Ecological Consequences of Island Colonization by Southwest Pacific Birds, I. Types of Niche Shifts

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Abstract. The land and fresh-water birds of the southwest Pacific islands derive mainly from New Guinea and offer a favorable situation for studying ecological consequences of island invasions. The reduction of competition on species-poor islands permits some colonizing species to expand their niches spatially, by occupying altitudinal bands, types of habitats, and/or vertical strata of the forest from which they are excluded by other species on species-rich islands. Expansions to higher altitudes, or from second-growth into forest, are especially frequent. Other colonists become more abundant in the same type of habitat preferred on New Guinea. Instances of a change in diet are rare. Changes in foraging technique are noted mainly for those colonists that have been isolated long enough to have undergone morphological divergence. Approximately half of the colonizing populations experience no niche shift.

One of the most distinctive features of island ecology is variation in the niche of a given species on different islands as compared to a mainland. For example, there are many instances in which a species of insect, reptile, bird, or mammal has been reported to be more abundant and/or to occupy a wider range of habitats on a small, isolated, species-poor island than on a species-rich island or on the mainland.[1-4] These island situations offer the possibility of determining to what extent the niche of a given species is determined by competition and to what extent by its intrinsic adaptations. Further questions of general biological interest that may be illuminated by analyses of island ecology include: which components of the niche are most plastic; which types of shifts require genotypic change, which do not; and what are the effects of factors such as population size, isolation, and longevity on fitness.

A favorable opportunity to study these niche shifts is provided by the land and fresh-water birds on the islands of the southwest Pacific. The Papuan, Melanesian, and Polynesian zoogeographical subregions consist of thousands of islands, ranging in size from a fraction of an acre up to 312,000 square miles; in number of resident bird species from 1 to 512; in elevation from flat atolls up to 17,000 ft; and in isolation from the colonization source area—from a few yards to 5000 miles. Most of the birds of the southwest Pacific islands are derived from the largest and most species-rich island, New Guinea, with a smaller number of species derived from Australia or New Zealand, whose avifaunas are, however, also closely related to that of New Guinea. The south-west Pacific

has the added advantage that its islands have been relatively well explored ornithologically, and its birds are relatively well understood taxonomically.[5,6] Furthermore, New Guinea itself behaves like an "island archipelago" as far as the distribution of montane birds is concerned, since New Guinea consists of mountain ranges of different sizes isolated from each other by a "sea" of uninhabitable lowlands.[7] Thus, by studying the same bird species on different islands or on different mountains, one may observe how its niche varies in the face of competition from only a few other species or from several hundred other species. The results presented here are derived from a program of explorations and ecological studies[7] that has encompassed the following islands, with the number of breeding land and fresh-water bird species in parentheses after the name of each island: New Guinea (512); New Britain (126) in the Bismarck Archipelago; Guadalcanal (94) in the Solomon Islands; New Zealand (91); Karkar (52) off northern New Guinea; Espiritu Santo (49) in the New Hebrides; Viti Levu (46) in the Fiji group; Admosin (46) and other islands of the Madang Archipelago off northern New Guinea; Upolu (30) in the Samoa group; and Bagabag (29) off northern New Guinea. This article summarizes the types of niche shifts observed.

1. **Altitudinal Shifts.** One of the commonest ecological sorting mechanisms among congeneric bird species on New Guinea is altitudinal. That is, there are many sequences of two to five congeneric species which inhabit mutually exclusive altitudinal bands as a result of interspecific competition but which are otherwise very similar ecologically.[9,10] On the smaller isolated ranges of New Guinea, or on mountainous Pacific islands smaller than New Guinea, one often finds that one or more members of these sequences have failed to establish themselves and that the remaining members have expanded their altitudinal ranges either upwards or downwards. Figs. *a*, *b*, and *c* illustrate examples, respectively, of a high-altitude species and a low-altitude species simultaneously expanding into the range of a missing middle-altitude congener, a low-altitude species taking over the range of a missing high-altitude congener, and a high-altitude species taking over the range of a missing low-altitude congener.

