalis waigiouensis*

*Eurystomus orientalis pacificus*

Dollarbird

**SPECIMENS EXAMINED:** Karkar: 1 ♀ (*pacificus*). Bagabag: 1 ♂ (*waigiouensis*), 1 ♀ (*pacificus*).

**MEASUREMENTS:** *E. o. waigiouensis*. Wing: ♂ 208. Tail: ♂ 108. Bill: ♂ 33.5. Tarsus: ♂ 19.5. Weight: ♂ 214. *E. o. pacificus*. Wing: ♀ 193. Bill: ♀ 30.0, 32.0. Tarsus: ♀ 18.5, 19.0. ♀ 172, 195.

**BREEDING AND MOLT:** The female from Bagabag was just completing primary molt; both females had the tail in molt.

**STOMACH CONTENTS:** Insects.

**TAXONOMY:** The three specimens collected by Meek on Karkar were originally listed as *Eurystomus orientalis crassirostris*, a large-billed form from the Bismarck Archipelago. They are, in fact, all three the smaller-billed *waigiouensis*, the resident breeding form of the New Guinea region (*pacificus* is an Australian wintering visitor).

**DISCUSSION:** This is an uncommon species in the lowlands of Karkar (up to 1700 ft.) and Bagabag.

*Pitta sordida novaeguineae*

Black-headed Pitta

**SPECIMENS COLLECTED:** Karkar: 1 ♀.

**MEASUREMENTS:** Wing: 102. Tail: 38. Bill: 24. Tarsus: 39. Weight: 74.

**BREEDING AND MOLT:** The specimen was not in molt. A nest was found that contained a single young bird.

**STOMACH CONTENTS:** Insects.

**TAXONOMY:** Hartert (1930, p. 92) described

*hebetior* as an endemic Karkar race from Meek's collection and characterized it as "duller, darker, on the breast, and the back is also slightly darker green in the series." Comparing Meek's six specimens from Karkar (including the type) with a large series of skins of *novaeguineae* from New Guinea, we find these characters not to hold. The individual variation in ventral color within *novaeguineae* is great and encompasses the variation found in the Karkar series. The more recently collected specimen is dorsally darker than any. Although the whole Karkar series does perhaps average slightly darker above than New Guinea birds, we consider the differences insufficient for taxonomic recognition. We therefore suggest synonymizing *hebetior* with *novaeguineae*.

DISCUSSION: This species is confined to the lowlands of New Guinea, but on Karkar it is confined to the mountains at elevations of 2300-3900 ft. It was solitary and shy, and generally seen only when it flew up from the ground and flew away just a few feet above the ground. Except for one individual on the boulders of a stream bed, all others were seen in forest.

*Hirundo tahitica frontalis*

Welcome Swallow

SPECIMENS EXAMINED: Bagabag: 3 ♂, 6 ♀, 3 ? sex.

MEASUREMENTS: Wing: ♂ 105; ♀ 108, 109, 110. Tail: ♂ 47.0; ♀ 47.5, 49.0, 51.0. Bill: ♂ 10.5; ♀ 12.0, 12.5. Tarsus: ♂ 8.5; ♀ 9.5, 9.5, 10.0. Weight: ♂ 15, 15, 17; ♀ 14-17 ( $15 \pm 1$ ,  $n = 6$ ); ? sex 15, 16, 16.

BREEDING AND MOLT: No molt. The males had gonads slightly enlarged.

TAXONOMY: These birds have the lighter underparts of *frontalis*; *ambiens* from New Britain is much darker below.

DISCUSSION: The Welcome Swallow was uncommon in the lowlands of Karkar and Bagabag, mainly along the coast. We often saw pairs perched on dead trees that had been washed onto the beach but were still resting partly in the water. An individual of *Haliastur indus*, perched in such a tree, was repeatedly dive-bombed by a swallow. One flew up from a puddle where it had apparently been drinking.

*Hirundo nigricans nigricans*

Tree Martin

DISCUSSION: Our sole record of this Australian wintering visitor was of a single individual flying at Karkar airport on June 7.

*Coracina tenuirostris muelleri*

Long-billed Graybird

SPECIMENS COLLECTED: Karkar: 11 ♂, 5 ♀.

MEASUREMENTS: Wing: ♂ 124-134 ( $130 \pm 3$ ,  $n = 7$ ); ♀ 125, 126, 126, 133. Tail: ♂ 106, 108; ♀ 103. Bill: ♂ 27.0, 28.0, 29.5, 29.5; ♀ 27.0, 28.0, 30.0. Tarsus: ♂ 23.0, 23.5, 24.0, 24.5; ♀ 23.5, 24.0, 25.0, 25.0. Weight: ♂ 68 - 80 ( $72 \pm 4$ ,  $n = 4$ ); ♀ 71-80 ( $76 \pm 3$ ,  $n = 5$ ).

BREEDING AND MOLT: Most specimens had the tail and the inner primaries in molt. None was in breeding condition, except that one male had testes slightly enlarged.

STOMACH CONTENTS: Insects (11 stomachs), fruit (4 stomachs).

TAXONOMY: The subspecies *heinrothi* from New Britain and *rooki* from Umboi Island are smaller than *muelleri* from New Guinea and Karkar, particularly in the females. In addition, the females of both *heinrothi* and *rooki* are browner above, particularly on the head, and less barred below. Males of *heinrothi* and *rooki* are a darker blue gray.

