Ecological Consequences of Island Colonization by Southwest Pacific Birds, II. The Effect of Species Diversity on Total Population Density

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Abstract. Among southwest Pacific birds colonizing a species-poor island from a species-rich island, spatial expansion of the niche to include a wider range of altitudes, habitats, or vertical strata is often an immediate response, while changes in foraging techniques and diet usually occur more slowly and require genotypic change. Despite occupation of spatially broader niches by some colonizing species and increases in abundance by others, the total population density of the whole avifauna is up to nine times lower on a species-poor island than in a comparable habitat on a species-rich island. Total population density varies among islands approximately linearly with the number of species in the lowlands, supralinearly at higher elevations. Part of the explanation is that many birds on small islands expand into niche space which is suboptimal for them and from which they would be excluded by species utilizing this niche space optimally on a species-rich island. The other suggested explanation is an intrinsic inefficiency or loss of fitness among populations on small Pacific islands compared to large-island populations, due to impoverished gene pools, reduced selection pressure, and low degree of endemism.

Islands with similar climate and similar habitat structure may support very different numbers of animal or plant species, depending upon the island's size and its distance from the colonization source area. Ecological comparisons of the faunas of such islands can provide insight into problems such as the effect of competition on niche breadth, abundance, and fitness. The land and freshwater birds on the islands of the southwest Pacific (New Guinea, Melanesia, and Polynesia) offer a particularly favorable situation for analyzing the ecology of island communities. In a previous report, based on ornithological exploration of 10 Pacific islands or island groups, it was shown that birds of New Guinea origin invading a species-poor island often expand their niches in one or more of the following ways: by expanding spatially, i.e., by occupying altitudinal bands, types of habitats, and/or vertical strata of the forest from which they are excluded on species-rich islands by other species; by becoming more abundant in the same type of habitat preferred on New Guinea; rarely, by broadening the diet; and by broadening the range of foraging techniques. The present article puts forward some generalizations based on the examples of niche shifts documented in the previous report, then discusses the effect of reduced species diversity on the total population density of the whole avifauna.

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Generalizations about Niche Shifts. The relative frequency of the various types of niche shifts documented previously may be illustrated by the following summary of niche shifts among the birds of Karkar Island as compared to the source island of New Guinea (or to the source island of New Britain in the case of three species). Nearly half of the species that colonized Karkar (23 out of 52) underwent no niche expansion of any kind. Among the 29 species that did expand, 22 did so spatially, by occupying a greater range of habitats (12 species), altitudes (13 species), or vertical foraging positions (5 species); 12 became more numerous in the same habitat they preferred on New Guinea; and only one species expanded its diet, and one its foraging technique. (The total instances of expansions add up to more than 29, since some species expanded in several ways. For example, the cuckoo-shrike Coracina tenuirostris, which is confined to lowland second-growth on New Guinea, became more abundant in this habitat on Karkar as well as expanding into the forest and to higher elevations.) Thus, spatial expansions and abundance increases are the commonest response to reduction in competition among southwest Pacific birds, as Crowell also found for the land birds of Bermuda and as I found for the land birds of the California Channel Islands.

Among southwest Pacific birds which suddenly find themselves relieved of competitors as a result of invading a species-poor island or mountain, spatial expansion without change in foraging technique is often a prompt response requiring little or no evolutionary change in the genotype, since it is often seen to have occurred in island populations that are not even subspecifically different from their mainland relatives. For instance, 18 of the 22 Karkar species that expanded spatially still belong to the same subspecies found on the New Guinea mainland. More prolonged isolation, and more marked genetic change reflected in differentiation at the subspecies and species level, is usually necessary for changes in diet or for changes in foraging tactics, such as the locomotor patterns that an arboreal species must acquire in order to be able to forage on the ground (ref. 2, p. 535). The interpretation that spatial shifts usually occur before shifts in feeding behavior is reinforced by analysis of ecological segregating mechanisms between sympatric congeners on New Guinea. Recently speciated relatives on New Guinea (e.g., semispecies whose geographical ranges are still largely allopatric) are usually very similar to each other in foraging technique and usually segregate in the zone of sympathy by completely excluding each other with respect to a single spatial variable—i.e., by utilizing contiguous but mutually exclusive altitudinal bands, habitats, or vertical strata. In general, then, when a species invades an island with few competitors, it may immediately expand spatially as a behavioral response requiring no genotypic change. Gradually the pressures of natural selection operating on it in its new niche produce genotypic changes which mold it better to this niche, modify its feeding strategy and diet, and enable it to achieve a higher population density in this niche.