Altitudinal expansions on small islands are also observed in the cases of species whose narrow altitudinal ranges on New Guinea cannot be attributed to competition from congeners. In these cases the expanding species must be taking over parts of niches which are occupied by less closely related species on New Guinea. One instance discussed below in which the missing competitor can be clearly identified proves to involve interactions between members of different families (the *Myzomela* honey-eaters and the *Nectarinia* sunbirds: see next section. A second example is that the thrush *Turdus poliocephalus*, the only species of its genus in the Pacific, is confined to altitudes above 9000 ft on New Guinea but descends to 4000 ft on Karkar and to sea-level on many other small islands, such as Espiritu Santo, Viti Levu, and Upolu. A third instance is provided by the white-eye *Zosterops atrifrons*, whose altitudinal range on New Britain is not only expanded upwards (correlated with the absence of *Z. fuscicapilla*) but also (in low numbers) downwards to sea-level (Fig. 1*b*), although there is no *Zosterops* in the New Guinea lowlands to explain its absence there.
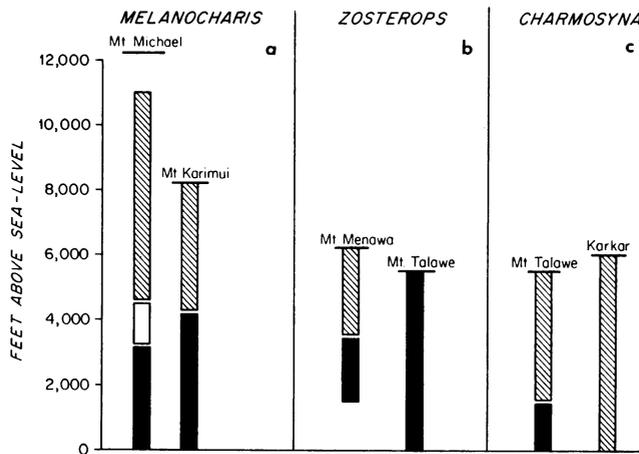
FIG. 1.   (a) Altitudinal ranges of three similar congeneric flower-peckers on two New Guinea mountains: *Melanocharis nigra,* solid shading; *M. longicauda,* un-shaded; *M. versteri,* diagonal striping.   The elevation of the summit of the mountain is indicated by a heavy horizontal line in this figure and in Figs. 1b and c.   On large mountains such as Mt. Michael (left), all three species are present and have mutually exclusive altitudinal ranges (0–3200, 3200–4550, 4550–11,000 ft).   On the smaller and more isolated Mt. Karimui (right) *M. longicauda* failed to establish itself, and the remaining two species expanded their ranges to fill the gap: *M. nigra* at 0–4200 ft, *M. versteri* from 4200 ft to the summit at 8200 ft.

(b) Altitudinal ranges of two congeneric white-eyes on mountains of two Pacific islands: *Zosterops atrifrons,* solid shading; *Z. fuscicapilla,* diagonal striping.   On New Guinea (e.g., Mt. Menawa, left), both species are present and have mutually exclusive altitudinal ranges, *Z. atrifrons* at 1500–3500 ft. and *Z. fuscicapilla* at 3500–6000 ft.   Only *Z. atrifrons* succeeded in colonizing New Britain (Mt. Talawe, right), where it occurs abundantly up to the summit at 5500 ft through the altitudinal range utilized by *Z. fuscicapilla* on New Guinea and thus 2000 ft higher than in the presence of its competitor, as well as extending in low numbers down to sea-level.

(c) Altitudinal ranges of two congeneric lorikeets on mountains of two Pacific islands: *Charmosyna placentis,* solid shading; *C. rubrigularis,* diagonal striping.   Both species are present on New Britain (Mt. Talawe, left) and have mutually exclusive altitudinal ranges, *C. placentis* at 0–1500 ft and *C. rubrigularis* at 1500–5500 ft.   Only *C. rubrigularis* succeeded in colonizing Karkar Island (right), where it extends down to sea-level, having expanded into the whole range of its absent competitor.

The instances in which a given species extends to higher elevations on New Britain or Karkar as compared to New Guinea outnumber the cases of expansion to lower elevations by 2:1 for New Britain and by 4:1 for Karkar.   For instance, of 49 bird species common to Karkar and New Guinea, nine tropical species extend to higher altitudes on Karkar than on New Guinea, two montane species extend to lower altitudes on Karkar than on New Guinea, and 38 species have essentially the same altitudinal range on both islands.   This predominance of upward expansions reflects the very limited area at higher elevations on Karkar and New Britain and hence the extreme reduction in truly montane species compared to New Guinea.   In both relative and absolute terms, New Guinea has far more area at high elevations, and far more montane species (birds which do not descend to sea-level), than other Pacific islands.   Thus, on New Guinea about 177 species, or 35% of the total breeding avifauna, are montane, while the

corresponding figures are 15 species or only 12% of the avifauna on New Britain, and six species or 12% of the avifauna on Karkar.   This preferential impoverishment of the true montane avifauna permits a preferential upwards spread of lowlands birds on the smaller islands, a feature which proves important in interpreting inter-island variations in total bird population densities in montane forest.[8]