DISCUSSION: We found *Coracina tenuirostris* on Karkar from the lowlands to 4500 ft., but rarely at sea level and commonly only above 2000 ft. Songs were never heard below 2000 ft. and were commonly heard only above 3000 ft. Most observations were in forest, though a few were in garden trees. In New Guinea this is an open-country lowland species, excluded from forest by several congeners that have not colonized Karkar. Absence of these competitors may explain the presence of *Coracina tenuirostris* in forest and at higher elevations on Karkar, but its failure to achieve a greater abundance in the Karkar lowlands than in the New Guinea lowlands is surprising. This is strictly a middle-story and canopy species, living at 20-70 ft.; no individual was mist-netted. Meek did not collect this species.

VOICE: The song is a ringing series of clear notes repeated at 3 per second for 10-30 sec-

onds, the series increasing slightly in volume. Like several congeners (*C. montana*, *C. schisticeps*) and relatives (*Campochaera sloetii*), a group of *C. tenuirostris* flying from one treetop perch to another give musical chirps and chattering calls.

*Coracina novaehollandiae* subsp.

DISCUSSION: Our sole record of this Australian wintering visitor was of a single individual seen June 7 in a tree in a lowland garden on Karkar.

*Turdus poliocephalus keysseri*  
Island Thrush

SPECIMENS EXAMINED: Karkar: 3 ♂, 2 ? sex.

MEASUREMENTS: Bill: ♂ 26.0, 26.0, 26.0; ? sex 24.0, 25.5. Tarsus: ♂ 35.0, 35.0, 36.0; ? sex 34.5, 35.5. See Table 10 for wing, tail, and weight.

PERISHABLE COLORS: Iris: brown. Bill: yellow. Legs: yellow.

BREEDING AND MOLT: The gonads were not enlarged in one male, only slightly enlarged in two males. There was no molt.

STOMACH CONTENTS: Fruit.

TAXONOMY: This species has subspeciated, sometimes markedly, on almost every island on which it occurs throughout its vast range in the Pacific. In the New Guinea area there are four

named populations on New Guinea itself (*papuensis*, *keysseri*, *erebus*, *versteegi*), *heinrothi* and *beehleri* from St. Matthias Island and New Ireland, respectively in the Bismarck Archipelago, and *canescens* from Goodenough Island. When we compared the material available to us, it quickly became apparent that the color of the skins changes with age. Specimens of *papuensis* collected by the Archbold Expedition in 1933 are noticeably darker than skins collected prior to 1913. Specimens of *erebus*, all collected in the 1950s, fall within the range of variation exhibited by *papuensis* collected in the 1930s. However, they are smaller, particularly the type (see table 10).

Our two skins of *keysseri*, collected in 1912 on the Huon Peninsula, are similar in color to the skins of *papuensis* collected before 1913; but they are considerably smaller, as are birds reported by Mayr (1931a) from the Huon Peninsula. The Karkar birds are similar in size and weight to *keysseri*, and are similar in color to the darker specimens of *papuensis* collected after 1930. The subspecies *keysseri* was originally separated from *papuensis* by Mayr (1931a) solely on the basis of its smaller size; no mention was made of color differences. Therefore it seems reasonable to assume that the differences between our birds and Huon Peninsula specimens are related to the time since collection of

TABLE 10  
Measurements of *Turdus poliocephalus*

	Sex	Wing	Tail	Weight
<i>versteegi</i>	♂	131-140 (n=3)	108	—
	♀	131-138 (n=3)	99-104 (n=3)	—
<i>papuensis</i>	♂	130-134 (n=7)	97-104 (n=7)	74, 80
	♀	126-128 (n=6)	92-97 (n=6)	77, 80
<i>erebus</i>	♂ (Type)	125	94	—
	♀	117, 127	88, 92	—
<i>keysseri</i>	♂	122	89	—
	♀	121	87	—
from Mayr (1931a)	♂	118, 124	—	69, 72
	♀	118, 119	—	71, 71
Karkar	♂	122, 122, 123	90, 91, 93	71, 78
	?	114	85	73
<i>heinrothi</i>	♂ (Type)	111	83	—

the specimens, as are the differences between specimens of *papuensis* of different ages.

We also examined the type of *heinrothi* from St. Matthias Island in the Bismarck Archipelago. It is a much smaller bird (table 10), very brownish in color (collected in 1923). We have not examined specimens of *beehleri* from New Ireland, but it is described as even smaller (Ripley, 1977).

The subspecies *canescens* from Goodenough Island is known from only three specimens in the Queensland Museum. They were probably collected by W.E. Armit on Mt. Oiamadawa (Mayr and Van Deusen, 1956). No other expeditions to Goodenough have encountered the species and we had no comparative material.

Specimens of *Turdus poliocephalus* collected by Diamond on Tolokiwa Island in the Bismarck Archipelago in the same year as the Karkar birds differ from them and from all other New Guinea populations in that the latter have the head and upper breast browner than the rest of the plumage with an obvious demarcation between the browner upper breast and the more blackish lower breast and abdomen. The Tolokiwa birds are overall more grayish black without an obvious difference, in most individuals, between the head and the rest of the body. They are also smaller. Both of these differences are in the direction of the small, very dark subspecies, *bougainvillei*. These differences will be discussed more fully in a subsequent report.

**DISCUSSION:** The Island Thrush was observed only in montane forest on Karkar between 3800 and 5000 ft.; uncommon there. Two collected in a fruiting tree had fruit in their stomachs. One was observed perched at heights of 6-20 ft. in forest 50 ft. tall.

