PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Bird Colonization of Anak Krakatau, an Emergent Volcanic Island

R. A. Zann, E. B. Male and Darjono

Phil. Trans. R. Soc. Lond. B 1990 **328**, 95-121
doi: 10.1098/rstb.1990.0110

Phil. Trans. R. Soc. Lond. B **328**, 95–121 (1990) [95]
Printed in Great Britain

BIRD COLONIZATION OF ANAK KRAKATAU, AN EMERGENT VOLCANIC ISLAND

BY R. A. ZANN[1], E. B. MALE[1] AND DARJONO[2]

[1] *Department of Zoology, La Trobe University, Bundoora, Victoria* 3083, *Australia*
[2] *Museum Zoologicum Bogoriense, Bogor, Indonesia*

(*Communicated by Sir David Smith, F.R.S. – Received* 8 *June* 1988)

CONTENTS

Bird colonization of Anak Krakatau in the 1980s serves as a model for the early colonization processes, which were mostly undocumented, that occurred on the archipelago in the first two decades of this century. Anak Krakatau, which emerged from the sea in 1930, also provides an opportunity to study the formation of an avian community *de novo*.

Thirty-seven species of birds have been recorded since 1951. Shore birds and aerial insectivores were the first species to exploit the newly emerged island. Plant succession, which is proceeding at different rates on different parts of the island, has provided niches for birds to permanently colonize. Species of open habitats (*Caprimulgus affinis*, *Centropus bengalensis*) were the first colonists, followed next by ecological generalists with good dispersal ability (*Pycnonotus goiavier*, *Halcyon chloris*); the next species were those that exploit casuarina woodland and forest and the most recent wave of colonists have been frugivores that arrived after figs began to bear fruit in 1985. Three raptors that hunt on the island have limited the colonization of three large frugivores. Most, but not all, colonists have come from the older islands, including those species denied open habitats by plant succession. Comparisons are made with the bird colonization of Rakata during the first two decades of this century.

Most birds on Anak Krakatau are insectivores and are restricted to two areas of trees some 12 hectares in total. Foraging methods and sites show little overlap, but dietary analysis in August 1986 showed some common prey items. The very high density of insectivores may be a function of insect abundance on the island and high fecundity and tolerance of crowding by early bird colonists.

1. Introduction

The recolonization by birds of the whole Krakatau archipelago is of considerable significance for island biogeography theory; nevertheless, ornithologists have been remiss in their efforts to record the process. Only four basic lists have been compiled in the 101-year interval before our visits in 1984, 1985 and 1986. Twenty-five years elapsed after the destructive eruption of 1883 before Jacobson (1909) made the first survey, and subsequent visits were made by ornithologists in 1919–20, 1930–3 and 1951–2. Unfortunately, observations of the earliest colonists of the bare open habitats are lacking, but more importantly, the dramatic rise in species numbers from 1908 to 1919 that coincided with the canopy closure was not documented. However, Anak Krakatau, which emerged from the sea in 1930, gives ornithologists the opportunity to study, in detail, the colonization *de novo* by birds of an island from the earliest stages of succession from bare ash and lava to the ultimate formation of secondary and, perhaps, primary rainforest. To some extent it provides a replicate, albeit on a smaller scale, of the colonization processes that operated on the archipelago in the first 50 years after 1883.

The successional sequence of vegetation communities likely to have taken place on Anak Krakatau since 1952 when all previous vegetation was destroyed by volcanic activity has been described by Partomihardjo (1983). There were two pioneer communities: the *Ipomoea*–

Ischaemum community colonized the beach zone and the *Saccharum* community pioneered the upper slopes of the volcano; these communities were still extant during our survey period. *Casuarina* and *Imperata* communities constituted the next stage that colonized the lower slopes and appeared to merge with the beach vegetation and, in some places, replace it. The grasses of the different communities and the scattered casuarinas formed a savannah grassland that was characteristic of much of Rakata in the early decades of this century (Richards 1982). Casuarinas gradually replaced *Imperata* and other grasses on the lower slopes to form a woodland on the Eastern Foreland and Northeastern Foreshore and these trees have recently colonized the Northern Foreland; they have also begun to colonize the exposed upper northern slopes. On the lower parts of the Eastern Foreland, secondary rainforest species have replaced patches of casuarinas and this represents the likely climax community for the island should destructive volcanic activity permit (Barker & Richards 1982). Before it was destroyed by the eruption of 1952, the vegetated area of the Eastern Foreland was predominantly grassland (70% of the area in some plots) with some 5% covered with casuarinas, up to 10 m in height (van Borssum Waalkes 1960); this was more advanced than the Northern Foreland during our survey period but less advanced than the Northeastern Foreshore.

Plant succession has not proceeded at the same rate on the three vegetated areas of the island; it is most advanced on the Eastern Foreland (now having some secondary rainforest components) and least on the Northern Foreland (savannah grassland), with the northeastern Foreshore intermediate (casuarina woodland). Plant succession on Anak Krakatau, therefore, appears to have proceeded at different rates at different locations, yet appears to be replicating the same stages that occurred on the older islands some 60–80 years ago and may provide insight into bird colonization during this important but undocumented period.

Birds of Anak Krakatau also provide a unique opportunity to study the formation and dynamics of an avian community that has developed *de novo*. The purpose of this paper is to detail the colonization of Anak Krakatau by birds since 1952 and to describe the abundance, foraging ecology and habitat use of the species that compose the avian community. The colonization process on Anak Krakatau will be compared with that documented for the older islands.

2. Methods

(*a*) *Surveys*

The first recorded visit by a zoologist to Anak Krakatau was that of Hoogerwerf on 12 October 1951 when he stayed for 8 h during his ornithological survey of the archipelago (Hoogerwerf 1953). He also visited the island briefly on 26 August 1952 and later revisited it on 16 November 1952 to record the effects of the devastating eruptions of the volcano in October 1952 that eradicated all vegetation (Thornton & Rosengren 1988). Given the paucity of vegetation on the island during this period, and Hoogerwerf's experience, we must assume that all species present were seen and identified correctly.

Hull University botanists made identifications of some bird species seen incidentally on Anak Krakatau during their expeditions to the archipelago on 13–15 September 1979 and 23–30 July 1983 (Bush & Newsome 1986). In July 1982 an Indonesian expedition of (mainly) invertebrate zoologists from Institut Teknologi Bandung spent part of one week on Anak Krakatau during which they identified some bird species sighted incidentally during their work (Ibkar-Kramadibrata *et al.* 1986). We do not assume that these expeditions made a complete

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

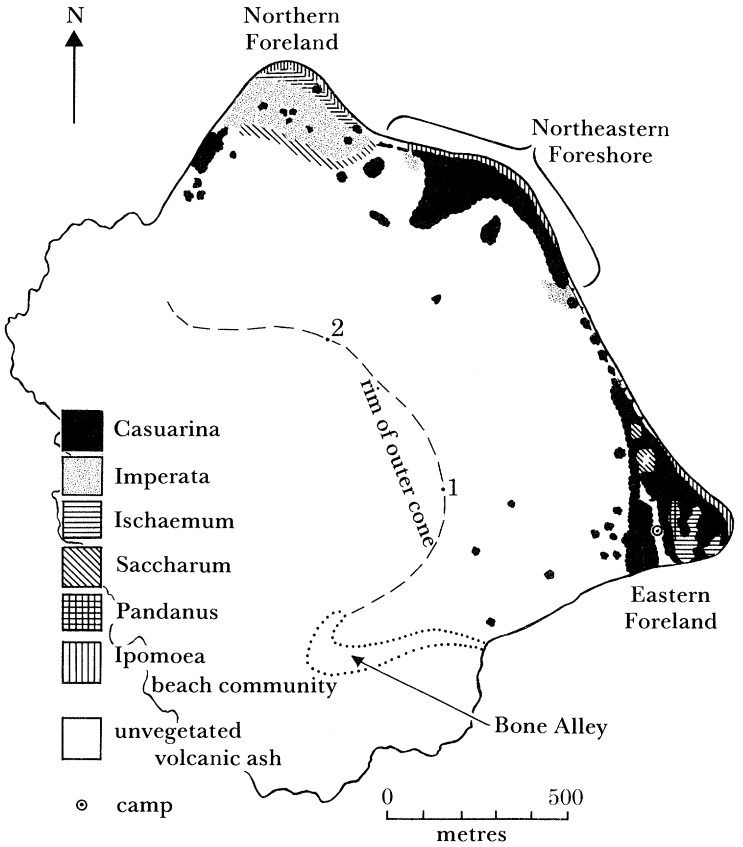

FIGURE 1. Distribution of plant communities on Anak Krakatau in 1986. Secondary rainforest trees are not shown but they occur in small patches among casuarinas on the eastern Foreland. Sparse scattered clumps of *Saccharum spontanum* on the northeastern slope of the outer cone are also not shown. 1 and 2 are concrete survey markers that are 515 m apart.

list of birds on the islands at the time, nor do we assume that all their identifications were correct.

Our surveys of Anak Krakatau in 1984 and 1985 were part of a general investigation of the avifauna of the archipelago (Zann *et al.* 1990) but in 1986 we concentrated exclusively on this new island. We surveyed birds on Anak Krakatau on the following dates: 1984: 10, 13, 20 and 21 September (G. Davison, M. Walker and R. A. Zann); 1985: 13–15, 20–22 August (R. A. Zann); 1986: 16–30 September (E. B. Male and Darjono). In 1984 we camped one night on Anak Krakatau and in 1985 and 1986 we camped on all the nights shown above. We also include incidental sightings made by Professor I. W. B. Thornton during a one-day visit on 11 February 1988.

General survey methods are described in Thornton & Rosengren (1988) and details are provided in tables 1 and 7 of Zann *et al.* (1990) and table 1 of Thornton *et al.* (1990). Each author's familiarity with the birds of the Lesser Sundas is given in the paper by Zann *et al.* (1990). To develop recognition skills for the 23 more cryptic species found on Anak Krakatau, sound recordings of 16 species made in 1984 and 1985 were familiarized by the 1986 survey team.

(*b*) *Study area*

Previous survey reports did not specify the locations on Anak Krakatau where observations were made but we may safely assume that most were made on the Eastern Foreland where most of the vegetation is found (figure 1). We too concentrated on the Eastern Foreland where we camped, but made regular surveys of the other vegetated areas and the non-vegetated parts of the island.

In 1986 the extent of the vegetation was mapped from 14 survey points located on the ash slopes some 20 m above the start of the vegetation; transects were run down to the shore and the presence and absence of the vegetation recorded (figure 1). Data were plotted on the 1981 Geologic Survey Map of Indonesia and the area of the island and vegetation measured on a digitizing tablet (table 1). The scale of the map was the distance between the two survey markers on the outer rim that was measured by a qualified surveyor with an electronic distance measurement device; this measurement was found to be 515 m.