2. **Habitat Shifts.** Broadening of habitat selection made possible by reduced competition on islands has been observed frequently[1-4] and is also conspicuous in southwest Pacific birds.   Three typical examples may be cited: (*a*) Two species of *Chalcophaps* ground-doves occur on New Guinea and Bagabag with mutually exclusive habitat selection, *C. indica* in light coastal forest, *C. stephani* in the lowland rainforest further inland.   On Karkar and New Britain, where *C. indica* is absent, *C. stephani* occupies the coastal forest as well as the interior. On Espiritu Santo, where *C. stephani* is absent, *C. indica* occurs in the interior forest as well as on the coast.   (*b*) On New Guinea and most neighboring islands the role of insectivorous gleaner in dry grassland is filled by one or more species of true grass-warblers (family Sylviidae).   None of these warblers has reached Guadalcanal, where one instead finds, inside tall dry grass, dense populations of the sunbird *Nectarinia jugularis*, confined to the forest edge and bushes or trees in open country in New Guinea.   (*c*) On New Guinea and New Britain there are two unrelated groups of small birds with elongated curved bills that congregate at flowers to drink nectar and take insects: the sunbirds of genus *Nectarinia*, strictly confined to the forest edge and open country in the lowlands, and the honey-eaters of genus *Myzomela*, in forest both in the lowlands and in the mountains.   Where sunbirds and honey-eaters meet, fights have been observed.[11]   On Karkar the sole species of honey-eater, *Myzomela sclateri*, is largely confined to elevations above 4000 ft, and the two species of sunbirds (*Nectarinia sericea* and *N. jugularis*) occur in the lowlands not only in open country but also in the forest interior, and extend up the mountain slopes to the elevation at which *Myzomela sclateri* appears.   The reverse situation, sunbirds absent and *Myzomela* honey-eaters appearing in open country of the lowlands as well as in forest, occurs on Espiritu Santo and Upolu (*Myzomela cardinalis*) and on Viti Levu (*M. jugularis*).

The overwhelmingly predominant pattern of habitat shifts is that species which are confined to second-growth or coastal forest on New Guinea move into the forest and the interior on islands with fewer species.   For instance, of the 49 Karkar species shared with New Guinea, 37 species (20 forest, 10 second-growth, 6 aerial, and 1 coastal species) show no habitat shift; of the 12 that do show a shift, 9 are confined to second-growth on New Guinea but enter the forest on Karkar, 2 are coastal on New Guinea but in the interior of Karkar, and only 1 interior species on New Guinea comes out to the coast on Karkar.   The result is that 10 of the 31 New Guinea species which occur in the forest interior on Karkar are absent from the forest interior on New Guinea.   Similarly, of the 13 New Guinea species which expanded their habitat preferences on colonizing New Britain, seven are New Guinea second-growth species which entered the forest on New Britain, 4 are coastal species that moved into the interior, 1 is

a grasslands species which spread into second-growth, and only 1 is an interior species that came out to the coast. Apparently New Guinea second-growth species are better colonizers than New Guinea forest species, because second-growth habitat comes in shifting bits, and species living in this habitat must evolve effective dispersal abilities to seek it out. When these second-growth birds invade smaller islands with many forest niches empty, they expand into the forest and eventually differentiate to become endemic forms confined to the forest. For example, of the 29 New Britain species endemic to it or to the Bismarck Archipelago, 20 live in lowland rainforest, 7 in montane forest, and only 2 in open country. A similar evolutionary transformation of New Guinea second-growth colonizing species into forest species endemic on small islands has been documented for ants by Wilson.[12]