Two unsexed specimens from Karkar have wide cinnamon tips on the feathers of the breast and abdomen. Recently collected sexed specimens often have narrow browner tips on these feathers, but the very wide tips may indicate immaturity.

This species was not collected by Meek.

**VOICE:** Calls include a soft, short, harsh rasp like that of *Monarcha cinerascens*, and a typical *Turdus* alarm call consisting of a rapid series of 2-6 notes "peak!" similar to the call

of *T. migratorius* (North America) but at a lower pitch. We heard no songs.

*Cisticola exilis diminuta*

Fantail Warbler

**SPECIMENS EXAMINED:** Bagabag: 4 ♂, 1 ♀, 3 ? sex.

**MEASUREMENTS:** Wing: ♂ 45.0, 45.5, 45.5; ♀ 42.0; ? sex 39.5, 45.0, 46.0. Tail: ♂ 42.5; ♀ 40.0; ? sex 38.5. Bill: ♂ 12.0, 12.5, 12.5, 13.0; ♀ 12.0; ? sex 12.0, 12.5, 13.0. Tarsus: ♂ 20.5, 21.0, 21.0, 21.5; ♀ 19.5; ? sex 20.0, 21.0, 21.0. Weight: ♂ 9.0, 9.0, 9.0, 9.0; ♀ 7.0; ? sex 8.0, 9.0.

**BREEDING AND MOLT:** Two individuals had the sixth and seventh primaries in molt. One male had somewhat enlarged gonads and three did not. The male with enlarged gonads and two of the other three were in the male breeding plumage; the remaining male and the female had a streaked crown.

**STOMACH CONTENTS:** Mostly insects, but two stomachs contained some grass seeds.

**DISCUSSION:** This is one of only two species resident on Bagabag but apparently absent on Karkar. It was confined on Bagabag to grassland.

*Gerygone magnirostris affinis*

Swamp Gerygone Warbler

**SPECIMENS EXAMINED:** Karkar: 3 ♂, 2 ? sex.

**MEASUREMENTS:** Wings: ♂ 52, 58; ? sex 54. Tail: ♂ 40, 41, 44. Bill: ♂ 13, 13. Tarsus: ♂ 16.0, 16.5, 18.0; ? sex 17.0. Weight: ♂ 9.0, 9.0; ? sex 9.0.

**BREEDING AND MOLT:** Two specimens had the central primaries in molt. Two of three males had enlarged gonads.

**STOMACH CONTENTS:** Insects.

**DISCUSSION:** *Gerygone magnirostris* was local and uncommon in the lowlands of Karkar up to 900 ft.; it was found singly or in pairs, at the forest edge and in gardens, and was absent from the forest interior. Individuals were seen at heights of 18-40 ft. One was seen to hover-glean.

**VOICE:** The song is a nasal repeated series of slurs, depicted elsewhere (Diamond, 1972a, p. 226 and 228).

*?Gerygone ruficollis*

## Red-necked Gerygone Warbler

DISCUSSION: Diamond twice thought he heard what appeared to be the distinctive song of this warbler (see Diamond, 1972a, p. 226) in forest at 4300 ft. on the crater rim of Karkar. There are no records of *Gerygone ruficollis* from surrounding islands, only from New Guinea itself. We mention this possible but doubtful record to alert future observers on Karkar; it should not be accepted without confirmation.

*Phylloscopus trivirgatus giulianettii*

## Island Leaf Warbler

SPECIMENS EXAMINED: Karkar: 5 ♂, 1 ♀.

MEASUREMENTS: Wing: ♂ 56, 57, 57, 58; ♀ 54. Tail: ♂ 39, 39, 41; ♀ 38. Bill: ♂ 11, 12, 13, 13; ♀ 12. Tarsus: ♂ 20.0 (4); ♀ 19.5. Weight: ♂ 8.5, 8.5, 9.0, 9.0, 9.0; ♀ 11.0.

BREEDING AND MOLT: No molt. All five males had enlarged gonads.

STOMACH CONTENTS: Five had eaten insects and one had apparently eaten vegetable matter.

TAXONOMY: Specimens from New Guinea (*giulianettii*), Goodenough (*hamlini*), and New Britain (*moorhousei*) were compared with the Karkar material. No differences were discernible between the Karkar specimens and mainland birds. Specimens of *hamlini* have the sides of the crown much blacker, and *moorhousei* is a much more bronzy green bird.

DISCUSSION: This species was fairly common in Karkar montane forest at 3600-4900 ft. on the outer crater wall and also on the crater floor. Individuals were seen from the lower story to the crowns, but mainly in the crowns. Songs were frequent. This species was not collected by Meek.

VOICE: A high, sibilant, formless warble lasting nearly one second and repeated at intervals of 4-5 seconds.

*Rhipidura leucophrys* subsp.

## Willie Wagtail

## Kamalo (Karkar)

DISCUSSION: Surprisingly rare: we saw only one individual on Bagabag and five (one of them singing) on Karkar. All were in open lowland habitats (beach, village, airport, dry stream beds). Karkar residents said that the

Willie Wagtail is rare in the dry season (the season of our visit) and more numerous in the wet season. Elsewhere in New Guinea too, Diamond was told that this species leaves or becomes less common in the dry season.

*Monarcha cinerascens impediens*

## Island Gray-headed Monarch Flycatcher

SPECIMENS EXAMINED: Karkar: 6 ♂, 4 ♀, 2 [imm.] ♂, 2 [imm.] ♀. Bagabag: 5 ♂, 3 ♀, 2 imm. ♂, 1 imm. ♀.