Table 1. Area of Anak Krakatau and the area covered in vegetation in September 1986 and shown in figure 1

(The very scattered clumps of *Saccharum spontanum* on the northern slopes are excluded.)

area	hectares
Anak Krakatau above the high-water mark	234
Eastern Foreland, including outlying clumps of vegetation	7
Northeastern Foreshore	4
Northern Foreland	6
total covered with vegetation	17
total covered with trees (excludes *Imperata* sp.)	12

(*c*) *Trapping*

Mist-nets were used to trap birds in 1984 and 1986 and four birds were caught in mist-nets set for bats in 1985 (table 2). All sixteen nets were set in the Eastern Foreland (figure 1) and birds were sampled in different vegetation types (table 3). The duration of trapping is shown in table 1 of Thornton & Zann (1990). Twelve nets sampled the first four metres above the ground and four were set in the canopy and sampled from about 20–25 m above the ground. In 1984 all birds were weighed and measured and the moult of the right wing was scored before the bird was released. In 1985 the four birds captured were colour banded. In 1986 all captives were given unique combinations of four colour bands and a numbered metal band provided by the Australian Bird Banding Scheme. Unfortunately, since 1986, no trapping has occurred, consequently, we cannot assess the longevity or sedentariness of these banded birds. Each animal was aged by using plumage and softparts, weighed (wt, in grams) and bill length (bl), bill depth (bd), head–bill length (h–b) and tarsus length (tl) were measured in millimetres. Measurements are given in the descriptions below with the mean and the standard deviation when the sample size was four or more, otherwise the median value is given. Morphometrics of species not captured were made on skins from the Museum Zoologicum Bogoriense; the skins chosen for measurement were from specimens taken on or adjacent to the Krakataus or areas close by. The cloacal protuberance of each captive was also examined to determine sex and the abdomen was examined for a brood patch. Finally, before release, the diet of most captives was investigated by 'stomach flushing' (Ford *et al.* 1982). This non-destructive method involved

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

the administration of a small quantity of freshwater into the stomach so that the bird would either regurgitate and/or defaecate food remains, which were preserved in 70% ethanol for later analysis. Sixty-seven birds from eight species were 'flushed' with no apparent ill-effect and twelve were recaptured and 'flushed' again.

TABLE 2. SPECIES OF BIRDS CAPTURED AND RECAPTURED ON ANAK KRAKATAU IN SEPTEMBER 1984 AND SEPTEMBER 1986

(Numbers in parentheses show rate of capture and recapture/10000 m² of mist-net × rain-free hours nets were set.)

species	1984 captures	1986 captures	1986 recaptures
Caprimulgus affinis	—	1	0
Halcyon chloris	7 (25.7)	15	4 (17.5)
Pycnonotus gioavier	8 (29.4)	14	2 (14.7)
Oriolus chinensis	—	2	0 (1.8)
Copsychus saularis	2 (7.3)	4	1 (4.6)
Gerygone sulphurea	1 (3.7)	5	0 (4.6)
Cyornis rufigastra	2 (7.3)	16	4 (19.3)
Pachycephala cinera	17 (62.4)	20	9 (35.9)
Lanius tigrinus	—	1	0 (0.92)
Nectarinia jugularis	4 (14.7)	2	0 (1.84)
Total	41	80	20

TABLE 3. NUMBER OF BIRDS CAPTURED ON ANAK KRAKATAU BY VEGETATION TYPE

(The value in parentheses shows capture rate/10000 m² of mist-net × rain-free hours nets were set.)

species	*Casuarina*	*Casuarina/Ficus*	*Erythrina/Pandanus*	*Ficus*
Halcyon chloris	5 (12.9)	0	2 (17.2)	8 (45.0)
Pycnonotus goiavier	10 (25.8)	3 (29.1)	0	3 (16.9)
Oriolus chinensis	2 (5.2)	0	0	0
Copsychus saularis	1 (2.6)	0	2 (17.2)	2 (11.2)
Gerygone sulphurea	4 (10.3)	1 (9.7)	0	0
Cyornis rufigastra	12 (30.9)	2 (19.7)	1 (8.6)	5 (28.1)
Pachycephala cinerea	9 (23.2)	5 (48.4)	5 (42.9)	9 (50.6)
Nectarinia jugularis	0	0	0	2 (11.2)
Total	43 (110.7)	11 (106.6)	10 (85.8)	29 (163)
effort (m² × hours)	3883	1032	1166	1778

(*d*) *Population estimates*

Absolute numbers of birds seen were used as an indicator of abundance where the species occupied open habitats and one could be sure all birds present were seen. Species in vegetation were surveyed by transect and mist-net and estimates made of the population size. In 1985 two transects sampled all the narrow strip of vegetation bordering the coastline of the Northeastern Foreshore and the Northern Foreland (figure 1). Pairs were identified and located by their song so that an accurate count of pairs was feasible. The number of pairs counted was extrapolated to account for the Eastern Foreland. In 1986 eleven strip transects were made from east to west taking in vegetation along the coast starting in the Eastern Foreland and moving parallel to the coast and finishing at the end of the vegetation in the Northern Foreland. Each transect was run in the morning and took from 2–3 h. All birds positively identified by either sight or sound were recorded and birds that moved forward from the observer were discounted. On the

Eastern Foreland a strip transect of 40 m width was necessary to sample the vegetation. Averages for each species were calculated from the eleven transects and extrapolation was used to account for the unsampled vegetation on the Eastern Foreland. Absolute numbers of different individuals captured and their rate of recapture were also used to determine population size.

(*e*) *Foraging behaviour*

In 1986 detailed observations were made of each bird encountered to determine habitat use and foraging techniques. These observations were usually made on the morning transects but many incidental observations were made at all times of the day and night during other activities. Species, date, time and location (ef, Eastern Foreland; nef, Northeastern Foreshore; nf, Northern Foreland; oc, outer cone; ba, Bone Alley and s–b, shore–beach) were always recorded. Other data recorded included: (*a*) habitat: casuarina woodland, secondary rainforest, grassland, shore, beach vegetation and desert–cliff; (*b*) plant species on which the bird was seen; (*c*) height of plant above ground (to the nearest metre); (*d*) height of bird to the nearest metre; (*e*) substrate in which the bird was seen ('air', 'lava/ash', tree: 'trunk', 'first-degree' branches, from trunk, 'second', other branches of tree, 'foliage'); (*f*) foraging method:

1. Aerial feeding: both the bird and the prey were flying when the prey was detected and attacked.
2. Hawking: the bird flies from a perch to take a flying insect.
3. Pouncing: the bird flies from a perch to take prey from the ground or lower vegetation.
4. Branch probe/glean: the bird extracts prey from within or on the branch it is hunting over.
5. Ground probe: the bird probes litter and the ground surface for prey.
6. Leaf glean: the bird hunts among foliage taking prey from the surface of leaves.
7. Fruit eating.

(*f*) *Habitats*

Habitats were defined as follows: Shore–beach up to the high-water mark. Cliff–desert, included all non-vegetated parts of the island and consisted of ash, lava and rocks.

The vegetation has been described in detail by Barker & Richards (1982, 1986), Partomihardjo (1983) and Tagawa *et al.* (1984). Plant succession is more advanced on the Eastern Foreland than elsewhere and is more complex and diverse; stands of grasses (*Ischaemum muticum* and *Saccharum spontaneum*) are interspersed with understorey shrubs and tall stands of *Casuarina* and elements of secondary rainforest (figure 27, Thornton & Rosengren 1988). We recognized the following six vegetation communities in our observations of feeding ecology:

1. Casuarina woodland. Dense pure stands of *Casuarina equisetifolia* were almost the sole constituents of the Northeastern Foreshore (figure 1) and formed an invading band on the higher slopes of the Eastern Foreland. The species dominated the lower more seaward aspects of the latter where other plant communities were slowly replacing it. Single trees and small clumps were found on the Northern Foreland and were sparsely distributed on the northern slopes of the outer cone. Some trees were over 35 m tall in 1986.
2. Secondary rainforest. This occurred on the eastern Foreland around the perimeter of open glades of the grass, *Ischaemum muticum*, and consisted of species of *Ficus*, *Erythrina* and other tree species normally associated with secondary rainforest (Barker & Richards 1982).
3. *Imperata* grassland. Dense pure stands of this pioneer were found on the Northern Foreland

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

and punctuated by small patches of *Pandanus*, *Saccharum* and *Ficus* (see figure 28, Thornton & Rosengren 1988).

4. *Saccharum* grassland. Dense stands of *S. spontaneum* were found in parts of the casuarina woodland and formed small 'islands' in the *Imperata* grassland; scattered tussocks occurred on the ash slopes of the outer cone but no birds were seen on these isolated plants.

5. *Ischaemum* grassland. Dense stands of *Ischaemum muticum* were found in glades and seaward patches on the Eastern Foreland; patches also occurred on the northern Foreland.

6. *Ipomoea pes-caprae* community. This beach association was found on the non-eroding northeastern shores (see Thornton & Rosengren 1988).

3. Foraging methods and habitat use

(*a*) *Foragers of the shore and littoral zone*

1. Pacific reef-heron, *Egretta sacra*. This solitary diurnal hunter of littoral animals was a sporadic visitor: two grey birds were seen in 1984 and two white ones in 1986. Three were on the shore and one on lava. The maximum population was two. Limb bones of three birds were found at Bone Alley (figure 1) in 1986 and some were broken, suggesting they had been taken by a predator.

2. Lesser golden plover, *Pluvialis dominica*; Mongolian plover *Charadrius mongolus*; whimbrel, *Numenius phaeopus* and great knot *Calidris tenuirostris*. These migrants were observed by Hoogerwerf (1953) on the shore in November 1952 soon after the volcanic eruption that destroyed the vegetation; they have not been recorded subsequently.

3. Common sandpiper *Actitis hypoleucos*. This migratory shorebird was first recorded by Hoogerwerf (1953) in 1951. We saw one in 1985 and another in 1986.

4. Great thick-knee, *Esacus magnirostris*. Observations: 1951, 1982, 1984–2, 1985–4, 1986–5; single birds, 1; pairs, 6; and threes, 2. Foraging: no observations, but it will eat crabs (Smythies 1981), beetles, grasshoppers and nestlings (Frith 1976). *Halcyon chloris* mobbed them on one occasion. Habitat: five observations on the beach, five on the ash slopes above the vegetation and two observations in casuarina woodland. Population in 1986: one pair.

5. Grey wagtail, *Motacilla cinerea*. Observations: 1951, 1986–2 (s/b); 1 (oc). Foraging: pouncing and gleaning insects. Habitat: Shoreline, *Ipomoea pes-caprae* beach vegetation and cliff–desert. Population in 1986: 1–2 individuals.

(*b*) *Frugivores*

1. Philippine glossy starling, *Aplonis panayensis*. Observations: 1985–1, 1986–2; only the distinctive calls were heard from the Northeastern Foreshore and eastern Forelands. These birds may have been transients. Habitat: Casuarina woodland. Morphometrics for $n = 4$ (museum specimens): bl = 16.0 ± 1.0, bd = 6.5 ± 0.4, hb = 44.0 ± 1.9, tl = 16.8, wt = 40 g. Population in 1986: one pair.

The starling, which was in extremely low numbers on Anak Krakatau, is principally a frugivore of the high tree tops, but will take ants, beetles and larvae (Hoogerwerf 1949, Smythies 1981). Numbers may increase as more fig trees begin to bear fruit.

2. Pink-necked pigeon, *Treron vernans*. Observations: 1986–4 (ef), 1 (oc); a pair of adults was observed three times and presumably the same pair with an immature seen twice. Habitat: on the Eastern Foreland three observations were of birds in upper branches of tall secondary rain

forest trees and one of flying birds in casuarina woodland; one observation was made of a pair sitting on the ash crest of the outer cone. Morphometrics for $n = 9$ (museum specimens): bl = 15.7±1.2, bd = 5.7±0.3, hb = 44.4±1.7, tl = 16.6±1.3, wt = 195 g. Population in 1986: one pair.

