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Colonization of Exploded Volcanic Islands by Birds: The Supertramp Strategy

Abstract. After volcanic explosions or tidal waves had defaunated several islands near New Guinea, bird species number rapidly returned to equilibrium on coral islets and rapidly returned to quasi-steady-state values limited by regrowth of vegetation in lowland forest of larger islands. However, reequilibration in montane forest has been limited by slow dispersal of the birds. Colonists have been drawn disproportionately from r-selected "supertramp" species, which maintain much higher population densities than do K-selected faunas, perhaps due to selection for resource overexploitation by the latter.

The repopulation of Krakatau (Indonesia) by plants and animals, after a volcanic explosion destroyed all life, furnished a classic natural experiment in island colonization. A similar opportunity may be provided by the re-colonization of Long and Ritter, two volcanic islands in Vitiaz and Dampier straits between the "source" islands of New Guinea and New Britain. On 13 March 1888 Ritter disintegrated in a cataclysmic explosion that removed more than 95 percent of its bulk and destroyed all vegetation and almost certainly all life on the remaining fragment (1, 2). Today Ritter supports pandanus trees up to 12 m high on its gentler slopes but is still bare in steeper areas, the regrowth of vegetation having been retarded by landslides, rain runoff, porous soil, and strong prevailing winds. Long was devastated about two centuries ago by an explosion that deposited a layer of ash up to 30 m thick or more (1, 3, 4). The forest in the lowlands of Long today is more open and savanna-like than on older volcanic islands, probably due to porous soil and the disappearance of streams during the prolonged annual dry season, and has remained in this arrested subclimax state for at least much of the 20th century. However, the montane forest above 900 m on Long is kept moist by standing cloud banks and is already similar in physiognomy to forest on the summits of older volcanic islands. Near Long and Ritter are "control" islands and "wave-defaunated" islands of varying sizes: the relatively undisturbed islands Umboi, Sakar, Tolokiwa, Crown, Malai, and Midi; and seven coral islets whose birds must have disappeared in a tidal wave set up by the Ritter explosion but which now support forest similar to that on remote islets. In 1972 I surveyed the birds of these 15 islands, examining all major types of habitat on each island from sea level to the summit. Since the survey party

consisted of six observers familiar with New Guinea birds and received much additional information from people living on the larger islands, our lists of presently resident bird species should be virtually complete. This report summarizes, for birds, the return to equilibrium species number, the types of colonizing species, and the striking contrast in population densities between the colonist avifaunas and older avifaunas.

In Fig. 1 the bird species numbers on the control islands are used to assess by comparison how far the defaunated islands have come toward equilibrium. For the seven larger control islands (represented by the seven closed circles on the right in Fig. 1) the number of lowland nonmarine bird species S increases very regularly with the island area A (in square kilometers) according to the empirical relation

$$S = 18.9 A^{0.18} \quad (1)$$

A linear logarithmic relation between species number and area similarly describes distributions of most plant and animal groups on most other archipelagoes (5). Such a relation is interpreted as meaning that island species numbers represent an equilibrium between extinction and immigration, larger islands reaching equilibrium at more species because of larger populations, lower extinction rates, and greater habitat diversity (5-7). Examination of the spe-

cies and races involved shows that most bird populations on the Vitiaz-Dampier islands are more immediately derived from the source island of New Britain than from New Guinea, although New Guinea is 20 times larger and approximately as close. The reason is that many New Guinea species are sedentary and rarely cross water gaps, but all New Britain species were originally derived by overwater colonization from New Guinea and were thus selected from New Guinea's pool of superior colonists. The same factor may underlie the high immigration rates implicit in the low value of the area exponent in Eq. 1 [0.18, compared to 0.22 for satellite islands of New Guinea (8) and 0.24 to 0.30 for many other archipelagoes (5)].