MEASUREMENTS: Wing: ♂ 87-94 (91 ± 2, n = 10); ♀ 83, 85, 86; [imm.] ♂ 83, 84, 84, 88\*; [imm.] ♀ 84, 84, 85, 86. Tail: ♂ 74-83 (78 ± 3, n = 10); ♀ 72, 72, 73; [imm.] ♂ 69, 69, 72, 74\*; [imm.] ♀ 71, 71, 73, 74. Bill: ♂ 23.0-24.5 (23.8 ± 0.5, n = 9); ♀ 23.0, 23.0, 23.5; [imm.] ♂ 22.5\*, 23.0, 23.0; [imm.] ♀ 22.0, 22.5, 23.0, 23.5. Tarsus: ♂ 21.5-23.0 (22.3 ± 0.5, n = 11); ♀ 21.5, 22.5, 22.5, 23.0; [imm.] ♂ 22.5\*, 22.5, 23.0, 23.0; [imm.] ♀ 21.0, 22.5, 22.5, 23.0. Weight: ♂ 24-35 (29.8 ± 3.1, n = 11); ♀ 24 - 41 (29.3 ± 4.0, n = 7); [imm.] ♂ 25, 26\*, 28, 31; [imm.] ♀ 24, 25, 26. (\* = molting into adult plumage).

BREEDING AND MOLT: Many individuals were in heavy body molt. Although wing molt was noted in several, most had fresh primaries. At altitudes above 3000 ft. on Karkar almost all males collected had large testes, one of them had the inner primaries in molt, and one female was nearly ready to lay. All individuals on Bagabag, and all except one in the lowlands of Karkar, had small gonads. The occurrence of immatures in the population, the presence of molt in some individuals of Meek's birds and of ours, and the occurrence of birds with enlarged gonads indicate that this species probably has an extended breeding season and an overlap of molt and breeding. In addition, breeding season evidently varies with altitude on Karkar.

STOMACH CONTENTS: Insects. One stomach contained a grasshopper. A stomach studied in detail contained several types of nonflying insects (a thrip, a collembolan, a small cockroach, many ants) and two seeds.

TAXONOMY: The race *nigrirostris* from Manam, Karkar and the coast of New Guinea from Tarawai to Huon Gulf was originally de-

scribed mainly on the basis of its black bill with horn base; whereas other races have a steel blue bill with light cutting edges and tip. However, our specimens from Karkar and Bagabag have bills of both types. Furthermore, the individuals having black bills with light bases also usually have a brownish edge to the primaries, secondaries and coverts, and a brownish wash on the rump and upper breast. Individuals with bluish bills with light cutting edges and tip do not have this brownish wash, and the rufous of the lower breast and abdomen is more sharply delineated from the gray of the upper breast. These characters do not correlate with locality or sex. They correlate with size in the males. One specimen with bluish bill is molting the primaries and brown-edged feathers are being replaced by all gray ones. It would seem that birds with black bills, lighter at the base, and with a brownish wash are immatures. The measurements of these birds have been given separately above. This interpretation holds for other subspecies as well (e.g., Mees, 1965b, p. 184).

The original series from Karkar and Manam, collected in February by Meek, and a specimen from Madang (October) all have black bills with light bases. Seven of these also have a brownish wash and are probably immatures. Six have black bills with light bases but adult plumage. It may be that these birds represent nonbreeding adults and that the bill changes color in the breeding season. All of the May and June adults in the present collection lack a light base to the bill.

Neumann (1929, p. 197) in his original description of *nigrirostris* mentions the fact that his specimens resemble the immatures of other races, but he had no specimens showing the bluish bills and so assumed that the black-billed birds represented the adult condition. Now that bluish-billed birds have been collected on Karkar, the status of the subspecies *nigrirostris* must be reassessed. However, our comparative material from New Guinea is scant. The few specimens of *fuscescens* and *inornatus* that we have seen have the lower abdomen paler rufous and the throat, neck, and upper breast lighter gray than our birds. *Rosselianus* has a heavier bill and *perpallidus* from the Bismarck Archipelago is much paler. Karkar and Bagabag

birds are inseparable from specimens of the widespread race *impediens*, from the Bismarck Archipelago and the Solomons, and extend the range of that subspecies westward. More comparative material is needed from New Guinea before a decision can be made on whether *nigrirostris* (type locality, Sattelberg) should be considered a synonym of *impediens*.

There is some tendency to increase in size with increase in altitude in adult males. Seven from sea level to 1000 feet measured: wing 88-91, tail 74-78; three from 3400-3600 feet on Karkar measured: wing 93-94, tail 80-83.

DISCUSSION: *Monarcha cinerascens* was fairly common on Karkar from the lowlands to 4800 ft., and on Bagabag nearly to the summit. Most foraging was done at heights of 20-60 ft., occasionally in the understory. Foraging techniques sometimes included sallying and hovergleaning but mainly consisted of plucking food items off leaves and branches. One individual repeatedly pounded a large insect held in its bill against a branch, then held the insect in its foot and tore it apart with its bill. Unlike *Myiagra alecto* but like *Pachycephala melanura*, this flycatcher moves by frequent short hops along a branch between flights. While perched, it frequently peers around. A group of three foraged for over 10 minutes in the same tree.