No foraging observations were made of this recent arrival on Anak Krakatau but it eats fruit, especially figs and berries (Kuroda 1933; Smythies 1981). The recently fruiting figs could easily support a breeding pair but we have no evidence that the free-flying immature was bred on the island. These birds may not have been the first of their species to colonize Anak Krakatau; the remains of two were found at Bone Alley in 1986. We searched the same area in 1984 and 1985 and so assume that the birds arrived between 1985 and 1986. The tibiotarsus of one was broken, so the predator may have been a large raptor such as *Haliaeetus leucogaster* rather than a small one such as *Tyto alba*.

3. Green-winged pigeon, *Chalcophaps indica*. Observations: the remains of one specimen from Bone Alley on 22 September 1986 is the only evidence of the existence of this species on Anak Krakatau. Morphometrics for $n = 1$ (specimen netted on Rakata in 1984): bl = 17, tl = 29, wt = 98 g. Population in 1986: zero.

We expected that the species would have been present as early as 1984 given the suitable habitat (dense undergrowth) and food resources for this ground feeder (fallen fruit and berries and fallen seed (Frith 1982), insects, ants and flies (Smythies 1981)) but extensive mist-netting, the best method of detection, failed to reveal it. The specimen at Bone Alley was probably a visitor or colonist that arrived between 1985 and 1986 and was taken by one of the two larger raptors, *Tyto alba* or *Haliaeetus leucogaster* on the island. It is unlikely that the bird was taken on another island and carried by the raptor to Anak Krakatau.

4. Sunda island cuckoo dove, *Macropygia phasianella*. Observations: 1985, one pair (ef); 1986, one (nef), seven (ef); six observations of pairs and three of a pair with an immature; 1988, one pair (nef). Foraging: only one observation was made when a pair was seen pecking at pebbles. They eat berries, fruit and seeds from trees and bushes (Smythies 1981; Frith 1982). Habitat: high in casuarinas in casuarina woodland. Morphometrics for $n = 5$ (museum specimens): bl = 16.2±1.1, bd = 5.2±0.1, hb = 46.2±1.3, tl = 17±0.0, wt = 145 g. Population in 1986: one pair.

This arboreal seed and fruit eater arrived in 1985, the year the figs fruited for the first time. It typically inhabits the middle story of shaded forest (Diamond 1975). The immature may have been bred on the island and we saw the parents courting once in 1986. At Bone Alley in 1986 the remains of three birds were found with some bones broken; we assume this was due to the large diurnal raptor, *Haliaeetus leucogaster*.

(*c*) *Insectivore–frugivores*

1. Yellow-vented bulbul, *Pycnonotus goiavier*. Observations: 1951, 1982, 1983, 1984, three (ef), 1985, five (ef), one (nef), one (nf), 1986, nine (ef), three (nef). Foraging: in nine observations the bird probed or gleaned first- and second-degree branches from 2–18 m above the ground in a variety of vegetation (*Casuarina*, *Ficus*, *Erythrina*, *Pandanus* and *Saccharum*). Thirty-four items were flushed from 14 birds: three grass seeds, 11 seeds of *Cassytha filiformis*, one unknown flower, three beetles, six wasps, two crickets, four dragonflies and four unidentified insect parts. Habitat: principally, casuarina woodland and occasionally casuarinas with elements of secondary rainforest (table 3); on the grassland of the Northern

Foreland it was only seen in the *Ficus–Pandanus* clumps. Captures: 1984, eight, 1985, two, 1986, 14 (one recaptured twice). The recapture rate was higher in 1984 than in 1986. Morphometrics for $n = 13$: bl = 16.1±0.7, bd = 5.4±0.5, hb = 38.8±1.0, tl = 16.5±0.8, wt = 33.9±2.6 g. Population for 1986: 15–20 pairs.

P. goiavier was extending its range on Anak Krakatau: it was one of two woodland species on the grassland of the Northern Foreland and it was the only species seen that flew over open ground between the vegetation of the Eastern Foreland and northeastern Foreshore. The low recapture rate in 1986 shows that the population estimate was an underestimate and was probably at least 15–20 pairs.

P. goiavier and *Caprimulgus affinis* were the only land birds, other than *Haliaeetus leucogaster*, that Hoogerwerf (1953) saw on his first visit to Anak Krakatau in 1951, but neither was seen in the following year, a month after the vegetation was destroyed by an eruption. *P. goiavier* was probably the first diurnal land bird to colonize the island, being an ecological generalist able to exploit both seeds and insects in all habitats of the archipelago (Zann *et al.* 1990).

2. Black-naped oriole, *Oriolus chinensis*. Observations: 1982, 1983, 1984, three (ef), 1985, two (ef, nef), 1986, seven (ef). Foraging: no observations but 29 food items were flushed from two captives taken in canopy nets: 14 remains of fruit of *Ficus septica*, one seed, one flower, 11 leaves of *Casuarina*, one cockroach and one cricket. Habitat: tops of the tallest casuarina and fig trees in casuarina woodland. Captures: two (adult male and a young male) in canopy nets set in casuarinas. Morphometrics for $n = 10$ (eight museum specimens): bl = 30.6±1.2, bd = 9.6±0.6, hb = 59.4±1.5, tl = 18.3±0.8, wt = 76.5 g. Population in 1986: 1–2 pairs.

Although this species prefers the tops of tall trees it will come down for foraging and with its diet of insects, fruit, flowers and leaves would be an early colonist.

(*d*) *Nectarivores–insectivores*

1. Olive-backed sunbird, *Nectarinia jugularis*. Observations: 1984, four (ef), 1985, three (ef), one (nef), 1986, seven (ef). Flocks of up to eight birds were seen but single birds or pairs were typical. Foraging: out of nine observations seven were leaf gleaning of insects in foliage and two probing for insects in second-degree branches; foraging heights ranged from 5–30 m in *Casuarina* (6), *Ficus* (1) and *Erythrina* (2). No nectar feeding was observed in 1986 as few plants were in flower. In August 1985 large flocks were seen taking nectar from a flowering *Erythrina* tree on Panjang. Habitat: six in casuarina woodland and two in secondary rainforest trees. Captures: 1984, four, 1986, two from nets set among fig trees. Morphometrics for $n = 7$ (five museum specimens): bl = 17.2±0.6, hb = 32.6±0.7, wt = 8.0 g. Population in 1986: 20–25 pairs; dependent young were seen in 1985.

The diet of this sunbird, according to Smythies (1981) is mainly nectar, with insects a minor component; the proportions of course would change depending on seasonal availability. On Anak Krakatau birds foraged the full height of vegetation, although Smythies (1981) states that they prefer lower foraging sites than the other sunbird, *Anthreptes malacensis*, also found on the island.

2. Brown-throated sunbird, *Anthreptes malacensis*. Observations: 1984, two (ef). Habitat: casuarina woodland. Morphometrics for $n = 4$ (museum specimens): bl = 15.8±0.5, bd = 3.9±0.2, wt = 12 g.

A pair were observed on 13 September 1984 but have not been seen since; the species is

probability extinct on the island. *A. malacensis* is larger than *N. jugularis* and eats pollen as well as insects and nectar; it hovers less than the latter and feeds at a greater height above the ground (Smythies 1981).

(*e*) *Omnivores*

1. House crow, *Corvus splendens*. Observations: 1986, one individual seen three times (ef). Foraging: kitchen scraps, figs and attempted to attack a bat. Habitat: shore and casuarina woodland. Population in 1986: one individual.

The house crow is an omnivorous opportunist that is extending its range in the Indian Ocean, frequently hitching rides on sea-going vessels (Ryall 1986). It had reached Ujung Kulon in 1984 (personal observation by R. A. Zann). It appeared on Anak Krakatau on 28 September 1986 and was not seen during the previous eleven days. We did not see it arrive on the island but it attempted to embark on our vessel when we left the island the next day. No *C. splendens* were seen by Thornton on 11 February 1988 so we must assume that the specimen seen in 1986 was a vagrant that died or moved off the island leaving no progeny.

2. Large-billed crow, *Corvus macrorhynchos*. Observations: 1983, 1984, one pair observed three times (ef); 1988, one pair observed once (nef). Foraging: no observations. Habitat: casuarina woodland and shore. Population in 1984 and 1988: one pair.

The pair in 1984 was not present on Anak Krakatau in 1985 and 1986 and the species was probably absent from the other islands of the archipelago as well because suitable habitat on these islands was well surveyed and the species is conspicuous. This must be considered an extinction and the pair seen in 1988 must be considered a re-colonization. *C. macrorhynchos* prefers open country with trees and shrubs (Hoogerwerf 1949; Smythies 1981) where it feeds on anything edible (Hoogerwerf 1949) on the ground to the tops of trees.

3. White-breasted waterhen, *Amaurornis phoenicurus*. Observations: 1982, 1984, three calls (ef); 1985, five calls, four sightings (ef); 1986, four sightings (ef). Habitat: casuarina woodland (ten observations), *Ischaemum* grassland (six observations); always on the ground. Morphometrics for $n = 6$ (museum specimens): bl $= 34.7 \pm 2.5$, bd $= 10.1 \pm 0.7$, hb $= 64.6 \pm 3.0$, tl $= 45.5 \pm 2.3$, wt $= 190$ g. Population in 1986: 2–3 pairs (based on calls of territorial birds).

On Anak Krakatau this large terrestrial omnivore preferred dense grass with a tree canopy but ventured out to scratch and probe in the bare ash and needles beneath the dense canopy of *Casuarina*. It feeds on small fish, grasshoppers and other insects and grass seeds (Smythies 1981). Skeletal remains including smashed tibiotarsi of three birds were found: at Bone Alley in 1986 and on the ash slope above the Eastern Foreland in 1985 and again in 1986. The predator was probably the eagle, *Haliaeetus leucogaster*.

4. Lesser coucal, *Centropus bengalensis*. Observations: 1982, one (nf), 1984, two calls (ef); 1985, one (ef), two (nf), five calls: two, (ef), three (nef); 1986, one sighting (ef), five calls (ef). Foraging: no observations. Habitat: sunny patches of grass, either *Imperata cylindrica*, *Ischaemum muticum* or *Saccharum spontaneum*. Morphometrics for $n = 4$ (museum specimens): bl $= 23.9 \pm 2.1$, bd $= 11.6 \pm 0.8$, hb $= 54.0 \pm 1.2$, tl $= 32.9 \pm 0.6$. Population in 1985: 5–8 pairs (assuming calling birds are territorial males).

Coucals eat seeds, grasshoppers, caterpillars, crickets, hemipterans, small reptiles, frogs, eggs and nestlings (Kuroda 1933; Frith 1976; Smythies 1981). *Pachycephala cinerea* mobbed a coucal in 1985 and this probably means that the coucal is a potential predator of *P. cinerea* eggs and young. The coucal was restricted to grassland on the island and was the only avian species

to exploit the expanse of *I. cylindrica* on the Northern Foreland. The estimate of 1–2 pairs in 1986 (table 4) was based on sightings as the species was less vocal than the previous year and is an underestimate.

5. Chestnut-capped thrush, *Zoothera interpres*. Observations: 1986, one (ef). Habitat: casuarina woodland. Foraging: no observations. Morphometrics for $n = 4$ (museum specimens): bl = 16.0±1.2, bd = 5.7±0.4, hb = 44.7±1.1, tl = 20.8±0.4, wt = 36 g. Population in 1986: one individual.