3. **Vertical Shifts.** Within the New Guinea forest the foraging ranges of most bird species are vertically restricted: many species remain in the treetops, others forage between 10 and 30 ft above the ground, and still others always remain within 5 ft. of the ground. Thus, if one randomly traps hundreds of bird individuals in the understory by means of nets extending from ground level to six feet above the ground, one finds that 50–80% of the species present in the vicinity are never netted (because they remain too high), while other species are caught with a frequency far out of proportion to their measured abundance. Five instances of these shifts will be cited: (*a*) The flycatcher *Myiagra alecto* is largely confined to the understory on New Guinea but ranges from the understory to the treetops on Karkar and Bagabag. (*b*) On New Guinea I have yet to catch in nets a single individual of the abundant honey-eater *Philemon novaeguineae*, the starling *Aplonis metallica*, or the cuckoo-shrike *Lalage leucomela*, because these species remain in the crowns. On New Britain these birds occasionally descend to the understory and are netted. (*c*) On the larger mountain ranges of New Guinea, where the whistler *Pachycephala hyperythra* shares much of its altitudinal range with the similar *Pachycephala soror*, *P. soror* spends much time in the understory and is often netted, while *P. hyperythra* remains 10 or more feet above the ground and is never netted. On the small and isolated North Coastal Range of New Guinea *P. soror* is absent, and *P. hyperythra* is regularly netted. (*d*) The warblers *Sericornis virgatus* and *S. arfakianus* coexist on the larger peaks of the North Coastal Range, *S. virgatus* foraging mainly in the understory, *S. arfakianus* in the middle story. On Mt. Turu, a small peak at the eastern end of the Range, *S. virgatus* occurs alone and is netted only half as often, in proportion to its censused abundance, as on other peaks of the Range (because it spends more time foraging above the height of the nets). (*e*) The white-eye *Zosterops lateralis* is the only member of its family, on New Zealand and in most of the habitats it selects in Australia, and ranges from the tree tops to the understory. On invading Espiritu Santo, it encountered an endemic white-eye, *Z. flavifrons*, and where the two species coexist in forest-edge habitats, *Z. lateralis* largely confines its foraging to within 15 ft of the ground, *Z. flavifrons* above 15 ft. This example reverses the usual trend, in that invasion of a small island led here to contact with more rather than fewer congeners and hence to niche contraction rather than expansion.

An extreme type of vertical shift, requiring a more marked change in foraging strategy, occurs when a normally arboreal bird descends to the ground (see *shifts in foraging technique*).

4. Abundance Shifts. The above three types of shifts (altitudinal, habitat, vertical) permit a species to occupy more space and thus, potentially, to achieve a larger population. In addition, one sometimes observes an abundance shift in a narrower sense: a species becomes more abundant on a small island in the same optimal type of habitat that it occupies on larger islands, regardless of whether it also occupies more habitat on the small island. For instance, the paradise kingfisher *Tanysiptera galatea* occupies essentially the same forested habitats and has the same vertical foraging range in the lowlands of Karkar as on New Guinea, but its population density is approximately twice as high on Karkar. The thrush *Amalocichla incerta* is a rare inhabitant of the forest floor above 5000 ft on the Central Range of New Guinea, relatively common in the same situation on the isolated, species-poor Mt. Menawa. Abundance increases in this narrowly defined sense have occurred among approximately 23% of the species on Karkar and 18% of the species of New Britain.

5. Dietary Shifts. Analyses of stomach contents on New Guinea, New Britain, Karkar, Bagabag, and the Madang Archipelago yielded only the following case of a major shift in diet. On New Guinea and New Britain an area of grassland almost always supports both a finch of genus *Lonchura* and a sylviid warbler, the species of finch and of warbler varying with the locality. Thus, Cape Gloucester on western New Britain has the finch *Lonchura spectabilis* and the warbler *Cisticola exilis;* the Madang lowlands of New Guinea, *Lonchura tristissima* and *Cisticola exilis;* and the mid-montane grasslands of southeast New Guinea, *Lonchura caniceps* and *Megalurus timoriensis.* In each of these cases the stomach contents of all finches examined consisted solely of seeds, while the contents of the warblers were solely insects. The grasslands of Karkar are inhabited by the finch *Lonchura tristissima* but no warbler, and the finch takes insects as well as seeds. The grasslands of Bagabag have no finch, only the warbler *Cisticola exilis*, which takes seeds as well as insects.

6. Shifts in Foraging Technique. Conspicuous differences in methods of foraging among populations of the same species on different islands are infrequent, but two sets of examples have been noted. The first involves birds that catch insects in mid-air. On most islands this activity is the specialty of two groups of birds: swifts and swallows, which remain in the air for minutes or hours at a time and forage in open spaces (large clearings, over water, or above the treetops); and flycatchers, particularly those of genus *Rhipidura*, which make brief sallies lasting only a few seconds from perches. On New Zealand, however, where there is no widespread swallow or swift,[13] the flycatcher *Rhipidura fuliginosa* may be seen spinning in the air to catch insects for long times in the air-space over ponds, a habitat which one expects to find monopolized by swifts and swallows elsewhere and where this flycatcher's behavior appears ludicrous to anyone familiar with the same species in Australia or with its New Guinea congeners. The opposite situation occurs on Karkar, where there is no forest *Rhipidura* and the swift *Collocalia esculenta* is found inside the forest,

hawking for insects in much more confined spaces and making much tighter turns than elsewhere. The likelihood that this behavior of the swift is a response to the absence of true flycatchers is reinforced by the situation on New Britain, where *Collocalia esculenta* is found at all altitudes but enters the forest only above the altitude at which the highest species of flycatcher, *Rhipidura dahli*, drops out (4700 ft).