Species numbers for the eight smaller islets ($A = 0.003$ to 0.07 km^2) lie generally below the species-area relation defined by the larger islands and show much more scatter. These islets are comparable in size to one territory for even the commoner bird species, and many of the populations on the islets were found to consist of only a single bird pair. Since it is thus marginal whether even species with minimal territory requirements can occur on these islets at all, S is lower than would be the case if the species-area relation could be extrapolated to the left by infinite subdivision of bird individuals. The deviation of the observed S value below the regression line of Fig. 1 is significant at $P < .05$ for six islets and at $P < .01$ for four islets. In addition, S is subject to fluctuation because of the small number of species (only four on some islets) as well as the small number of individuals. The seven islets defaunated by tidal wave (Fig. 1, triangles) have S values similar to that of the noninundated control islet (Fig. 1, closed circle on the left) and may already have achieved equilibrium. This was to be expected because they have

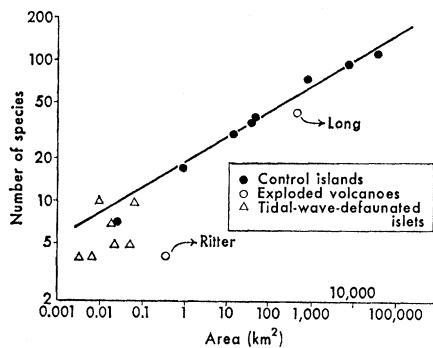


Fig. 1. Number of resident, nonmarine, lowland bird species, S , on Vitiaz-Dampier islands, plotted as a function of island area, A , on a double logarithmic scale. (Closed circles) Relatively undisturbed "control" islands (from left to right, Midi, Malai, Crown, Sakar, Tolokiwa, Umboi, New Ireland, and New Britain); (open circles) exploded volcanoes; (triangles) coral islets inundated by the Ritter tidal wave. The straight line $S = 18.9 A^{0.18}$ was fitted by least mean squares through points for the seven larger control islands.

already regained climax vegetation and because their tiny population sizes and hence high natural turnover rates restrict successful colonization to the most rapidly dispersing species. Rapid equilibration is unequivocally demonstrated by the fact that after experimental removals of birds from a small islet the bird species number returned to its original value within times as short as a few days and with initial colonization rates of approximately one species per hour.

Lowland species numbers on the two exploded volcanoes lie below the line for control islands. Ritter has only four species, far below the 16 species predicted for its area from Eq. 1 or the 17 species observed on a control island of similar size, Malai. No other ornithologically explored island of the tropical southwest Pacific deviates so far below the species-area relation for its archipelago as does Ritter. Long has only 43 species, considerably fewer than the 57 species predicted from Eq. 1 and nearly matched by the 40 species observed on the control island Tolokiwa, which is ten times smaller than Long. Although the deviation below the

control curve (Eq. 1) is less striking for Long than for Ritter, the deviation for Long is still significant at $P < .001$. A priori, these deficits could be due either to slow colonization by birds or to the postexplosion forest not yet having regained the climax structure found on older volcanoes. The latter explanation is surely the correct one. The arrival at Ritter of species that could not establish resident populations, because of sparse vegetation and lack of wind shelter, was documented both by direct observation and by feathers at the plucking perch of a resident peregrine falcon. On Long, my party found 40 species in the same habitats where Coulta (4) had already found 37 species in 1933. The difference between 37 and 40 is insignificant, probably arose because Coulta was working alone rather than in a party of six, and suggests that the species number on Long scarcely changed from 1933 to 1972. The species turnover rate on Long, calculated as in table 1 in (6) from apparent immigration and extinction rates between 1933 and 1972, is 0.18 percent per year. This is even less than the turnover rate of 0.32 percent

per year for a similar-sized, older volcano, Karkar (9), whose species number is at equilibrium (8, 10). Thus, by 1933, about a century and a half after the explosion, the bird species number on Long had built up to 75 percent of the equilibrium value, become "stuck" in this quasi-steady state, and ceased to turn over more rapidly than on old islands. Since the open, savanna-like lowland forest of Long should hold fewer species than the more structured rainforest of old islands (11), the arrested equilibration of the Long lowlands with bird species may be attributed to the arrested development of forest. The more marked deficit in species number on Ritter than on Long is consistent with Ritter's much sparser vegetation.

On mountainous southwest Pacific islands, each 1000 m of elevation enriches the avifauna by a number of montane species equal on the average to 8.9 percent of the species number at sea level (8, 10). For the control islands Crown, Tolokiwa, and Umboi, this formula predicts 2, 5, and 11 montane species, in good agreement with the 2, 4, and 9 observed, respectively. For Long, however, the actual number of montane species, 2, is far below the predicted 7, this deficit being greater than that for any other known mountainous island of the southwest Pacific. Unlike the lowland deficit, the montane deficit cannot be attributed to arrested vegetation, since the montane forest of Long is already structurally mature. Colonization by montane birds must be much slower than colonization by lowland birds and must be limited by dispersal of the birds themselves. In agreement with this conclusion, the montane birds of New Britain are much more distinct from their New Guinea relatives than are the lowland birds, suggesting lower rates of gene flow.