This thrush was a rare, furtive bird on the Krakataus and only one was trapped in thick *Neonauclea* forest on Rakata in 1984 (Zann *et al.* 1990). On Java it is a ground bird of dark, dense forests (Kuroda 1933; Hoogerwerf 1970) and was entirely unexpected on Anak Krakatau. It eats fruit, berries and insects from the ground (Smythies 1981). The single individual we observed on 29 September was an immature; it was not seen on the previous 12 days of the survey and may have just arrived on the island. We assume the bird was a dispersing visitor and not a resident.

(*f*) *Predator of ground and littoral invertebrates*

1. Collared kingfisher, *Halcyon chloris*. Observations: 1982, 1983, 1984, two (ef); 1985, four (ef); 1986, three (ef), one (nef), one (nf), two (ba). Foraging: three ground probes, four pounces on the ground, one pounce on a shore crab. No birds were sighted more than 8 m above the ground. Thirteen items were flushed from 14 birds: seven unknowns, one cockroach, one chrysomelid beetle, one wasp, one cricket and two crabs. Habitat: casuarina woodland (eight observations), shore (two), grassland (one), desert (two). In the last two habitats the kingfisher was always associated with the few small trees that were colonizing the area. Captures: 1984, seven, 1986, 15 (four recaptures). Morphometrics for $n = 15$: bl = 45.4±2.2, bd = 13.1±0.5, hb = 81.0±2.5, tl = 10.7±0.7, wt = 71.1 g±6.3. Population in 1986: 8–12 pairs.

Kingfishers had numerous nesting holes in termite nests and the sides of gullies and mobbed *Haliaeetus leucogaster* and *Esacus magnirostris*, which may be potential predators of adults and nestlings, respectively. This species appears to be extending its range on the island; by 1986 a few birds had moved into the expanse of grassland on the northern Foreland and on two occasions birds were seen at the barren lava and ash site, Bone Alley. The ability to forage on a variety of terrestrial and aquatic invertebrates in a range of habitats makes this species an early and successful colonizer.

(*g*) *Aerial insectivores*

1. Savanna nightjar, *Caprimulgus affinis*. Observations: 1951, 1982, 1984, one (ef); 1985, six (ef), 1986, two (ef). Foraging: up to six birds could be seen to hawk for insects each dusk. Six items were flushed from one capture: one cerambycid beetle and five tortricid moths. Habitat: birds may have roosted on the ash slopes of the island; they foraged just above the canopy of the casuarina woodland. Captures: 1986, one. Morphometrics for $n = 3$ (two museum specimens): bl = 8.0, bd = 3.2, hb = 40.5, wt = 61.0 g. Population in 1986: 3–4 pairs.

The nightjar was one of the first two land bird colonists on the island and was recorded by Hoogerwerf (1953) during his visit in 1951.

2. White-breasted wood-swallow, *Artamus leucorhynchus*. Observations: 1982, 1984, three (ef); 1985, four (ef), one (nf); 1986, eight (ef), one (nef); 1988, nef. Foraging: four observations of hawking flying insects above the canopy. Habitat: casuarina woodland. Birds invariably perched on the second degree branches at the top of 20–30 m casuarinas where they often

clumped in groups of 2–12 individuals. Morphometrics for $n = 4$ (museum specimens): bl = 17.6±0.9, bd = 8.7±0.5, hb = 43.6±1.3, wt = 40 g. Population in 1986: 4–5 pairs.

The species was a breeding resident on the island as dependent young have been observed. They fed on the diurnal insects that flew above the canopy in casuarina woodland. Woodswallows mobbed *Falco severus* and *Haliaeetus leucogaster*, which are probably potential predators. They would have been early colonists given their preference for trees fringing beaches (Smythies 1981; Zann *et al.* 1990).

3. Pacific swallow, *Hirundo tahitica*. Observations 1984, one (ef), one (oc); 1986, three (ef), one (nf). Foraging: hawking flying insects. Habitat: above the canopy in casuarina woodland and less often high above the shore. Population in 1986: 1–2 pairs.

The swallow was not seen perching on Anak Krakatau and we saw no evidence to suggest that it bred on the island. We assume that the few birds we saw were on a foraging expeditions and bred elsewhere on the archipelago.

4. Barn swallow, *Hirundo rustica*. Observations: 1984, one (oc); 1985, one (oc); 1986, one (nf), one (ef). Foraging: hawking flying insects. Habitat: high above casuarina woodland, Imperata grassland and the outer cone. Population in 1986: 1–2 pairs.

Only a few vagrants of this migrating species were seen gliding over the coast and outer cone. It appears to be less restricted to foraging above vegetation than *H. tahitica*.

5. Edible-nest swiftlet, *Collocalia fuciphaga*. Observations: 1984, two (s/b); 1985, two (s/b); 1986, two (s/b); 20 birds were seen in total ranging in flock size from 1–9. Foraging: hawking flying insects, typically at dawn and dusk. Habitat: high above the shore. Population in 1986: 2–5 pairs.

We found no caves on Anak Krakatau and assume that *C. fuciphaga* breeds elsewhere on the archipelago, such as Panjang where there are caves.

6. House swift, *Apus affinis*. Observations: 1984, one (oc); 1985, two (oc); flocks of six, one and five. Foraging: not observed, but we assume they took flying insects. Habitat: cliffs of the Outer Cone. Population in 1985: 3–4 pairs.

The cliffs of Anak Krakatau are probably not suitable for nesting by the swift but those of the other islands of the archipelago should be. No significance should be attached to their absence in 1986 since the Outer Cone was not often surveyed that year.

(*h*) *Insectivores of foliage and twigs*

1. Flyeater, *Gerygone sulphurea*. Observations: 1984, four (ef); 1985, four (ef), one (nef), one (nf); 1986, nine (ef), one (nf); 1988, one (nef). On 12 out of 16 occasions birds were in pairs. Foraging: 11 observations: five gleaning twigs, five gleaning foliage and one hovering. Four items were flushed from three birds: two small beetles and two spiders. Habitat: Casuarinas (10 out of 11 observations) in casuarina woodland, in foliage or second-degree branches at a height of 3–5 m, sometimes as high as 15 m. Captures: 1984, one; 1986, five (no recaptures). Morphometrics for $n = 14$ (nine museum specimens): bl = 8.5±0.6, bd = 2.8±0.2, hb = 25.3±0.9, tl = 12.8±1.0, wt = 6.0 g±0.6. Population in 1986: 20–25 pairs.

The flyeater is a specialist gleaner of insects from leaves and twigs of *Casuarina equisetifolia*; it may take insects on the wing. In conjunction with the casuarinas they are extending their range up the ash slope of the Outer Cone and to the Northern Foreland where two or three large trees are sufficient to support a territorial pair. Active nests were found in 1984 and 1985 and one capture had a brood patch in 1986.

2. Leaf-warbler, *Phylloscopus* sp. Observation: 1983, one (Bush & Newsome 1986). *P.*

coronatus and *P. trivirgatus* are the only species that range to the Sunda Strait (King *et al.* 1975) and both are migratory.

(*i*) *Insectivores of branches*

1. Mangrove blue flycatcher, *Cyornis rufigastra*. Observations: 1982; 1984, two (ef); 1985, three (ef); 1986, 13 (ef). Foraging: in all nine observations the bird was less than 3 m above the ground and flew down to pounce on prey. Nine items were flushed from five birds: four beetles, two ants, two crickets and parts of an unidentified insect. Habitat: five observations in casuarina woodland and four in rainforest trees all of which were over 5 m; four observations on first-degree branches, four on second-degree branches and one on a trunk. Captures: 1984, two; 1985, one; 1986, 16; four were recaptured including one banded the previous year. Morphometrics for $n = 12$: bl $= 13.9 \pm 1.0$, bd $= 5.0 \pm 0.7$, hb $= 36.8 \pm 1.2$, tl $= 15.5 \pm 1.0$, wt $= 20.2$ g ± 1.6. Population in 1986: 10–15 pairs.

This resident species bred on the island (three immatures observed in 1986) and was restricted to denser vegetation (Eastern Foreland only) with a tall canopy where it foraged by pouncing on insects less than three metres off the ground. It was captured more frequently in 1986 than in 1984 (table 2) and caught as frequently in casuarina vegetation as in *Ficus* (table 3).

2. Magpie robin, *Copsychus saularis*. Observations: 1982, one; 1984, two (ef); 1985, two (ef), one (nef), one (nf); 1986, four (ef); nine pairs and three single birds were sighted. Foraging: probing branches (two observations), trunk (one) and ground (one); eight items were flushed from five birds: two beetles, three wasps, one cricket, one spider and one unidentified insect. Habitat: casuarina woodland from the ground to 2 m. Captures: 1984, one; 1985, one; 1986, four (one recapture banded in 1985). Morphometrics for $n = 8$ (four museum specimens): bl $= 19.1 \pm 1.1$, bd $= 6.1 \pm 0.2$, hb $= 48.9 \pm 1.6$, tl $= 23.2 \pm 1.3$, wt $= 42.5$ g. Population in 1986: 5–6 pairs. This must be an underestimate since in 1985, when the species was more vocal, five pairs were identified by song from the Northeastern Foreshore; 10–15 pairs would be a more realistic number.

The robin specializes in probing for larger insects within 2 m of the ground in shaded locations where cover is good and the ground clear. In September 1985 it was strongly territorial and there was much counter-singing.

3. Tiger shrike, *Lanius tigrinus*. Observation: 1986, one (ef). Foraging: no observations, but according to Smythies (1981), it flies down from a prominent perch to pounce on crickets and beetles on the ground. Habitat: casuarina woodland. Capture: 1986, one. Morphometrics for $n = 10$ (nine museum specimens): bl $= 14.8 \pm 0.7$, bd $= 9.2 \pm 0.5$, hb $= 40.4 \pm 1.0$, tl $= 17.6 \pm 1.0$, wt $= 25$ g. Population in 1986: one bird.

The shrike was captured on the last day of the 1986 expedition and it is possible the bird had just arrived on Anak Krakatau on its migration to Java (Smythies 1981).

4. Mangrove whistler, *Pachycephala cinerea*. Observations: 1984, eight (ef); 1985, three (ef), one (nef), one (nf); 1986, ten (ef), one (nef), one (nf). Foraging: eight observations of probing first- and second-degree branches and three leaf gleans all in casuarinas at a mean height of 7.9 ± 5.4 m (range 2–18 m); 28 items flushes from 23 birds: one beetle, eleven wasps, four spiders, two ants, eight unidentified insect parts, one unidentified fruit and one unidentified flower part. Habitat: all observations in casuarina woodland. Captures: 1984, 17 (two immatures); 1986, 20 (five immatures) and nine recaptures. Morphometrics for $n = 19$: bl $= 14.0 \pm 1.0$, bd $= 5.3 \pm 0.2$, hb $= 37.5 \pm 0.8$, tl $= 14.9 \pm 0.8$, wt $= 20.7 \pm 1.6$. Population in 1986: 20–25 pairs.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

The whistler is an insectivore of the mid to low levels of *Casuarina equisetifolia* where it probes branches for insects. It is common on the island and has the highest rate of capture (table 2). It is extending its range and is one of the few woodland species to be found on the sparsely treed Northern Foreland.