VOICE: The song (fig. 8) is a repeated, loud, mellow, slurred note, with a quality similar to the calls of *M. frater* or *Oriolus szalayii*, and a pattern sometimes very similar to that of *M. frater*. The calls include squawks, loud squeaking notes, and a repeated scolding note suggestive of a squirrel. Foraging groups call often and loudly and in this respect are reminiscent of the warbler *Mohoua ochrocephala* of New Zealand.

*Myiagra alecto chalybeocephalus*  
Shining Flycatcher  
Sibogbog (Bagabag)

SPECIMENS COLLECTED: Karkar: 8 ♂, 6 ♀, 3 imm. ♂. Bagabag: 5 ♂, 2 ♀.

MEASUREMENTS: Wing: ♂ 86-94 (90 ± 3, n = 13); ♀ 84-89 (86 ± 2, n = 7). Tail: ♂ 72-79 (75 ± 2, n = 13); ♀ 70-74 (72 ± 1, n = 7). Bill: ♂ 19.5-22.5 (21.3 ± 1.0, n = 11); ♀ 20.5-22.0 (21.3 ± 0.5, n = 6). Tarsus: ♂ 18.0-20.5 (19.5 ± 0.8, n = 13); ♀ 19.0-20.5

Monarcha cinerascensFIG. 8. Voice of *Monarcha cinerascens*.

(19.6 ± 0.6, n = 7). Weight: ♂ 24-31 (27.2 ± 4.0, n = 13); ♀ 20-32 (24.6 ± 4.0, n = 8); imm. ♂, 22, 22, 25.

**BREEDING AND MOLT:** No molt was observed, except that in one male collected on May 28 primaries 8 and 9 were growing in. Testes were enlarged, sometimes very large, in more than half of the males, but others had very small testes. Three immature males still in female-like plumage were collected.

**STOMACH CONTENTS:** Insects in most specimens, fruit in two.

**DISCUSSION:** The Shining Flycatcher was common on Karkar from the lowlands to 3600 ft., and occasionally to 4000 ft.; very common on Bagabag from the lowlands to 900 ft., and occasionally higher. In New Guinea, where there are several dozen competing species of flycatcher, this one is mainly confined to second growth and waterside habitats. On Karkar and Bagabag, which *Myiagra alecto* shares with only one other resident flycatcher, it occurred commonly in lowland and montane forest as well as in coconut groves. It foraged between 3 and 80 ft. above the ground, but mainly at 10-60 ft. This foraging range also represents a niche expansion compared to the situation in New Guinea, where it usually remains below 30 ft. Its foraging technique is to hold a perch for 8 to 36 seconds, occasionally to hover-glean, then to fly several feet (occasionally 30 ft.) to the next perch.

**VOICE:** The commonest song is a rapid whistled trill generally rising in pitch, occasionally all on the same pitch. A less common song is a slow nasal trill dropping in pitch, similar in quality to notes of the drongo *Dicrurus hottentottus*. The commonest call is a very harsh rasped note that crescendos greatly; less often, two or three notes "tuck" with a quality as of a xylophone, spaced at intervals of one-half second.

*Myiagra cyanoleuca*  
Satin Flycatcher

**DISCUSSION:** In the Karkar lowlands a female was seen on June 4, an immature male on June 8. Meek collected one in female-like plumage on March 7. Other records of this wintering visitor from Australia on islands north of New Guinea are for Manam, Umboi, New Britain, and Lihir. In contrast, there are only a few records for the mainland of north New Guinea itself.

One of these individuals was at 50-80 ft. in a roadside tree, the other at 80 ft. in a tall forest tree overhanging a dry narrow stream bed. At intervals of half-a-minute these birds made short sallies, remaining within 5 ft. of the vegetation and returning to the same or a nearby perch. They snapped repeatedly and occasionally hovered in midair. On perching after each sally, they quivered the tail. One sallied for many minutes from the crown of the same tree.

*Aplonis cantoroides*  
Singing Starling

**SPECIMENS EXAMINED:** Karkar: 2 ♂, 3 ♀, 1 ? sex, 2 imm. ♀.

**MEASUREMENTS:** Wing: ♂ 102, 103; ♀ 97; ? sex 100; imm. ♀ 96. Tail: ♂ 69, 69; ♀ 64; ? sex 68; imm. ♀ 63. Bill: ♂ 25.0, 25.0; ♀ 23.5; ? sex 24.0; imm. ♀ 24.0. Tarsus: ♂ 23.0, 23.5; ♀ 21.0; ? sex 23.0; imm. ♀ 23.0. Weight: ♂ 56, 59; ♀ 48, 53, 55; ? sex 56; imm. ♀ 47, 54.

**PERISHABLE COLORS:** Iris: orange-red.

**BREEDING AND MOLT:** Gonads were considerably enlarged in one male, slightly enlarged in the other. There was no molt.

**STOMACH CONTENTS:** Fruit.

**DISCUSSION:** In the lowlands of Karkar, where the starling *A. metallica* was abundant, we encountered *A. cantoroides* only twice. On

Bagabag, where *A. metallica* was similarly abundant, *A. cantoroides* was absent. However, above the altitudinal range of *A. metallica* on Karkar *A. cantoroides* occurred in small numbers through gardens at 1900 ft., in montane forest up to the crater rim at 3900 ft., and on the hot cone in the center of the crater. *A. cantoroides* is absent from forest on New Guinea.

*Aplonis metallica metallica*

Metallic Starling

Syen (Karkar)

SPECIMENS EXAMINED: Karkar: 8 ♂, 11 ♀, 5 imm. ♂, 3 imm. ♀. Bagabag: 1 ♂, 5 ♀, 2 imm. ♂, 4 imm. ♀.