The observed niche shifts indicate competitive interaction not only between close relatives, such as recently speciated congeners, but also between more distant species. That is, many colonists expand into spaces, or increase their abundance in spaces, where there was no congener to exclude them or to depress
their abundance on the source island. The *Myzomela-Nectarinia* case discussed previously (ref. 2, p. 532) shows that the missing competitors may even belong to different families. A similar example on the California Channel Islands is the expansion of the warbler *Vermivora celata* (family Parulidae) into chaparral in the absence of the wren-tit *Chamaea fasciata* (family Timaliidae) and the bush-tit *Psaltriparus minimus* (family Aegithalidae). In other cases the missing competition may be diffuse, i.e., may come from many species with only moderate ecological resemblance rather than from one or two ecologically very similar species.

Certain groups of birds appear more likely than others to undergo certain kinds of niche shifts, or to experience no shift at all. For instance, on Karkar proportionately almost twice as many nonpasserines (mostly the older orders of birds) than passerines (recently evolved perching songbirds) failed to expand their niches, suggesting that passerines are on the whole more plastic and more recently speciated, and have their distributions determined to a greater extent by interspecific competition rather than by intrinsic limitations. One frequently finds several species of flycatchers (family Muscicapidae) of the same size in the same space, employing different methods of catching insects. In contrast, sympatric similar-sized species of white-eyes (genus Zosterops) always sort out spatially (by habitat, altitude, or vertically), implying that all the Pacific white-eyes have essentially the same foraging technique, which no species has been able to modify enough to permit broad spatial overlap with another species. More work will be necessary to provide a secure basis for generalizations about correlates of plasticity.

**Total Bird Population Density.** It may finally be asked what is the effect of reduced competition on the summed population density of all bird species. Field observations made it immediately obvious when we transferred activities from New Guinea to the first satellite island surveyed, Karkar, that the total density of birds was considerably lower on Karkar than in similar habitats on New Guinea, and that this reduction was particularly extreme at higher altitudes. In the temperate zones, where breeding seasons of almost all species are highly synchronized, the usual method of determining population densities quantitatively is to count singing territorial males in a given area. This method is inapplicable on the southwest Pacific islands surveyed, where breeding of a given species may be spread over much of the year, different species have peaks at different times, and many bird individuals in most localities at most times are nonbreeding and nonterritorial. The rate at which birds were caught in nets with a surface area of 250 ft² (22.5 m²), set up under standardized conditions, was therefore taken as the basis for comparing total population densities in habitats of similar structure on different islands. The relation between catching efficiency and total population density of course depends upon the structure of the habitat (e.g., upon the height of the forest, and upon the amount of vegetation in the understory where the nets are erected), but the role of this variability in inter-island comparisons was minimized by comparing yields from habitats matched for similarity of structure on different islands. The coefficient of variation of yield determinations (expressed in birds caught per net-day) in
Table 1. Rate of catching land birds in nets on different southwest Pacific islands: an index of bird population densities.