(*j*) *Predators of vertebrates*

1. White-bellied sea-eagle, *Haliaeetus leucogaster*. Observations: 1951, one; 1982, one; 1985, one (ef), three (oc); 1986, one (ef), one (ba), three (oc), two (s/b); 1988, one (nef); an adult pair and an immature were observed together in 1986. Foraging: no observations of prey but all but one sighting were of slowly soaring birds, presumably searching for prey. The eagle was mobbed by *Falco severus*, *Halcyon chloris* and *Artamus leucorhynchus* and presumably these are potential prey. The following skeletal remains were also likely to have been the results of predation by the sea-eagle because of their size, location and the fact that the long bones were broken: *Egretta sacra* (three skeletons at Bone Alley), *Amaurornis phoenicurus* (two skeletons above the Eastern Foreland and one at Bone Alley), *Macropygia phasianella* (three skeletons at Bone Alley), and one sea-snake skeleton at Bone Alley. The eagle was seen perching on a laval outcrop at Bone Alley in 1986. Habitat: shore, cliff–desert and casuarina woodland. Population in 1986: one pair.

The eagle did not breed on Anak Krakatau but the island was part of its home range and judging from Hoogerwerf's (1953) observation the species has been hunting there since 1951. We have seen increasing exploitation of the island since 1984 when we found no remains of prey attributable to the sea-eagle; in 1985 we found skeletons of two prey and in 1986 eight, of which five were land birds and five shore birds. We have seen a pair and an immature together but did not know from which island they came.

2. Oriental hobby, *Falco severus*. Observations: 1986, four (ef), three (rim of Outer Cone). Foraging: one unsuccessful stoop on an unidentified small bird; *Artamus leucorhynchus* mobbed the falcon twice in 1986 and presumably is potential prey. Habitat: casuarina woodland as a hunting area and the cliffs of the outer cone. The species may have nested on these cliffs as a pair was seen perching and also mobbing *Haliaeetus leucogaster* there. Population in 1986: one pair.

The falcon has colonized the island since 1985–86 and it is possible that the pair may become permanent residents; the biomass of suitable flying prey (small birds, bats, and insects, Kuroda 1933) that appears to be available would support a pair.

3. Barn owl, *Tyto alba*. Observations: 1982, one (ef, calls); 1986: sighting of one pair and a single bird at Bone Alley; 15 calls (ef). Foraging: flying birds which called over the Eastern Foreland were presumably hunting. The following remains were found at Bone Alley near the site at which owls were sighted and where uric acid stains indicate roosting sites: 1984, pellets of 25 *Rattus rattus* (distinguished from *R. tiomanicus* by skull features); 1985, pellets of 25 *R. rattus*; 1986, in addition to the pellets of 11 *R. rattus*, the skeleton of the bat *Rousettus amplexicaudatus* was found as well as feathers and skeletons with unbroken bones of one of each of *Treron vernans*, *Macropygia phasianella* and *Chalcophaps indica*. Habitat: casuarina woodland for hunting and lava outcrops for roosting. Population in 1986: one pair.

Owls were not present on the island in September 1984 and August 1985 but pellets collected from Bone Alley on each expedition showed that owls had been present some time previously. It is likely that all the non-rodent prey remains found at Bone Alley were of animals taken on Anak Krakatau as barn owls normally eat prey at the site of capture (Bunn *et al.* 1982). It is possible that owls ate the rats on Rakata, the only island in the archipelago with *Rattus rattus*

other than Anak Krakatau (Iwamoto 1986), and commuted across the 4.5 km of sea to roost on Anak Krakatau each morning. This is unlikely, however, as according to Bunn *et al.* (1982), barn owls normally hunt close to the roost. The density of *Rattus rattus* was low on Anak Krakatau. Only one has ever been caught on the island (in 1985) and it is likely that the owls have switched from their preferred rodent diet to birds and bats.

Table 4. Prey items extracted from eight insectivores mist-netted on Anak Krakatau in 1986

(*n* is the number of birds sampled.)

species	*n*	seeds	fruits	flowers	leaves	ants/wasps	beetles
Caprimulgus affinis	1	—	—	—	—	—	1
Halcycon chloris	14	—	—	—	—	1	1
Pycnonotus goiavier	14	3	11	1	—	6	3
Oriolus chinensis	2	—	15	—	11	—	—
Copsychus saularis	5	—	—	—	—	3	4
Gerygone sulphurea	3	—	—	—	—	—	2
Cyornis rufigastra	5	—	—	—	—	2	4
Pachycephala cinerea	23	—	1	1	—	13	1

species	*n*	crickets	dragonflies	spiders	moths	cockroaches	crabs
Caprimulgus affinis	1	—	—	—	5	—	—
Halcycon chloris	14	—	—	—	—	1	2
Pycnonotus goiavier	14	2	4	—	—	—	—
Oriolus chinensis	2	1	—	—	—	1	—
Copsychus saularis	5	2	—	1	—	—	—
Gerygone sulphurea	3	—	—	2	—	—	—
Cyornis rufigastra	5	2	—	—	—	—	—
Pachycephala cinerea	23	—	—	4	—	—	—

4. Community organization

Figure 2 shows species in relation to habitat, foraging method and substrate. The data upon which this is based (§3) are too limited in quantity and scope (only the months of August and September sampled) to warrant quantitative treatment and to make strong inferences about niches. Nevertheless, if we ignore the shore foragers (including *Esacus magnirostris*) we see a consistent pattern where there is some overlap for these dimensions of the niche but this is reduced if the principal foraging method of each species is considered; it is further reduced if size differences are taken into account. The diet of eight mist-netted insectivore species showed much overlap of prey items; beetles were found in gut contents of all but one of the eight species, wasps in five, crickets and ants or wasps in four and spiders in three (table 4). Therefore, despite different foraging methods and substrate there appears to be some dietary overlap among the species during our limited sample, although it is impossible to tell if they are taking exactly the same species of prey item.

Foraging niches of two insectivores appear to overlap more than any other, *Cyornis rufigastra* and *Copsychus saularis*: both hunt on branches close to the ground by pouncing on beetles, crickets and ants. Furthermore, they are the only species that occasionally hunted on tree trunks. The former requires a denser more shaded habitat than the latter and is not found in casuarinas where the canopy does not overlap. Competition between the two is reduced on Rakata where both species are found together only in *Neonauclea* forest below 400 m; *C. rufigastra* is found in all other habitats on the island except casuarina forest (Zann *et al.* 1990).

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

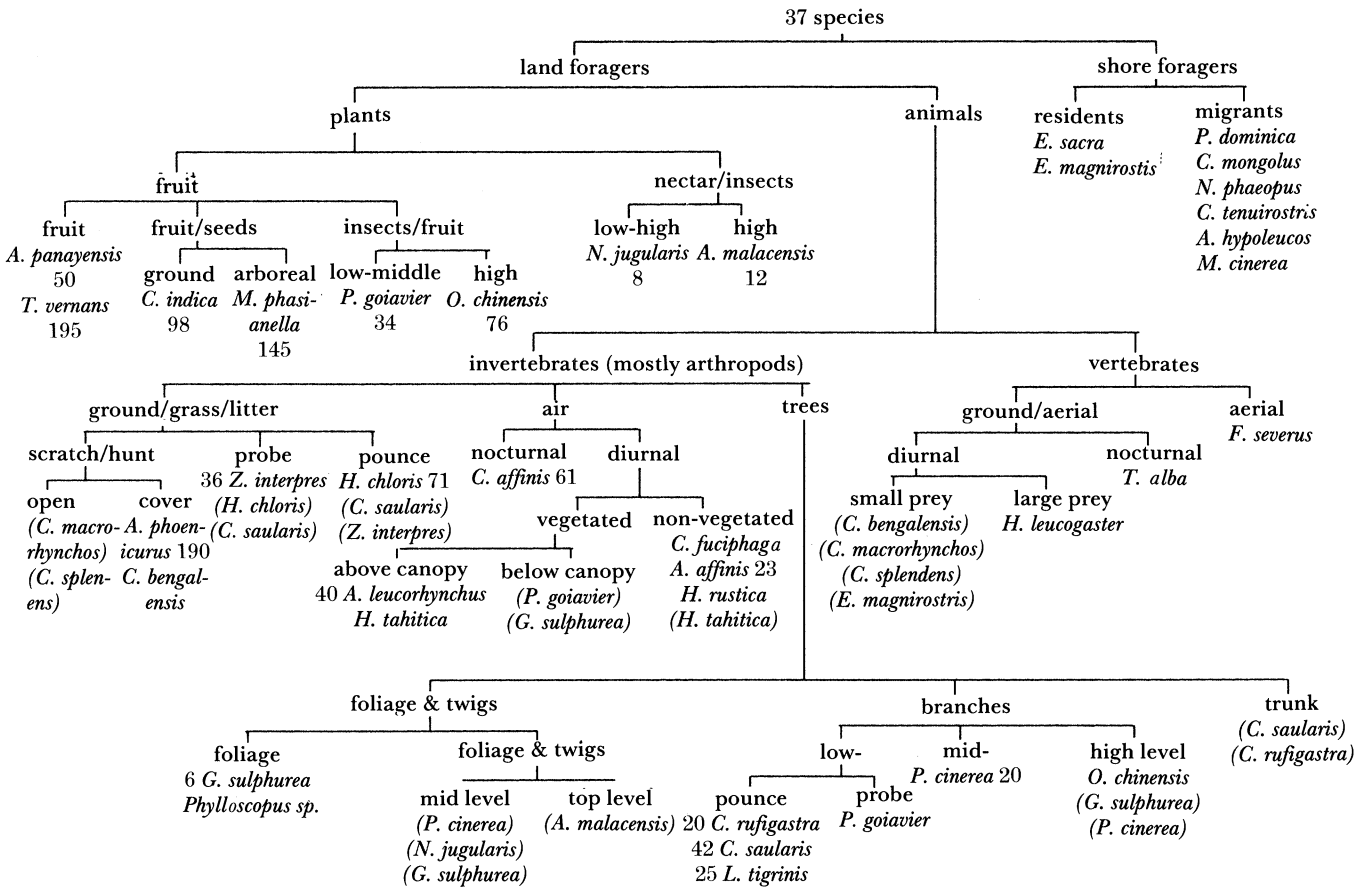

FIGURE 2. Community organization of birds on Anak Krakatau arrayed by habitat, foraging substrate and foraging method. Parentheses show supplementary method of foraging. Numbers show the mean or median weight in grams of each species where it is known.

5. POPULATION SIZE

The estimated size of the bird population on Anak Krakatau is shown in table 5. The differences between 1985 and 1986 are due principally to the different methods used and the fact that birds were more vocal in the former year because of pronounced breeding activity. The higher value for each species over both years is probably the more accurate estimate.

Density estimated by mist-netting on Anak Krakatau appears high by comparison with other islands and habitats but sampling bias (table 9, Zann *et al.* 1990) makes this difficult to prove. Nevertheless, if we consider only insectivore densities on the island estimated by transect we find higher than predicted values. Canopy height is considered a simple and reliable estimator of insectivore densities of woodlands and low forests because it is an index of structural complexity. For eucalypt forests and woodlands in Australia the regression equation for this relation is $y = 2.6x + 0.77$, where y = number of pairs per ten hectares (ha†) and x = canopy height in metres (Gilmore 1985). Applying this prediction to casuarina woodland on Anak Krakatau (area 12 ha, table 1) and assuming an average canopy height of 20 m, we get an estimate of 52 pairs of insectivores per 10 ha^{-1}. However, if we take the lowest realistic value

† 1 hectare = 10^4 m^2.