The other set of examples is provided by originally arboreal birds which spend part of their time foraging on the ground on some islands where specialized ground-dwelling competitors are few or absent. This shift has come to my attention in four groups of birds: (*a*) On New Guinea, New Britain, and Karkar the *Erythrura* finches (*E. trichroa*, *E. papuana*) forage in bushes and trees, mainly in the forest, while open ground is exploited by various species of *Lonchura* finches. The latter have spread only as far as the Bismarck Archipelago. Further east in the Pacific one finds their role as ground-hopping finch taken over by *Erythrura trichroa* (endemic subspecies) on Efate in the New Hebrides and by the related *Erythrura cyanovirens* (endemic Pacific species) on Viti Levu. (*b*) The cuckoo-shrike genus *Lalage* is represented on New Guinea by two species, *L. leucomela* and *L. atrovirens*, which are confined to the treetops. On New Britain *L. leucomela* descends to the lower story, and the related *L. leucopyga* on Espiritu Santo and *L. maculosa* on Samoa (both of them endemic Pacific species) forage on the ground as well as throughout the whole vegetational column. (*c*) The three species of *Zosterops* on New Guinea and New Britain, and *Zosterops lateralis* on Australia and New Zealand, are arboreal, but the endemic subspecies of *Z. lateralis* on Espiritu Santo often forages on the ground. (*d*) On New Guinea, where ground-dwelling forest warblers of the genus *Crateroscelis* are abundant, there are six widespread, abundant warblers of the genus *Sericornis*, which are often seen within 1 ft of the ground but not on the ground itself. In Australia the genus *Crateroscelis* is absent, and several species of *Sericornis* (one subspecifically distinct, the rest specifically distinct, from the New Guinea populations) regularly forage on the ground.

The shift to ground foraging by an originally arboreal bird may be considered an extreme case of vertical shifts (see above) but requires much more marked changes in locomotion, hence more morphological change (e.g., longer and stronger legs, as documented for the *Sericornis* warblers by Galbraith and Parker[14]), more evolutionary differentiation, and more time, than a shift from the treetops to the lower story. Thus, all the instances of tree-to-ground shifts cited in the previous paragraph involve populations that have become distinct either subspecifically or specifically from their arboreal ancestors, whereas many of the vertical shifts discussed above have taken place without even subspecific differentiation, and presumably in much shorter times.

Some generalizations about these niche shifts, and the effect of reduced species number on the total population density of the whole avifauna, are discussed elsewhere.[8]

Dean Amadon and Hobart Van Deusen, for permission to use the facilities of the American Museum of Natural History; and more individuals than can be mentioned by name, for making possible the field work in the southwest Pacific.

[1] Mac Arthur, R. H., and E. O. Wilson, *The Theory of Island Biogeography* (Princeton, N. J.: Princeton University Press, 1967).

[2] Mayr, E., *Animal Species and Evolution* (Cambridge: Harvard University Press, 1963).

[3] Crowell, K., *Ecology*, **43**, 75 (1962).

[4] Williams, E. E., *Quart. Rev. Biol.*, **44**, 345 (1969).

[5] Mayr, E., *Birds of the Southwest Pacific* (New York: MacMillan, 1945).

[6] Rand, A. L., and E. T. Gilliard, *Handbook of New Guinea Birds* (London: Weidenfeld and Nicolson, 1967).

[7] Diamond, J. M., *Explorers J.*, **46**, 210 (1968).

[8] Diamond, J. M., *Proc. Nat. Acad. Sci. USA*, in press.

[9] Diamond, J. M., *Amer. Mus. Novitates*, No. 2362 (1969).

[10] Diamond, J. M., and J. W. Terborgh, *Auk*, **85**, 62 (1968).

[11] Ripley, S. D., *Amer. Naturalist*, **93**, 127 (1959).

[12] Wilson, E. O., *Amer. Naturalist*, **95**, 169 (1961).

[13] The swallow *Hirundo tahitica* recently colonized New Zealand from Australia but had not yet spread to any of my New Zealand study areas.

[14] Galbraith, I. C. J., and S. Parker, *Emu*, **69**, 212 (1969).