<table>
<thead>
<tr>
<th>Habitat type</th>
<th>Island</th>
<th>Locality</th>
<th>Local number of species</th>
<th>% Tropical species</th>
<th>Yield (birds caught per net-day)</th>
<th>Yield per species (birds per net-day per species)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coastal lowland rainforest</td>
<td>New Guinea</td>
<td>Madang</td>
<td>132</td>
<td>100</td>
<td>0.82</td>
<td>0.0062</td>
</tr>
<tr>
<td></td>
<td>New Britain</td>
<td>Cape Gloucester</td>
<td>88</td>
<td>100</td>
<td>0.48</td>
<td>0.0055</td>
</tr>
<tr>
<td></td>
<td>Admosin</td>
<td>Admosin</td>
<td>49</td>
<td>100</td>
<td>0.35</td>
<td>0.0071</td>
</tr>
<tr>
<td></td>
<td>Karkar</td>
<td>Duc-Bulu</td>
<td>48</td>
<td>100</td>
<td>0.30</td>
<td>0.0063</td>
</tr>
<tr>
<td></td>
<td>Bagabag</td>
<td>Badilu</td>
<td>31</td>
<td>100</td>
<td>0.19</td>
<td>0.0061</td>
</tr>
<tr>
<td>Montane forest</td>
<td>New Guinea</td>
<td>Mt. Albert Edward, Avios</td>
<td>59</td>
<td>8</td>
<td>1.41</td>
<td>0.024</td>
</tr>
<tr>
<td></td>
<td>New Britain</td>
<td>Mt. Talawe, Agathis camp</td>
<td>31</td>
<td>77</td>
<td>0.21</td>
<td>0.0068</td>
</tr>
<tr>
<td></td>
<td>Karkar</td>
<td>Outer Crater</td>
<td>27</td>
<td>73</td>
<td>0.15</td>
<td>0.0056</td>
</tr>
<tr>
<td>Subalpine mossy forest</td>
<td>New Guinea</td>
<td>Mt. Albert Edward, Tsidib Amul</td>
<td>31</td>
<td>3</td>
<td>0.71</td>
<td>0.023</td>
</tr>
<tr>
<td></td>
<td>New Britain</td>
<td>Mt. Talawe, Middle Peak</td>
<td>17</td>
<td>45</td>
<td>0.15</td>
<td>0.0088</td>
</tr>
</tbody>
</table>

Column 6 gives the netting yield (birds of all species caught per net-day in nylon mist-nets erected under standardised conditions) in the habitat listed in column 1 on the island listed in column 2 at the locality listed in column 3. Column 4 gives the number of bird species present at the locality; column 5, the percentage of those species that are tropical, i.e., that descend to sea-level (note that tropical species make up a much higher percentage of the avifauna in montane forest and subalpine mossy forest on New Britain and Karkar than on New Guinea). Column 7, the yield per species, is calculated as column 6 divided by column 4. The netting yield is determined by the bird population density and by the habitat structure, so that the ratio of the yields in the same type of habitat on different islands (but not in different habitats on the same island) should be approximately equal to the ratio of the bird population densities. Comparison of columns 4 and 6, or consideration of column 7 alone, shows that in a given habitat type the yield (and hence bird population density) increases linearly or supralinearly with species number.
different stands of the same type of habitat on New Guinea was ±25%. The results obtained by this method are given in Table 1 and Fig. 1. Comparison of coastal lowland rainforest on New Guinea, New Britain, Admosin, Karkar, and Bagabag, where the local number of bird species declines respectively from 132 to 31, shows that yields decline in direct proportion to the number of species. In montane forest at higher altitudes (New Guinea, New Britain, and Karkar compared) the yield decreases even more rapidly than the number of species, so that Karkar montane forest, with 46% as many species as New Guinea montane forest, has only 11% as large a yield. Similarly, in the stunted subalpine mossy forest below timberline (New Guinea and New Britain compared) the yield declines even more rapidly than the number of species. These results, which show that netting yields (and presumably population density) in the understory are up to nine times lower on a species-poor island than in a similar habitat on a species-rich island, are in agreement with our qualitative impressions of these large and obvious abundance differences throughout the whole vegetational column, based on field observations.

Given the fact that there are some island species (e.g., 23% of those on Karkar) that become more abundant in the type of habitat they prefer on New Guinea, and others that expand their habitat selection, it may seem initially surprising that the total population density declines as fast as or faster than the number of species on the Pacific islands—i.e., that the average density of individuals per species remains constant or declines. There may be two types of factors underlying this effect.