Table 5. Estimated number of pairs of each bird species on Anak Krakatau in 1985 and 1986

(1-One pair sighted in 1984 and again in 1988, 2-one single individual observed 3-bones found. Values in italic are the lowest realistic values for insectivores (see §5).)

species	estimated number of pairs 1985	1986
Egretta sacra	1	1
Haliaeetus leucogaster	1	1
Falco severus	—	1
Amaurornis phoenicurus	4–5	2–3
Actitis hypoleucos	2	1
Esacus magnirostris	3	1–2
Treron vernans	0	1
Macropygia phasianella	1	1
Chalcophaps indica (3)	—	—
Centropus bengalensis	5–8	1–2
Tyto alba	1	1
Caprimulgus affinis	4–6	3–*4*
Collocalia fuciphaga	5	*3*–5
Apus affinis	*2*–3	—
Halcyon chloris	6–8	*10*–12
Hirundo tahitica	2	*1*–2
H. rustica	2	1
Pycnonotus goiavier	*15*–20	8–12
Oriolus chinensis	*5*–7	1–2
Corvus macrorhynchos (1)	—	—
C. splendens (2)	—	—
Copsychus saularis	*10*–15	5–6
Zoothera interpres (2)	—	1
Gerygone sulphurea	15–20	*20*–25
Cyornis rufigastra	5–10	*15*–20
Pachycephala cinerea	10–15	*25*–30
Artamus leucorhynchus	*10*–15	4–5
Motacilla cinerea (2)	—	1
Lanius tigrinus (2)	—	1
Aplonis panayensis	1	1
Anthreptes malacensis	1	—
Nectarinia jugularis	10–15	*20*–25

for each pair of insectivores in table 5 we find that the island has 117 pairs 10 ha^{-1}; more than twice that predicted. This result must be tempered by the fact that the equation was established for subtropical eucalypt habitats that may not apply in the tropics (Karr 1971); nevertheless first colonists, typical *r*-selected species, have a high reproductive potential and maintain very high population densities (Diamond 1975). Thornton & New (1988) found insect diversity on Anak Krakatau was unexpectedly high in the vegetated areas and suggested this may be partly because airborne insects that landed on the island gravitated to these restricted areas; if the same phenomenon affects insect abundance the high insect biomass in the vegetation may permit high insectivore numbers.

6. Sequence of bird colonization of Anak Krakatau

(*a*) *Pre-vegetation species*

Shorebirds would have been the first to exploit the shoreline of the newly emerged island for resting and scavenging and, indeed, Hoogerwerf (1953) found four species (*Pluvialis dominica*,

Charadrius mongolus, *Numenius phaeopus* and *Calidris tenuirostris*) present in November 1952 exploiting this niche, one month after volcanic eruptions had destroyed all vegetation and reduced the island to barren volcanic ash (table 6). When he first visited the island the previous year, Hoogerwerf (1953) had also seen *Haliaeetus leucogaster* (a D-tramp in the Bismarck archipelago (Diamond 1975)) and *Esacus magnirostris*, two species capable of hunting on land and shore.

Before Anak Krakatau became colonized by the first plants it would have also provided a niche for small aerial insectivores that exploit airborne arthropods blown from nearby islands; species that currently exploit this resource on Anak Krakatau include *Apus affinis*, *Hirundo*

TABLE 6. BIRDS OF ANAK KRAKATAU 1951–1986

(×, observation; ×* also observed in 1988 (I. W. B. Thornton, personal communication); 1, *Collocalia* sp., 2, introduced but did not establish; 3, species not recorded for the archipelago; 4, incidental sighting in 1983 (Bush & Newsome 1986); 5, also recorded by Jacobson (1909) on the Krakataus in 1908; sh, shorebird; mi, migrant; lb, land bird.)

	1951[a]	1952[a]	1982[b]	1984[c]	1985[c]	1986[c]
1. *Actitis hypoleucos* (sh, mi) 5	×	—	—	—	×	×
2. *Esacus magnirostris* (sh)	×	—	×	×	×	×
3. *Haliaeetus leucogaster* (lb)	×	—	×	—	×	×*
4. *Pycnonotus goiavier* (lb) 4, 5	×	—	×	×	×	×
5. *Caprimulgus affinis* (lb) 5	×	—	×	×	×	×
6. *Motacilla cinerea* (mi)	×	—	—	—	—	×
7. *Hirundo rustica* (mi)	×	—	—	×	×	×
8. *Pluvialis dominica* (sh, mi)	—	×	—	—	—	—
9. *Charadrius mongolus* (sh, mi)	—	×	—	—	—	—
10. *Numenius phaeopus* (sh, mi)	—	×	—	—	—	—
11. *Calidris tenuirostris* (sh, mi)	—	×	—	—	—	—
12. *Egretta sacra* (sh)	—	—	×	—	×	×
13. *Amaurornis phoenicurus* (lb)	—	—	×	×	×	×
14. *Centropus bengalensis* (lb) 5	—	—	×	×	×	×
15. *Tyto alba* (lb)	—	—	×	×	×	×
16. *Collocalia fuciphaga* (lb) 5	—	—	×1	×	×	×
17. *Halcyon chloris* (lb) 4, 5	—	—	×	×	×	×*
18. *Oriolus chinensis* (lb) 4, 5	—	—	×	×	×	×
19. *Copsychus saularis* (lb)	—	—	×	×	×	×
20. *Cyornis rufigastra* (lb)	—	—	×	×	×	×
21. *Artamus leucorhynchus* (lb) 5	—	—	×	×	×	×*
22. *Gallus domesticus* (lb)	—	—	×2	—	—	—
23. *Dicaeum trochileum* (lb)	—	—	×3	—	—	—
24. *Phylloscopus* sp. (mi) 4	—	—	—	—	—	—
25. *Apus affinis* (lb)	—	—	—	×	×	—
26. *Hirundo tahitica* (lb)	—	—	—	×	—	×
27. *Corvus macrorhynchos* (lb) 4, 5	—	—	—	×*	—	—
28. *Gerygone sulphurea* (lb)	—	—	—	×	×	×*
29. *Pachycephala cinerea* (lb)	—	—	—	×	×	×*
30. *Anthreptes malacensis* (lb)	—	—	—	×	—	—
31. *Nectarinia jugularis* (lb)	—	—	—	×	×	×
32. *Macropygia phasianella* (lb)	—	—	—	—	×	×
33. *Aplonis panayensis* (lb)	—	—	—	—	×	×
34. *Treron verans* (lb) 5	—	—	—	—	—	×
35. *Zoothera interpres* (lb)	—	—	—	—	—	×
36. *Corvus splendens* (lb)	—	—	—	—	—	×
37. *Lanius tigrinus* (lb, mi)	—	—	—	—	—	×
38. *Falco severus* (lb)	—	—	—	—	—	×
39. *Chalcophaps indica* (lb) 5	—	—	—	—	—	×

Sources of data: [a] Hoogerwerf (1953); [b] Ibkar-Kramadibrata *et al.* (1986); [c] Zann *et al.* (1990).

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

rustica, *H. tahitica* (one of Diamond's (1975) C-tramps) and *Collocalia fuciphaga*. These airborne insects also provide fallout on the ground (Thornton *et al.* 1988) and these are currently taken by species such as *Motacilla cinerea* and *Actitis hypoleucos*. In 1951 Hoogerwerf (1953) recorded only *H. rustica* and *M. cinerea* but may have recorded other predators of airborne insects had he surveyed more extensively (table 6).

(*b*) *Movement of birds between islands*

No species that exploited Anak Krakatau before it became vegetated could have obtained sufficient resources to permanently reside and breed on the island. Furthermore, given the proximity to the other islands, none might need to. Even when the island had reached the savannah grassland stage of succession in 1951 Hoogerwerf (1953) placed no significance on his list of species because of the proximity factor (table 6). This is certainly true in the case of *Haliaeetus leucogaster* and the migrants *Actitis hypoleucos*, *Hirundo rustica* and *Motacilla cinerea* but not necessarily the case for *Esacus magnirostris*, *Caprimulgus affinis* and *Pycnonotus goiavier*.

It is difficult to assess the degree of movement of birds between islands of the archipelago. Despite considerable vigilance we saw no birds flying between any of the islands during our three expeditions but they obviously do so fairly frequently. For example, three birds appeared to arrive on Anak Krakatau during our 1986 visit (*Corvus splendens*, *Zoothera interpres* and *Lanius tigrinus*) and, of course, the barn owl pellets indicated that they too vacated and returned to the island at certain times of the year. The aerial insectivores (*Apus affinis*, *Hirundo tahitica* and *Collocalia fuciphaga*) must also hunt over the other islands of the archipelago. Nevertheless, this situation contrasts with the observation made by Diamond (1975) on a small islet of New Guinea where the recolonization rate was one species per hour after he had experimentally defaunated it. We have proof that some species are resident on Anak Krakatau: in 1985 we banded only four birds, yet we recaptured two in 1986 (one *Cyornis rufigastra* and one *Copsychus saularis*).

In 1951 Anak Krakatau would have furnished sufficient of the requirements of *E. magnirostris* and *C. affinis* for feeding and nesting. *Pycnonotus goiavier*, in contrast, would have required tree cover for food, shelter and nesting and it is difficult to determine if all its requirements for survival and reproduction would have been met on the island in 1951, although its ability to eat both fruit and insects would facilitate its early and permanent colonization. Shelter and nesting sites would have been available in the *Saccharum* and casuarinas, some of which were about 10 m high (van Borssum Waalkes 1960). The creeper, *Cassytha filiformis*, which parasitizes pioneering plant species, was common in 1951 (van Borssum Waalkes 1960) and it has a succulent fruit, the seeds of which were flushed from three *P. goiavier* we captured in 1986. Thus some suitable food plants were definitely present in 1951; this plant is now common on the Northern Foreland (Thornton & Rosengren 1988).

(*c*) *Colonizers of pioneer plant communities*

The first vegetation on the island (pioneer communities of *Ipomoea-Ischaemum* on the beach and *Saccharum* on the inland slopes) would have provided food resources for insects (see Dammerman 1948) of which the larger flying nocturnal beetles and moths would have constituted a resource for the nocturnal aerial insectivore, *Caprimulgus affinis*. Hoogerwerf (1953) recorded it on the first survey of the island in 1951. This species has minimum nesting requirements making it one of the first species to nest on the island.

The other colonizers of the pioneer plant communities are unknown but by examining those that have colonized the early successional stages of vegetation now found on the Northern Foreland we can make an educated guess; plant succession is now at a stage similar to that reached by the Eastern Foreland about a decade ago (Thornton & Rosengren 1988) and resembles the vegetation in 1951 before it was destroyed by volcanic activity in 1952 (van Borssum Waalkes 1960). *Centropus bengalesis*, the coucal, was the only species we found in the extensive stands of *Imperata cylinderica* on the Northern Foreland and is likely to have been an early colonist; it was not recorded by Hoogerwerf (1953) in 1951 and was first recorded on the island on the Northern Foreland in 1982, during the next survey (Ibkar-Kramadibrata *et al.* 1986). In contrast, other species of birds we found on this foreland were few in number and associated with the few trees and shrubs that have recently become established and are likely to have arrived after the coucal. These were *Halcyon chloris*, *Pycnonotus goiavier*, *Copsychus saularis*, *Gerygone sulphurea*, *Pachycephala cinerea* and *Artamus leucorhynchus* of which only the first two are ecological generalists. The others were strongly associated with casuarina woodland on the island and exploited insects in various niches in this habitat and would have required a minimum tree cover and tree size. Of these predicted early colonists, only *P. goiavier* was present in 1951 (Hoogerwerf 1953), but *C. bengalensis* and *H. chloris* would probably have soon followed to constitute the first wave of permanent colonists with *C. affinis* and *P. goiavier*. *Corvus macrorhynchos*, an omnivore of open habitats may have been the next species to colonize; it was absent in 1982, 1985 and 1986 but present in 1983, 1984 and 1988.