A remarkable finding of the surveys was the spectacularly high population densities of birds on Long and two other islands. This finding, which was qualitatively obvious within a short time of our landing on Long, was quantitated by mist-netting techniques (12, 13). Figure 2 shows that on most control islands the combined population densities of all bird species increase with the local number of species present, linearly in lowland forest and supralinearly in montane forest. Values for two Vitiaz-Dampier control islands,

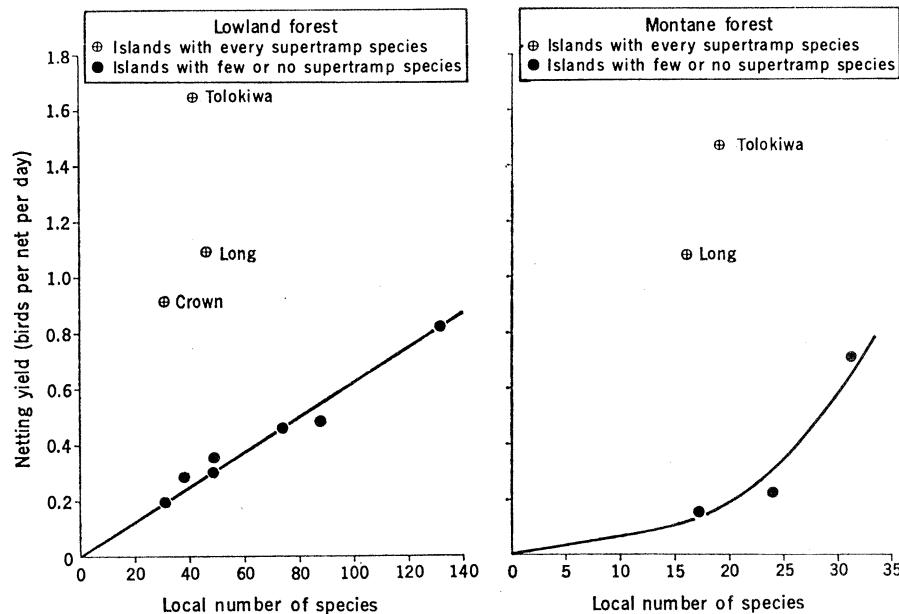


Fig. 2. Ordinate: rate of catching land birds under standardized conditions in mist nets on a particular island (expressed in birds caught per net per day), in lowland forest (left) or montane cloud forest (right). Abscissa: local number of species present on the island. If one compares the same type of habitat on different islands (but not if one compares different habitats), this catch rate is proportional to the combined population densities of all species present (12, 13). (Closed circles) Control islands with not more than three supertramp species [values for Umboi and Sakar are from this report; other values are from table 1 and figure 1 in (12)]; (crossed circles) the exploded volcano of Long and two control islands, which support all nine supertramp species. Note that, on islands with few supertramps, netting yields (and total population densities) increase with the local number of species, and that islands with all the supertramp species have much higher yields than islands with the same total number of species but few supertramps.

Umboi and Sakar (61 and 93 km from Long, respectively), fall on the curve defined by other New Guinea satellite islands and interpreted previously (12). On the exploded volcano of Long and the two nearest control islands Crown and Tolokiwa (12 and 37 km, respectively, from Long), population densities are 4 to 11 times those on more distant control islands with similar species numbers. This pattern could not be explained by postulating that these three islands share exceptionally fertile soil deposited as an ash blanket by the Long explosion, since ash fallout on Tolokiwa was slight (1).