The first factor is that the competition between 512 species on New Guinea confines each species to that optimal fraction of niche space which it can exploit.
most efficiently and in which it can maintain the highest population density. On a species-poor island some of the species present succeed in expanding into additional niche space, from which they are excluded on New Guinea by species that can exploit this space more efficiently but failed to colonize the small island. The expanded species would not be expected to maintain as high population densities in this (for them) suboptimal niche space than could its New Guinea occupants (e.g., a second-growth species might enter the forest in the absence of true forest species but would not be able to exploit the forest as efficiently). The importance of this factor is clearly expressed in the fact that the density of individuals per species on small islands is reduced even further at high altitudes than in the lowlands. As discussed previously (ref. 2, p. 532), the preferential impoverishment of the New Guinea montane avifauna on mountainous satellite islands means that many of the species found at higher elevations on small islands are actually tropical species that have been able to spread upwards because of the greatly reduced competition. As summarized in column 5 of Table 1, most of the species occurring in Karkar and New Britain montane forest, and half of the species in New Britain subalpine mossy forest, are tropical species, while only 3–8% of the species in these high-altitude habitats on New Guinea are tropical. The tropical species at high altitudes on Karkar and New Britain are probably much less well adapted to the cool conditions, and are able to maintain only much lower population densities, than the specialized New Guinea montane species they are replacing.6

It is questionable, however, whether utilization of suboptimal niche space provides the whole explanation for low population densities on small islands. Considerably more than half of the species inside lowland rainforest on Karkar or New Britain are native to this habitat on New Guinea, yet some of these species still suffer declines of population density in this optimal habitat on the smaller islands compared to New Guinea. Thus, there may be an additional type of factor operating, an intrinsic inefficiency of small-island populations that counterbalances or more than counterbalances the expansions of some species. Three causes can be suggested that would tend to make small-island populations less efficient than large-island populations: impoverished gene pools, lower selection pressure, and lower degree of endemism. (1) *Impoverished gene pools*. The chance of any given favorable mutation arising is proportional to the first power, and the chance of any given polygenic recombinant proportional to a higher power, of population size. In addition, island populations are generally the descendants of a small number of colonizing individuals. Hence exceptionally fit individuals are much less likely to arise in the small, impoverished gene pools of small islands than of large source islands. (2) *Reduced selection pressure*. The smaller the island, the fewer individuals will there be in the island population of a given species, and also the smaller will be the total number of species. Hence the pressures of both intraspecific and interspecific competition to select for fitness will be reduced. (3) *Low endemism*. The degree of endemism decreases with decreasing island size in the Pacific,7 implying that expected survival time decreases and extinction rates increase with decreasing size, as expected theoretically.1 For example, on New Guinea (512 species) 21%
of the species are endemic at the level of the genus, 31% at the level of the species, 29% at the level of the subspecies, and the remaining 18% belong to subspecies extending beyond New Guinea. The corresponding figures for New Britain (126 species) are 0, 22, 40, and 38%, while Karkar (52 species) has no endemic genera or species and only 8% of its subspecies are endemic. Thus, New Britain birds and especially Karkar birds must have had much shorter times to adapt to the local conditions of their islands than have New Guinea birds. In general, the inverse relation between extinction rate and population size means that few bird populations on small Pacific islands survive long enough for natural selection to mold them optimally to the environmental conditions of their particular island.

For comparison with the results of the present study, the relation between species number and total population density has been studied in two other island situations. On the Pearl Islands off Panama, bird censuses carried out by R. H. MacArthur showed (personal communication) that total population densities stand in approximately the same ratio as the species numbers, in agreement with the pattern observed in coastal lowland forest of the southwest Pacific islands. In contrast, Crowell found that total bird population densities on the Bermuda Islands, which have an impoverished North American avifauna, are even higher than those in similar North American habitats—the opposite of the finding for Pacific birds. A factor that may protect Bermudan birds against loss of fitness is high selection pressure maintained by large annual influxes of many migrant species from North America, whereas very few migrant land bird species reach the southwest Pacific islands and none of these occurs inside forest. More studies are required before one can generalize on what kinds of islands and for what groups of animals total population densities decrease on islands, and which of the suggested contributing factors are the most important.

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5 Thus, although Table 1 indicates differences in netting yields on New Guinea between coastal lowland rainforest, montane forest, and subalpine mossy forest, it would be impossible to decide without further information which of these habitats supported the densest populations.
6 A parallel case in California is that on the mainland the Bewick’s wren Thryomanes bewickii is confined to chaparral and is excluded from riparian woodland by the house wren Troglodytes aedon. On the Channel Islands, where the house wren is absent, the Bewick’s wren expands into riparian woodland but achieves much lower population densities in this marginal habitat than does the house wren on the mainland.