(*d*) *Colonizers of casuarina woodland and forest*

Casuarina woodland was the dominant vegetation of the Northeastern Foreshore during the 1984–86 survey period and bird species found here could be representative of those that colonized the casuarina woodland as it formed on the Eastern Foreland some 10–15 years earlier. Species generally confined to this habitat were: *Copsychus saularis*, an insect forager of the ground and low branches; *Pachycephala cinerea*, an insect forager of branches of the mid level, *Gerygone sulphurea*, a gleaner of insects from foliage, *Artamus leucorhynchus*, a hawker of flying insects above the tree canopy and *Oriolus chinesis*, a frugivore–insectivore that hunts for insects on the topmost branches of tall casuarianas. The gerygone would have been the first to colonize the casuarinas when they were part of the earlier savannah woodland stage; during the 1984–86 survey period this species established territories in small isolated clumps of casuarinas that were colonizing the upper slopes of the Northeastern Foreland. The need for tall casuarinas would make *O. chinensis* and *A. leucorhynchus* the last of this group to colonize.

When the canopy of the woodland began to close it created conditions suitable for another three species. *Amaurornis phoenicurus*, the rail, was confined to the Eastern Foreland and largely to heavily shaded locations under casuarinas with nearby patches of *Ischaemum* grass. *Cyornis rufigastra*, one of the most abundant species on Anak Krakatau, was confined to the Eastern Foreland where it foraged on insects below 3 m in shrubs and dense shady casuarinas; it also foraged to a lesser extent among trees of secondary rainforest. *Nectarinia jugularis*, a nectarivore/insectivore, also abundant was largely confined to the Eastern Foreland but seen on one occasion on the Northern Foreland; it foraged for insects among the foliage of casuarinas but could exploit the nectar of the secondary rainforest species.

Unfortunately, no lists of birds are available between 1952 and 1982 to confirm the above predictions. Furthermore, there is some doubt that the 1982 list, made by the Bandung

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

expedition is complete. For example, if we exclude three aerial insectivores that may easily have been missed in such a short survey, made without a bird specialist, three species which we found conspicuous, abundant and breeding in 1984 (tables 3 and 4) were not listed in 1982: *G. sulphurea*. *P. cinerea* and *N. jugularis* (table 6). We must assume that these species were present in 1982 and were not more recent colonists. This is especially likely for *N. jugularis*, which has high dispersal rates (D-tramp in the Bismarck archipelago (Diamond 1975)).

(*e*) *Colonizers of secondary rainforest habitats*

Secondary rainforest plants were already present on Anak Krakatau before 1979 but appeared to have only a marginal effect on the avifauna until figs began to bear fruit in 1985. Two frugivores, *Aplonis panayensis* and *Macropygia phasianella* were recorded for the first time in August 1985. Only a few calls of *A. panayensis* were heard in 1985 and 1986 so little comment can be made on its status on the island except that the population was extremely small. In contrast, a pair of *M. Phasianella* was seen in 1985 and another pair with an immature in 1986, so we conclude the species has successfully colonized the island, at least in the short term. This pigeon not only digests the flesh of figs and other fruit, but also the seeds, for which they need grit. In 1986 the bones of three *M. phasianella* were found at Bone Alley and we infer that these colonists were taken by the sea-eagle *Haliaeetus leucogaster*.

Treron vernans, another pigeon, arrived on the island in 1986; a pair and an immature were seen several times. They are obligate frugivores that eat the flesh of figs and berries (Smythies 1981). The remains of two individuals were found at Bone Alley in 1986, presumably the result of predation by *H. leucogaster*. This pigeon has the potential to be a successful colonist given the suitable food source now available and sites for nesting, and providing predation does not eliminate the recruits. There is evidence of a third pigeon on the island. In 1986 remains of *Chalcophaps indica* were found at Bone Alley; this appears to be the only individual to have reached the island and was probably killed by a raptor. This pigeon, almost a food generalist, can eat insects, ants and flies (Smythies 1981) as well as seeds, fallen fruit and berries (Frith 1982) and prefers dense, shady understorey. We predicted it to have been the first pigeon to colonize Anak Krakatau.

(*f*) *Raptor colonists*

Three species of raptors were found on Anak Krakatau during the survey period. *Haliaeetus leucogaster*, the sea-eagle, used the island for hunting before plant colonization began but it is not resident. It requires a territory of some 8–24 km^2 (Diamond 1975) and hence must breed elsewhere on the archipelago. *Tyto alba*, the second raptor, is resident for part of the year and has been present since 1982. Its survival depends on the abundance of *Rattus rattus* that has diminished in numbers since 1985; fewer rat pellets were found in 1986 and more remains of birds. The third raptor, *Falco severus*, was first recorded in 1986: a pair gave the impression they might have a nest (by frequently perching on the rim of the Outer Cone and mobbing *H. leucogaster* there). The island appears to have sufficient small birds for a pair of falcons to survive and breed and become successful colonists.

(*g*) *Unsuccessful colonists*

A pair of *Anthreptes malacensis* was observed in 1984 but not seen subsequently. We must assume these pioneers failed to colonize for unknown reasons. Perhaps the population was too small or the nectar resource too patchy.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Single birds of *Corvus splendens* and *Zoothera interpres* were observed in 1986; without mates they could only be regarded as potential but unlikely colonists at this stage. The house crow, an omnivore, was not seen in 1988 and probably failed to colonize, presumably because it had no mate or was taken by a predator or left the island. This species is a highly successful, but destructive, colonist that is extending its range round the Indian Ocean (Ryall 1986) and conditions on Anak Krakatau should have sufficed for its survival and reproduction. Had it colonized successfully this voracious opportunist may have had a significant effect on the avian community. The thrush, *Zoothera interpres*, was an immature and would not be expected to stay as it is an inhabitant of dark, dense rainforests (Kuroda 1933; Hoogerwerf 1970).

(*h*) *Future colonization*

The major constraint on bird colonization of Anak Krakatau is the extent and frequency of volcanic activity that can destroy, and indeed has destroyed, the vegetation upon which birds depend. Accidental bush fires from visitors constitute the other major threat to the habitat. Furthermore, there are also biological constraints, one of which is the premature arrival of two major predators, *Haliaeetus leucogaster* and *Tyto alba* that appear to be harvesting large potential new founder colonists (*Macropygia phasianella*, *Treron vernans* and *Chalcophaps indica*) before they can become established. Perhaps their size and the limited and open habitat makes them easy prey. Bone remains show that of six *M. phasianella* to reached the island between 1985 and 1986 three were killed by predators; five *T. vernans* arrived in 1986, yet two have been killed, and finally, it appears that the only *C. indica* individual to arrive was also killed. The owl appears to have switched to bird prey as a consequence of the reduced abundance in 1985–86 of its preferred prey, rodents, and their numbers will determine whether or not bird predation by owls will continue. Iwamoto (1986) believed that the rat population on Anak Krakatau is too small to be stable and this may explain the apparent fall in their numbers. In contrast to the owl and eagle, the falcon *Falco severus* appears to be well adjusted to the abundance of small bird prey available on the island in the 1980s and should not affect future colonization.

Most species that have colonized Anak Krakatau have come from populations already present on the older islands and these should constitute the major source of future colonists. The fruiting of figs on Anak Krakatau appears to be responsible for the arrival of the three pigeons mentioned above and this could also attract four other fruit-eaters present on the older islands, although this is unlikely in the near future. *Dicaeum trigonostigma* and *Ptilinopus melanospila* prefer rainforests that are as yet only incipient on Anak Krakatau, furthermore, these species do not appear to be good dispersers. The former is still only found on Rakata, although it arrived in 1908–1919, and the latter now occurs on Rakata and Panjang although it arrived in the archipelago between 1932–1951. Two other pigeons, *Ducula bicolor* and *Ducula aenea*, which eat fruit at the very tops of tall trees, especially in the *Barringtonia* zone, cannot be expected to arrive on Anak Krakatau for many years; the same can be said for the woodpecker *Picoides moluccensis* that also requires large trees.

The two species most likely to be the next colonists from the older islands are *Lalage nigra* and *Collocalia esculenta*. *L. nigra* arrived early (1908–1920) on the archipelago and was common up to 1929 (Dammerman 1948) but is now rare and restricted to rapidly diminishing remnant areas of casuarinas on Panjang and Rakata (Zann *et al.* 1990); suitable casuarina habitat has long been available on Anak Krakatau and the species might have been expected to have colonized before our surveys. The small population of *L. nigra* on the older islands may account

for its lack of colonists on the new island. The second species, *C. esculenta*, is an aerial insectivore of coast and cliff and a C-tramp in the Bismarck archipelago (Diamond 1975) that has probably hunted over Anak Krakatau but been missed by surveys; there may be caves among the lava fields suitable for nesting. Finally, from the older islands, we can expect the brown sunbird *Anthreptes malacensis* to recolonize Anak Krakatau in the near future but not the scarlet sunbird *Aethopyga mystacalis*, which is a poor disperser by comparison and an inhabitant of secondary rainforest (Zann *et al.* 1990).

Younger, more open habitats on Anak Krakatau not only provided an 'ecological rescue' effect (Thornton *et al.* 1990) for species denied these habitats by plant succession on the older islands but it also provides suitable habitat for open country colonists new to the archipelago. *Tyto alba*, *Corvus splendens* and *Lanius tigrinus* are species of open habitats that have arrived on Anak Krakatau, although only the first species is a resident for part of the year. Other potential colonists are listed in table 10 of Zann *et al.* (1990) as inhabitants of casuarina and open habitats on the island of Sebesi and Panaitan, and the first colonists would be those with the best dispersal ability.

7. Comparisons with the colonization of Rakata

Anak Krakatau can serve as a model for the bird colonization of Rakata to the extent that plant succession on Anak Krakatau appears to be at a stage comparable to that reached by the older islands some 60–80 years ago (summarized by Richards 1982). On the older islands, after the pioneer beach communities, dense grasslands (comparable to the northern Foreland) dominated in 1897, and by 1906 a coastal woodland of casuarinas and other species had formed (slightly more advanced than the Northeastern Foreshore). By 1909 some patches of woodland included some secondary rainforest species such as *Ficus* and *Macaranga* (comparable to the Eastern Foreland). One important difference, however, is that the *Barringtonia* coastal formation failed to develop to any extent on Anak Krakatau (except for the *Pandanus* element) whereas it was an important and stable pioneering community of Rakata.