What does set Long, Crown, and Tolokiwa apart is the unusual, shared species composition of their avifaunas. Bird species of the Bismarck Archipelago (New Britain and its neighbors, including the Vitiaz-Dampier group) may be divided according to their dispersal strategy into three somewhat arbitrary categories: (i) "sedentary species," confined to the larger islands; (ii) "tramps," present on not only the larger islands but also many smaller and more remote islands; and (iii) "supertramps," nine species which are confined as residents mainly to small islands and virtually absent as residents (although often recorded as vagrants) from the larger islands (14). In the terminology of MacArthur and Wilson (5), sedentary species represent the extreme of K selection (selection for competitive ability at the expense of dispersal ability), while supertramps represent the extreme of r selection (selection for dispersal ability and reproductive potential at the expense of competitive ability). Tramps comprise most species on all the Vitiaz-Dampier islands. On most islands, except for Long, Crown, and Tolokiwa, there are only a few supertramp species. These three islands are unique in the whole Bismarck Archipelago in supporting all nine supertramps.

These distributional patterns suggest the following interpretation of the supertramp strategy. Supertramps specialize in rapid breeding and overwater colonization, but they have paid a price for these adaptations and are excluded from most islands by competitors that can harvest resources more thoroughly and tolerate lower resource levels. Whenever the supertramps find islets too small for stable populations to persist for a long time, or else an empty island recently devastated by a tidal

wave or volcanic explosion, they breed on a nearly year-round basis (15), fill the island, and generate new emigrants. By the time these populations have disappeared or been squeezed out by more efficient later arrivals, the supertramps have already ensured their survival as species by finding other transiently empty islands. With the explosion of a large island like Long, the supertramps "struck it rich" as first arrivals. For some of the supertramp species, the colonization of Long quadrupled the area inhabited by all populations of that species combined. The frequency with which I saw groups of land birds over mid-ocean around Long, or else leaving land and disappearing out of sight, suggests that Long is producing numerous emigrants and that these colonists have inundated parts of the former avifaunas of the two nearest islands, Crown and Tolokiwa. However, on islands more distant from Long, where the flood of colonists is lower, more efficient residents have been able to exclude the supertramps.

The excess population densities in the supertramp-rich avifaunas of Long, Crown, and Tolokiwa largely represent the abundances of the supertramp species themselves, even though they comprise only about one-quarter of the species present (16). At first it seems paradoxical that the supertramps maintain much higher population densities than the more efficient competitors which exclude them from older islands. However, there is increasing reason to suspect that "self-renewing resources can be exploited to the detriment of the predator's population, and this overexploitation will be a natural consequence of competition among the predator species" (17, p. 31; see pp. 56-57 for a simple model). That is, competition in a species-rich fauna selects for species that can reduce resource levels below the point where other species can survive, even though this diminishes the rate of resource production and hence the population density of harvesting species. For instance, K-selected species of insectivorous birds, by finding and catching insects more efficiently than do supertramps, may be depressing sustainable insect yields far below the level that exists on supertramp-rich islands. K-selected frugivores may eat fruits which are not yet full-sized and are more unripe than supertramps tolerate, even though this reduces the caloric value of the fruit crop. This "non-

overexploitation" interpretation of high supertramp densities on the Vitiaz-Dampier islands is the mirror image of Elton's explanation (18), in terms of heavy predation pressure, for the low total abundance (despite high diversity) of insects in the most species-rich community on Earth, the neotropical rainforest.

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- The supertramps are *Ptilinopus solomonensis*, *Ducula pistrinaria*, *Macropygia mackinlayi*, *Halcyon chloris stresemanni*, *Monarcha cinerascens*, *Pachycephala melanura dehli*, *Myzomela sclateri*, *Myzomela pammelaena*, and *Zosterops griseotincta*. On Long, all of these species are widespread in virtually all habitats with bushes or trees, from sea level to the summit, and from gardens to savanna to cloud forest. The supertramps lack resident populations in the corresponding habitats of most species-rich islands, although they are often present on islets a few kilometers or less distant. Since vagrants, dispersing juveniles, or transient populations have by now been recorded for most supertramp species on the best-studied large islands such as New Britain and Umboi, the supertramps must be excluded on a permanent basis by competitors. In some cases the competitors can be identified from details of distributional patterns. For example, *Macropygia mackinlayi* is excluded by *M. nigrirostris* and certain combinations of other cuckoo doves, *Ducula pistrinaria* by *D. rubricera*, *Monarcha cinerascens* by certain combinations of six other flycatchers, *Pachycephala melanura dahli* by *P. pectoralis* or by certain combinations of other flycatchers, and *Myzomela sclateri* and *M. pammelaena* by certain combinations of other myzomelids and sunbirds.
- Compare observations on year-round breeding by five of the supertramp species [O. Meyer, *J. Ornithol.* 78, 19 (1930)]. A single pair of the tramp flycatcher *Rhipidura leucophrys* has been observed to rear six broods within 6 months [R. Mackay, *The Birds of Port Moresby and District* (Nelson, Melbourne, 1970), p. 46].
- More individuals were netted of the territorial supertramp species than of the non-territorial ones, because the latter happen to be species that forage largely above the height

- of the nets. Thus, wanderings of nonterritorial supertramps are unlikely to have significantly inflated the mist-net yields. Predators of birds are more diverse and far more abundant on Long than on control islands, so that supertramp abundance cannot be attributed to reduced predation pressure.
17. R. H. MacArthur, *Geographical Ecology* (Harper & Row, New York, 1972).

18. C. S. Elton, *J. Anim. Ecol.* **42**, 55 (1973).
 19. I thank the National Geographic Society and the Sanford Trust of the American Museum of Natural History for support; E. E. Ball and R. W. Johnson for discussions of Long Island; and many New Guinea residents for making fieldwork possible.

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spine (but not rheumatoid arthritis), thalamic pain, causalgia, brachial plexus avulsions, trigeminal neuralgia, and so forth.

Patients completed a Minnesota Multiphasic Personality Inventory (MMPI), a short Health Index (2), gave a pain estimate in which they rated the average intensity of their pain on a scale from 0 to 100, and took a tourniquet pain test (3). The latter produces arm ischemic pain and is our adaptation of the submaximum effort tourniquet technique (4). It yields two direct measures: the time at which the average clinical pain is matched in severity (clinical pain level), and the time to reach the unbearable level of pain (maximum pain tolerance).

Twenty-three variables were collected from each patient for factor analysis. These included the ten clinical scales of the MMPI, the four scales of the Health Index, the pain estimate, and the clinical pain level and maximum pain tolerance of the tourniquet pain test. Four derived variables were computed: the difference between the clinical pain level and the maximum pain tolerance; the ratio of the clinical pain level to the maximum pain tolerance, computed by dividing the maximum pain tolerance value into the clinical pain level, and multiplying the quotient by 100; the difference between the pain estimate and the ratio just described; and the total of the four Health Index scales. The final two variables were age and sex.

The data were intercorrelated, forming a 23 by 23 matrix which was subjected to a factor analysis by using the principal components method with unities in the main diagonal. Seven factors were extracted with eigenvalues greater than 1, and these factors were rotated by means of the oblique rotation method, in which the obliqueness control was set to zero. The program used in this analysis is a part of a computer data analysis package of social sciences programs (5).

Of the patients, 81 were males and 38 were females; values for all the other variables are presented in Table 1. These data show that the neurotic scales of the MMPI [hypochondriasis (Hs), depression (D), and hysteria (Hy)] are elevated in a psychophysiological pattern which is characteristic of patients with chronic disease; the character disorder [psychopathic deviate (Pd) and masculinity-femininity (Mf)] and psychotic scales [paranoia (Pa), psych-

Table 1. Values for factored variables.

Variable	Average value	Standard deviation
Tourniquet test		
Clinical pain level	3.25 minutes	3.50 minutes
Maximum pain tolerance	6.75 minutes	4.83 minutes
Ratio, $(\frac{\text{clinical}}{\text{maximum}} \times 100)$	46	28
Difference (maximum - clinical)	3.50 minutes	3.50 minutes
Pain estimate - ratio	10	25.6
Pain estimate (0 = no pain, 100 = worst possible)	57	19
Health Index		
Invalidism	2.9	2.4
Manifest depression	7.7	4.3
Pain preoccupation	5.2	1.8
Pain games	3.7	2.2
Total	19.5	8.4
MMPI		
Hs (hypochondriasis)	75	13
D (depression)	72	16
Hy (hysteria)	74	10
Pd (psychopathic deviate)	64	13
Mf (masculinity-femininity)	56	11
Pa (paranoia)	57	9
Pt (psychasthenia)	63	14
Sc (schizophrenia)	64	15
Ma (hypomania)	60	11
Si (social introversion)	52	9
Age	45.7 years	12.6 years