MEASUREMENTS: Wing: ♂ 106, 111, 113, 113, 117; ♀ 104-115 ( $108 \pm 4$ ,  $n = 9$ ). Tail: ♂ 101, 104, 106, 110, 111; ♀ 85-106 ( $96 \pm 7$ ,  $n = 7$ ). Bill: ♂ 22.0, 22.5, 25.0; ♀ 22.5-25.0 ( $23.6 \pm 0.9$ ,  $n = 8$ ). Tarsus: ♂ 22.0, 23.0, 23.0, 23.0, 23.5; ♀ 21.0-23.0 ( $22.4 \pm 0.7$ ,  $n = 7$ ). Weight: ♂ 50-65 ( $59 \pm 5$ ,  $n = 9$ ); ♀ 49-70 ( $58 \pm 6$ ,  $n = 16$ ); imm. ♂ 54-67 ( $60 \pm 4$ ,  $n = 7$ ); imm. ♀ 45-70 ( $56 \pm 10$ ,  $n = 5$ ).

BREEDING AND MOLT: Most adult males, and some immature males, had testes somewhat but not greatly enlarged. Two females were nearly ready to lay. No adults were in molt.

STOMACH CONTENTS: Fruit.

TAXONOMY: Karkar and Bagabag birds have the large purplish metallic spot in the middle of the back characteristic of *metallica*; in specimens from Umboi and New Britain this spot is smaller (subspecies *nitida*).

DISCUSSION: *Aplonis metallica* was common in the lowlands of Karkar (up to 2000 ft.) and Bagabag, inside forest as well as in open habitats. On Karkar we found several colonial nesting trees. On Bagabag we found only one nesting tree, in Matiu-number-1 village, where both immatures and adults were collected and from which they ranged over the whole length of the island. Most were seen in the canopy, several groups were netted in the understory, and a group of three was seen on the beach.

*Nectarinia sericea sericea*

Black Sunbird

SPECIMENS EXAMINED: Karkar: 15 ♂, 9 ♀, 1 juv. ♂. Bagabag: 12 ♂, 3 ♀, 1 imm. ♂.

MEASUREMENTS: Wing: ♂ 60-65 ( $62 \pm 1$ ,  $n = 20$ ); ♀ 54, 54, 56, 56. Tail: ♂ 35.0-40.0 ( $37.4 \pm 1.2$ ,  $n = 18$ ); ♀ 29.0, 31.0, 32.5, 32.5. Bill: ♂ 19.0-22.0 ( $20.7 \pm 0.9$ ,  $n = 12$ ); ♀ 18.0, 19.5, 20.0, 21.0, 21.0. Tarsus: ♂ 15.0-16.0 ( $15.5 \pm 0.4$ ,  $n = 22$ ); ♀ 14.0, 14.5, 15.0, 16.0. Weight: ♂ 9.0-12.0 ( $10.6 \pm 0.8$ ,  $n = 16$ ); ♀ 8.0-10.0 ( $9.5 \pm 0.7$ ,  $n = 12$ ).

BREEDING AND MOLT: A number of individuals had the wings in molt. Most adult males had the gonads enlarged, but none of the nine adult males examined for molt showed molt. One male in female-like plumage, presumably an immature, also had enlarged gonads. Perhaps the breeding season in this species was just starting, as one juvenile male was collected with primaries still in sheath, and males outnumbered females 2:1 in the collection.

STOMACH CONTENTS: Insects and fruit pulp.

TAXONOMY: These birds have the iridescence of the throat purplish and of the back more greenish as in *sericea* of mainland New Guinea. The subspecies *eichhorni* from Feni has the purplish throat patch but is more bluish on the back; the subspecies *caeruleogula* from New Britain and Umboi islands (Mees, 1965a, p. 43) and *corinna* from the rest of the Bismarck Archipelago have the throat bluish.

DISCUSSION: We found this species common on Karkar in the lowlands, and in lower numbers up to about 4100 ft. On Bagabag it was the most abundant bird species at all elevations from sea level to the summit. Like its congener *N. jugularis*, this sunbird occupies open habitats in New Guinea but expands into forest on Karkar and Bagabag in the absence of competitors except at high elevations, where it is replaced by the honeyeater *Myzomela sclateri*. Individuals occasionally descended to the understory, where six were netted. Foraging individuals hover-gleaned at leaves, probed with the bill at bases of leaves, and fed in flowering trees with lories.

Two individuals both in female plumage were observed to display together for several minutes, with one of these individuals repeatedly singing. Possibly immature males breed while still in female-like plumage, as suggested by one collected with enlarged testes.



*Nectarinia jugularis frenata*  
Yellow-bellied Sunbird

SPECIMENS EXAMINED: Karkar: 11 ♂, 5 ♀.  
Bagabag: 4 ♂, 1 ♀, 1 ? sex.

MEASUREMENTS: Wing: ♂ 56-59 ( $57 \pm 1$ ,  $n = 15$ ); ♀ 54-55 ( $54 \pm 0$ ,  $n = 6$ ). Tail: ♂ 37.0-40.0 ( $38.7 \pm 1.0$ ,  $n = 13$ ); ♀ 34.0-36.5 ( $35.4 \pm 0.9$ ,  $n = 6$ ). Bill: ♂ 20.0-24.0 ( $22.6 \pm 1.1$ ,  $n = 10$ ); ♀ 20.0-23.0 ( $21.5 \pm 1.0$ ,  $n = 6$ ). Tarsus: ♂ 15.0-16.5 ( $15.6 \pm 0.5$ ,  $n = 15$ ); ♀ 15.0-15.5 ( $15.3 \pm 0.3$ ,  $n = 6$ ). Weight: ♂ 9.0-12.0 ( $10.3 \pm 0.7$ ,  $n = 13$ ); ♀ 8.0-11.0 ( $9.1 \pm 0.9$ ,  $n = 5$ ).

BREEDING AND MOLT: No molt. Virtually all males had the gonads enlarged.

STOMACH CONTENTS: Mostly insects, sometimes fruit, once flowers.

TAXONOMY: Specimens collected by Meek were assigned by Rothschild and Hartert to the subspecies *flavigaster*, which has the yellow of the underparts deeper than does *frenata* from New Guinea. In looking at a larger series, one becomes aware that there is much overlap in color of the underparts, very deep yellow individuals occurring in both subspecies. But *flavigaster* has more of these deep yellow individuals, and often the upperparts of these birds are more yellowish green. The Karkar birds are not the very deep yellow on the underparts and it seems best for the present to consider them *frenata*.

DISCUSSION: On Karkar *Nectarinia jugularis* was common up to about 3300 ft. and in the crater, and rarely to 3900 ft.; on Bagabag it was fairly common in the lowlands and occasionally up to the summit. In New Guinea this sunbird is strictly confined to open habitats, but both on Karkar and Bagabag it occurs regularly in forest as well as in open habitats. Together with its congener *N. sericea* it takes over the niches of New Guinea's numerous forest warbler and meliphagid species. Its virtual disappearance around 3300 ft. is probably related to the appearance at that altitude of the abundant, ecologically similar meliphagid *Myzomela sclateri*, and possibly of the warbler *Phylloscopus trivirgatus*. Most observed were at heights of more than 5 ft., but four individuals were netted in the understory.

VOICE: The song is a very rapid, jumbled twitter.

*Myzomela sclateri*  
Sclater's Myzomela

SPECIMENS EXAMINED: Karkar: 15 ♂, 4 ♀, 4 imm. ♂, 3 imm. ♀.

MEASUREMENTS: Wing: ♂ 61-66 ( $64 \pm 2$ ,  $n = 11$ ); ♀ 58, 59, 59, 60. Tail: ♂ 40.0-44.5 ( $42.2 \pm 1.3$ ,  $n = 15$ ); ♀ 37.0, 38.0, 38.0, 38.0, 39.5. Bill: ♂ 17.0-18.0 ( $17.5 \pm 0.5$ ,  $n = 13$ ); ♀ 16.0, 17.0, 18.0. Tarsus: ♂ 16.0-18.5 ( $17.6 \pm 0.7$ ,  $n = 15$ ); ♀ 17.5, 17.5, 17.5, 18.0. Weight: ♂ 10.5-12.0 ( $10.9 \pm 0.4$ ,  $n = 10$ ); ♀ 10.0, 10.0, 10.0, 11.0.

BREEDING AND MOLT: One female had the inner primaries in molt. All immature males had the tail in molt but none of the adults showed tail molt. Many of the males, both adult and immature, had heavy molt on the head. Gonads were enlarged in all except one of the males collected; no females had enlarged gonads. The fact that many more immatures and males than females were collected may indicate that breeding was in progress. Males outnumbered females 2:1, as is apparently true for some other myzomelid species (Rand and Gilliard, 1967, p. 533; Diamond, 1972a, p. 361).

STOMACH CONTENTS: Insects, fruit, and flower parts.

TAXONOMY: Mayr (1955, p. 41) has already noted the wide variation in back color between individuals in the same series. The red of the throat is also variable within the same series. We have made wing, tail, bill, and tarsus measurements of the 22 specimens in the American Museum of Natural History from six localities and find no consistent size differences.

DISCUSSION: *Myzomela sclateri* was observed only in Karkar montane habitats: a few individuals down to 3400 ft., common at 3800 ft., the most abundant bird species above 3900 ft., and the sole bird species in the stunted shrubbery in Karkar's summit. In the forest in the lower part of its altitudinal range it foraged mainly above 10 ft., occasionally descending to the understory, but was nonetheless abundant in

summit shrubbery less than 10 ft. tall. *Myzomela sclateri* frequently hover-gleaned. Its gleaning was unsystematic and punctuated by frequent flights of 15-30 ft. Of all New Guinea bird species that we have encountered, this one spished up most infallibly to small noises we made to attract birds. At each spishing sound we made above 4500 ft., half-a-dozen *Myzomela sclateri* flew up, followed us, and flew from perch to perch in a circle around us.

Ecologically and biogeographically, *Myzomela sclateri* is the most remarkable bird population of Karkar. The species is confined to islands along the north coasts of New Britain and New Guinea but has never been recorded from these two large islands themselves. The Karkar population is the westernmost known population. Most of the islands on which *Myzomela sclateri* occurs are low, tiny, coral islets, except for the recently defaunated volcanic island of Long and its neighbors Tolokiwa and Crown, where the species occurs from sea level to the summits at 2000-4500 ft. *Myzomela sclateri* is an extreme example of a "super-tramp" (Diamond, 1975a): a species of high dispersal ability, reproductive potential, and ecological amplitude but low competitive ability, confined to small species-poor islands where population turnover is high and competitors few, and to recently defaunated volcanoes which it can recolonize ahead of its competitors.

In colonizing Karkar, *Myzomela sclateri* underwent a drastic niche shift, from strand forest on warm coral atolls to the cool, damp, moss-hung summit forest and shrubbery above 3300 ft. on Karkar. Its altitudinal floor on Karkar correlates approximately with the altitudinal ceiling of the ecologically similar sunbirds *Nectarinia jugularis* and *N. sericea*, so that its absence below 3300 ft. is probably due to competition from these two species combined (see Diamond, 1975a, pp. 404-406 and 418-420, for analysis of the complex competitive relations among these species). Thus, the Karkar population of *Myzomela sclateri* gave up its usual coastal niche and shifted into a very different habitat. It remains a puzzle why such a vagile species, having made the 70-mile overwater

colonizing jump from the nearest population (on Crown Island) to Karkar, has not established itself on Bagabag, only 14 miles from Karkar, and 50 miles from Crown.

*Dicaeum pectorale rubrocoronatum*

Red-capped Flowerpecker

SPECIMENS EXAMINED: Karkar: 3 ♂, 4 ♀, 1 imm. ? sex.

MEASUREMENTS: Wing: ♂ 53, 54; ♀ 48.0, 49.5, 51. Tail: ♂ 25, 27; ♀ 21, 23, 24. Bill: ♂ 11.0, 12.0; ♀ 11.0, 11.5, 12.0. Tarsus: ♂ 11.0, 11.5; ♀ 11.0, 11.5, 12.5. Weight: ♂ 7.0, 7.5, 8.0; ♀ 7.0, 8.0, 8.0, 8.5.

BREEDING AND MOLT: Gonads enlarged in all three males; no molt apparent.

STOMACH CONTENTS: Small fruits.

TAXONOMY: Salomonsen (1960, pp. 27-31) has considered *D. pectorale*, *D. geelvinkianum*, and *D. nitidum* conspecific, whereas other authors have considered *pectorale*, at least, to be a distinct species. The geographical distribution of these three forms and the occurrence of populations obviously intermediate between *pectorale* and *geelvinkianum* are strong arguments in favor of Salomonsen's view. The presence of greenish head color in *pectorale* and some individuals with a rusty cap also would seem to indicate relationship to the red-capped populations.

The Karkar birds belong to the widespread subspecies *rubrocoronatum*.

DISCUSSION: This species occurred in modest numbers in forest on Karkar up to about 3400 ft., and on Bagabag up to the summit; heard much more often than seen.

VOICE: The call is a short, weak, unmusical, unvoiced note "tsik." The note is distinctive, but so slight and brief that courage and practice are required to identify this species by voice.

*Erythrura trichroa sigillifera*

Blue-faced Parrot Finch

SPECIES EXAMINED: Karkar: 2 ♂, 2 ♀, 1 ? sex.

MEASUREMENTS: Wing: ♂ 61; ♀ 58, 61; ? sex 62. Tail: ♂ 48.5; ♀ 42.0, 43.0; ? sex 36.5. Bill: ♂ 13.0, 14.0; ♀ 11.5, 13.5; ? sex 12.0. Tarsus: ♂ 17, 18; ♀ 16, 17; ? sex 16.

Weight: ♂ 16.0, 16.5; ♀ 15.0, 16.5; ? sex 13.0.

**BREEDING AND MOLT:** One male had the outer primaries in molt. Both males had slightly enlarged gonads.

**STOMACH CONTENTS:** Mostly fruit with some seeds; insects in one stomach.

**TAXONOMY:** Rothschild and Hartert listed the Karkar birds as subspecies *goodfellowi*, but Mayr (1931b, p. 5) has shown that *sigillifera* is the older name.

**DISCUSSION:** *Erythrura trichroa* was uncommon and inconspicuous in Karkar montane forest between about 1000 and 4200 ft.; it was once observed at sea level, and once in a garden. One individual was seen drinking water, another was feeding at the flower of the limbun palm, and two were netted.

*Lonchura tristissima calaminoros*

Streak-headed Mannikin

**SPECIMENS EXAMINED:** Karkar: 1 ♂, 2 ♀, 1 ? sex.

**MEASUREMENTS:** Wing: ♂ 48.0, ♀ 47.0, 49.0; ? sex 48.5. Tail: ♀ 35; ? sex 34. Ex-

posed culmen: ♂ 11.0; ♀ 11.0, 11.5; ? sex 11.0. Tarsus: ♂ 14.0; ♀ 13.0, 14.0; ? sex 13.5. Weight: ♂ 10; ♀ 10; ? sex 8.

**BREEDING AND MOLT:** Gonads of the male were slightly enlarged. The specimens were not in molt.

**STOMACH CONTENTS:** Insects and seeds.

**TAXONOMY:** We agree with Mayr (1931a, p. 654) in assigning Karkar birds to the widespread subspecies *calaminoros*, replaced only in west New Guinea by other races.

**DISCUSSION:** On Karkar this mannikin occurred uncommonly in groups of up to six at altitudes up to 1700 ft., in gardens, grass, second growth, and forest at the edge of watercourses, but not inside dense forest. On the New Guinea mainland, where *Lonchura* mannikins and sylviid warblers coexist in grassland, the former take almost exclusively seeds, the latter insects. On Karkar, which lacks a grass-warbler, *Lonchura tristissima* expands its diet to include insects. Similarly, the grass-warbler *Cisticola exilis* on Bagabag, which lacks mannikins, takes seeds as well as insects.

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