Thirteen species of land birds were found on the archipelago in 1908 when Jacobson (1909) conducted the first bird survey and all but three species were found on Rakata in all subsequent surveys (table 2, Thornton *et al.* 1990) so that they could have served as the source of colonists for Anak Krakatau both when the island was first colonized in the 1940s and later recolonized after its defaunation in 1952. In the 1980s these 10 species were all found on Anak Krakatau. *Alcedo caerulescens*, *Pycnonotus aurigaster* and *Lanius schach* have not been seen on the archipelago since 1921 and therefore did not constitute part of the source of potential colonists for Anak Krakatau. Of these 10 early colonists of the archipelago after 1883, aerial insectivores should have been the first species to colonize Rakata: *Collocalia fuciphaga*, then *Caprimulgus affinis* around 1900 ('bird zero' Thornton *et al.* 1990), soon to be followed by *Centropus bengalensis*, *Pycnonotus goiavier* and *Halcyon chloris*. *Corvus macrorhynchos* probably came next to be followed by the woodland species, *Oriolus chinensis* and *Artamus leucorhynchus*. Jacobson (1909) remarked several times on the abundance of the oriole during his visit, so this species may have arrived earlier than we suggested and exploited the *Barringtonia* formation. The pigeons *Treron vernans* and *Chalcophaps indica* that were also found on Rakata in 1908, appear to have colonized the archipelago a little early by comparison with the Anak Krakatau model, where they arrived after the first fruiting of figs. On the older islands of the archipelago,

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

however, these pigeons were strongly associated with the *Barringtonia–Terminalia* strand formation (Dammerman 1948; Zann *et al.* 1990) that began to form by 1902; it is still poorly developed on Anak Krakatau, possibly because the unstable coastline (Bird & Rosengren 1985) hampered its establishment. Furthermore, the first report of figs in fruit on Rakata was by Ernst (1908) in 1906 so that there must have been food at least in small quantities for the obligate frugivore *Treron vernans*.

The 11–12 years after 1908 saw a fairly rapid change on the lower parts of Rakata from savannah woodland to mixed secondary rainforest (Thornton & Rosengren 1988). The oriole was still abundant in 1919 and *Treron vernans*, *Chalcophaps indica* and *Caprigulmus affinis* had become so, others like *Corvus macrorhynchos* remained uncommon. More importantly, 17 new species of land birds colonized Rakata during this brief period (table 2 and figure 3, Thornton *et al.* 1990). This stage of plant succession on Anak Krakatau's Eastern Foreland began only in the 1980s, yet of these 17 species of birds, six can already be found there. These species might be regarded as the likely early arrivals of this wave of colonists to Rakata. The beach specialist, *Esacus magnirostris* would have colonized early. New open country species, *Lalage nigra*, *Geopelia striata* and *Hirundo tahitica* continued to arrive as did specialist insectivores of casuarinas and *Barringtonia*, such as *Pachycephala cinerea* and *Copsychus saularis*, but the completion of the canopy in places probably made new habitats suitable for *Amaurornis phoenicurus*. The growth of large trees would have provided a niche for the trunk specialist, *Picoides moluccensis*, and nectarivores (*Nectarinia jugularis* and *Anthreptes malacensis*) and frugivores (*Dicaeum trigonostigma*, *Aplonis panayensis*, *Eudynamys scolopacea*, *Ducula bicolor*) would also have arrived to exploit the increasing resource provided by flowering and fruiting trees. *N. jugularis*, *A. panayensis* and *D. bicolor* may have been the first of the nectarivores and frugivores as they exploit the early *Barringtonia* zone on the coast, whereas the other three species occupy the dense interior forest (Zann *et al.* 1990, table 4) that developed later. Of course, dispersal ability and chance rather than availability of specialist habitat would also have affected the order of colonization. This seems to be the reason that *Cyornis rufigastra*, *Gerygone sulphurea* and *Macropygia phasianella* failed to colonize the Krakataus until the 1921–1932 period, despite the existence of a suitable habitat for some 20–30 years. *Macropygia amboinensis* a is a C-tramp in the Bismarck archipelago (Diamond 1975) and is considered synonymous with *M. phasianella* (Frith 1982), so one might expect it to have good dispersal abilities and to have colonized Krakatau earlier than records show.

Three raptors colonized the archipelago for the first time during the 1908–19 period, probably as a result of the increasing availability of prey and nesting sites: *Accipiter trivirgatus* and two species which are D-tramps in the Bismarck archipelago (Diamond 1975), *Haliastur indus* and *Haliaeetus leucogaster*. Only the last species now exploits Anak Krakatau but does not breed there. *A. trivirgatus* became extinct between 1932 and 1952 but *H. indus* still exists in low numbers (Zann *et al.* 1990). Four more raptors have colonized the archipelago but the two larger species (*Spilornis cheela*, *Ictinaetus malayensis*) have not appeared on Anak Krakatau, probably due to insufficient prey, whereas the two smaller species (*Tyto alba*, *Falco severus*) have colonized the new island.

We thank Professor I. W. B. Thornton, who conceived the project and led the expeditions, for inviting us to participate and for checking the manuscript. We thank the Director of the Museum Zoologicum Bogoriense, Indonesia for allowing one of us (Darjono) to join the 1986 expedition and also for providing access to the museum's bird collection. Tim New, Mark

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Walker, Geoffrey Davison, Asep Adhikerana and Mark Hutchinson provided their bird sightings. Tim New checked the manuscript and identified the insect items taken from the birds; Jenny Browning prepared figure 1. Finally, it is our pleasure to sincerely thank the many financial supporters of the expeditions (Thornton & Rosengren 1988) and Lembaga Ilmu Pengetahuan Indonesia (L.I.P.I.) and Lembaga Biologi Nasional (L.B.I.) for permission to work on the islands.

References

Barker, N. & Richards, K 1982 The vegetation of Anak Krakatau. In *The Krakatoa Centenary Expedition* (ed. J. R. Flenley & K. Richards) (*Univ. Hull Dept. Geogr. misc. Ser.* no. 25), pp. 143–164.

Barker, N. & Richards, K. 1986 Notes on the present ecology and biogeography of Anak Krakatau. In *Krakatoa Centenary Expedition 1983. Final Report* (ed. M. Bush, P. Jones & K. Richards) (*Univ. Hull. Dept. Geogr. misc. Ser* no. 33.), pp. 167–181.

Bird, E. C. F. & Rosengren, N. J. 1985 The changing coastline of the Krakatau Islands, Indonesia. *Z. Geomorph.* (N.F.) **28**, 347–366.

Borssum Waalkes, J. van 1960 Botanical observations on the Krakatau Islands in 1951 and 1952. *Annls Bogor* **4**, 5–63.

Bunn, D. S., Warburton, A. B. & Wilson, R. D. S. 1982 *The barn owl.* Carlton: T. & A. D. Poyser.

Bush, M. & Newsome, D. 1986 A check-list of the birds seen on Krakatoa during the 1979 and 1983 Centenary Expedition. In *Krakatoa Centenary Expedition 1983. Final Report* (ed. M. Bush, P. Jones & K. Richards) (*Univ. Hull Dept. Geogr. misc. Ser.* no. 33.), pp. 217–218.

Dammerman, K. W. 1948 The fauna of Krakatau 1883–1933. *Verh. K. ned. Akad. Wet.* (tweede sectie) **44**, 1–584.

Diamond, J. M. 1975 Assembly of species communities. In *Ecology and evolution of communities* (ed. M. L. Cody & J. M. Diamond), pp. 342–444. Cambridge: Belknap Press.

Ernst, A. 1908 *The new flora of the volcanic island of Krakatau.* Cambridge University Press.

Ford, H. A., Forde, N. & Harrington, S. 1982 Non-destructive methods to determine diet of birds. *Corella* **6**, 6–10.

Frith, H. J. 1976 *Reader's Digest complete book of Australian birds.* Sydney: Reader's Digest Services.

Frith, H. J. 1982 *Pigeons and doves of Australia.* Sydney: Angus and Robertson.

Gilmore, A. M. 1985 The influence of vegetation structure on the diversity of insectivorous birds. In *Birds of eucalypt forests and woodlands* (ed. A. Keast, H. F. Recher, H. Ford & D. Saunders), pp. 21–31. Chipping Norton: Surrey Beatty.

Hoogerwerf, A. 1949 *De avifauna van de Plantentium te Buitenzorg* (*Java*). Buitenzorg (Bogor): De Kon. Plantent van Indonesie.

Hoogerwerf, A. 1953 Notes on the vertebrate fauna of the Krakatau islands, with special reference to the birds. *Treubia* **22**, 319–348.

Hoogerwerf, A. 1970 *Udjung Kulon. The land of the last Javan rhinoceros.* Leiden: E. J. Brill.

Ibkar-Kramadibrata, H., Soeriaatmadja, R. E., Syarif, H., Paryatmo, W., Surasana, E., Sutisna, M., Galih, D., Syarmidi, A., Widolo, S. H. & Birsyam, I. 1986 *Explorasi biologis dan ekologis dari daerah daratan di gugus kepubuan Krakatau memjelang 100 tahun sesudah peletusan.* Bandung: Institut Teknologi Bandung.

Iwamoto, T. 1986 Mammals, reptiles and crabs on the Krakatau islands. *Ecol. Res. Jap.* **1**, 249–258.

Jacobson, E. R. 1909 De nieuwe fauna van Krakatau. *Jversl. topogr. Dienst Ned.–Indië* **4**, 192–206.

Karr, J. 1971 A comparative study of the structure of avian communities in selected Panama and Illinois habitats. *Ecol. Monogr.* **41**, 207–233.

King, B., Woodcock, M. & Dickison, E. C. 1975 A field guide to the birds of south-east Asia. London: Collins.

Kuroda, N. 1933 *Birds of the island of Java.* Tokyo: Kuroda.

Partomihardjo, T. 1983 The pioneer vascular vegetation on Anak Krakatau and a comparison with the lower part of Sertung. In *Proceedings of the workshop on coastal resources management of Krakatau and the Sunda Strait region, Indonesia* (ed. E. C. F. Bird, A. Soegiarto, K. Soegiarto & N. Rosengren), pp. 187–205. Jakarta: Indonesian Institute of Sciences and the United Nations University.

Richards, K. 1982 Introduction. In *The Krakatoa Centenary Expedition* (ed. J. R. Flenley & K. Richards) (*Univ. Hull Dept. Geogr. misc. Ser.* no. 25.), pp. 1–8.

Ryall, C. 1986 Killer crows stalk the Seychelles. *New Scient.* **112**, 48–49.

Smythies, B. E. 1981 *The birds of Borneo.* Kuala Lumpur: The Sabah Society and the Malay Nature Society.

Tagawa, H., Suzuki, E., Partimohardjo, T. & Suriadarma, A. 1984 Vegetation and succession on the Krakatau islands. In *Researches on the ecological succession and the formation process of volcanic ash soils on the Krakatau Islands* (ed. H. Tagawa), pp. 48–68. Kagoshima: Kagoshima University.

Thornton, I. W. B. & Rosengren, N. J. 1988 Zoological expeditions to the Krakatau islands, 1984, 1985: general introduction. *Phil. Trans. R. Soc. Lond.* B **322**, 273–316.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Thornton, I. W. B., Zann, R. A. & Stephenson, D. G. 1990 Colonization of the Krakatau islands by land birds and the approach to an equilibrium number of species. *Phil. Trans. R. Soc. Lond.* B **328**, 55–93. (This volume).

Thornton, I. W. B. & New, T. R. 1988 Krakatau invertebrates: the 1980s fauna in the context of a century of recolonization. *Phil. Trans. R. Soc. Lond.* B **322**, 493–522.

Thornton, I. W. B., New, T. R., McLaren, D. A., Sudamen, H. K. & Vaughan, P. J. 1988 Air-borne arthropod fall-out on Krakatau and a possible pre-vegetation pioneer community. *Phil. Trans. R. Soc.* B **322**, 471–479.

Zann, R. A., Walker, M. V., Adhikerana, A. S., Davison, G. W., Male, E. B. & Darjono 1990 The birds of Krakatau (Indonesia) 1984–86. *Phil. Trans. R. Soc. Lond.* B **328**, 29–54. (This volume.)

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES