PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

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THE TERRESTRIAL VERTEBRATE FAUNA OF THE KRAKATAU ISLANDS, SUNDA STRAIT, 1883–1986

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CONTENTS

The results of terrestrial vertebrate collecting on the Krakatau Islands, Sunda Strait, during La Trobe University-L.I.P.I. expeditions in 1984, 1985 and 1986 are reported and previous records from the islands are consolidated and reviewed. Since the 1883 eruption of Krakatau, 15 species of terrestrial vertebrates (13 reptiles and 2 mammals) have been recorded from the Krakatau Group. Two of the species records (*Crocodylus porosus* and *Cosymbotus platyurus*) are only incidental but the remaining thirteen species have at some stage established breeding populations on one or more islands.

In the first 50 years up to 1933, ten species (eight reptiles and two mammals) reached the islands, eight of which (*Hemidactylus frenatus*, *Lepidodactylus lugubris*, *Emoia atrocostata*, *Mabuya multifasciata*, *Varanus salvator*, *Python reticulatus*, *Rattus rattus* and *Rattus tiomanicus*) had established breeding populations. Results of collections made over the period 1982–1986 showed that two of the species (*L. lugubris* and *E. atrocostata*) with breeding populations in 1933 had become extinct, whereas five new species (*Gekko gecko*, *Gekko monarchus*, *Hemiphyllodactylus typus*, *Chrysopelea paradisi* and *Ramphotyphlops braminus*) have reached the islands and established breeding populations. Therefore at the end of 100 years, eleven species of terrestrial vertebrates have extant breeding populations on one or more islands in the Krakatau group; two species have become extinct; and two species have incidental records.

Significant ecological changes in the development of the present day terrestrial fauna are discussed. These include canopy closure of the forests and continual marine erosion of the coasts that together have eliminated most of the open habitats on Rakata, Sertung and Panjang; heavy ash falls from volcanic eruptions on Anak Krakatau that have periodically disrupted successional stages and habitats on Sertung, Panjang and Anak Krakatau.

The dispersal of terrestrial vertebrates in the Sunda Strait is discussed in the light of the heavy boat traffic and the predominant southwest ocean currents. It is concluded that dispersal by human agency on boats is highly significant, seven of the 15 recorded species (46 %) being most likely to have reached the islands in this way; and the prevailing southwest flow of water in Sunda Strait makes Sebesi and Sumatra the probable source areas for the eight species most likely to have dispersed on ocean currents by swimming or rafting.

Anak Krakatau, the volcanic island that became permanent in Aug. 1930, has three species of terrestrial vertebrates (*H. frenatus*, *V. salvator* and *C. paradisi*) all of which have established breeding populations on Rakata, Sertung and Panjang. The early arrival of *H. frenatus* and *V. salvator* and their present abundance on all four islands distinguishes them as the most successful terrestrial vertebrate colonizers of the Krakatau group.

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1. Introduction

This paper reviews the occurrence of terrestrial vertebrate species on the Krakatau Islands and Sunda Strait, over the century since the explosive eruption of 27 Aug. 1883, which is believed to have extirpated at least the macrobiota of the then existing islands of Rakata, Sertung and Panjang, situated some 44 kilometres (km) from the coasts of the large islands of Java and Sumatra. The fourth island of the archipelago, Anak Krakatau, is an active volcano that first emerged as a permanent island in 1930, 2–4 km from the three older islands; it was subjected to very damaging ashfalls in 1952 and several other eruptions since then. Its terrestrial biota thus represents approximately 30–50 years of colonization. Thornton & Rosengren (1988) provide a general background to the expeditions of which this is a partial report.

The first systematic faunal survey, including terrestrial vertebrates, was not made until 1908, 25 years after the eruption (Jacobson 1909). Further surveys were made between 1919 and 1924, and 1928 and 1934, by Dammerman and his colleagues and are reported in the monograph *The fauna of Krakatau 1883–1933* (Dammerman 1948). Hoogerwerf (1953) provided information on terrestrial vertebrates seen on his visit of 5–15 Oct. 1951, Expeditions by Institut Teknologi Bandung (I.T.B.) of 7–13 Jly 1982 (Ibkar-Kramadibrata *et al.* 1986) and by Kagoshima University and Lembaga Ilmu Pengetahuan Indonesia (L.I.P.I.) from July to August and from October to November 1982 (Yukawa *et al.* 1983, 1984; Iwamoto 1986) provided valuable information on some species, particularly rats. Dieter Plage, in July 1982, in the course of making a film on the archipelago, obtained records on film of five reptile species from Rakata and one from Anak Krakatau (Plage 1983).

(*a*) *La Trobe University – L.I.P.I. expeditions*

Visits were made in 1984 (9–23 Sep.), 1985 (13–26 Aug.) and 1986 (16–30 Sep.) (Thornton 1985–1987), and a total of 57 man-days were available for surveying terrestrial vertebrates (26 in 1984, Rawlinson & Brown; 28 in 1985, Rawlinson & Agus Widjoya; 3 in 1986, Hutchinson).

On the archipelago we concentrated on species surveys; ecological data were obtained only incidentally. Our aims were to establish the extant terrestrial vertebrate fauna of each island of the archipelago and thus obtain insights into patterns of dispersal and the rate of colonization, extinction and turnover on the archipelago.

(*b*) *Collection of distributional and ecological data*

Systematic searches were made of the major habitats and their microenvironments on each island. Voucher specimens were taken of each species encountered for confirmation of identification and as a permanent record.

Distributional and ecological information was obtained by both direct evidence (specimens collected and examined, definite sight records, identifiable calls, carcasses, sloughed skin, skeletal material) and indirect evidence (faecal pellets, identifiable tracks, identifiable burrows or nests). At night spotlighting was used and calls were recorded.

The search pattern in the day was based on a systematic examination of habitats, altitudinal zones and microenvironments. These were repeated at night when spotlighting, but on a more limited time schedule. Mammal traps were set at dusk and cleared in the early morning.

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A detailed list of all terrestrial vertebrate records from the Krakatau islands since 1883 (including localities, dates and numbers of specimens where possible) is shown below. Previously published records are listed with the appropriate author's name and the year of publication. As the data in Dammerman 1922 and 1929 are substantially repeated in Dammerman 1948, the former two references have been omitted from the list. La Trobe University – L.I.P.I. expedition species identifications were all made by the authors unless otherwise shown after the appropriate record. 'First records' of a species for an island are provided with full details, 'additional records' are provided in abbreviated form.

2. Terrestrial vertebrate species recorded since 1883

Class Reptilia

Order Crocodilia

Family Crocodylia

(*a*) *Crocodylus porosus* Schneider

A very large aquatic carnivore (up to 7 m in length, Cogger 1983) widely distributed through southeast Asia and the Indo-Australian archipelago; recorded from Java and Sumatra (Cogger 1983; De Rooij 1915). *C. porosus* is a very active swimmer known to readily cross ocean barriers (Dammerman 1948).

Rakata. First records: Zwarte Hoek, 'red eyes' spotlit in beach surf for 30 min, Sep. 1986 (D. Kitchener); 'serrated tail' sighted at sea in caldera, Sep. 1986 (N. Rosengren).

Sertung. First record: brackish lake, northern spit, Jly. 1924, one male, 2.80 m long, collected (Dammerman 1948).

Status. The 1924 and 1986 records are considered to be incidental and not indicative of resident breeding populations. In each case dispersal would have resulted from active swimming. Although *C. porosus* is largely aquatic, it is included here as a terrestrial species because it can occupy inland waters and feed on terrestrial animals.

Order Squamata

Suborder Sauria

Family Gekkonidae

(*b*) *Cosymbotus platyurus* (Schneider)

A small insectivore (up to 66 mm snout–vent, 127 mm total length, De Rooij 1915) widely distributed through southeast Asia and the Indo-Australian archipelago; recorded from Java and Sumatra (Auffenberg 1980; Brown & Alcala 1978; De Rooij 1915; Whitten *et al.* 1984). The species is a common 'house gecko' in Java and Sumatra (Brown & Alcala 1978; Dammerman 1948; Whitten *et al.* 1984).

Rakata. First record: May 1928, one collected (Dammerman 1948, as *Hemidactylus platyurus*).

Status. The 1928 record for Rakata is incidental and not indicative of a resident breeding population. The close association of *C. platyurus* with human settlements shows that dispersal by human agency on a boat was most likely, but rafting on driftwood or flotsam is also possible.

(*c*) *Gekko gecko* (Linnaeus)

A medium-sized insectivore/carnivore (up to 171 mm snout–vent, 350 mm total length, De Rooij 1915) widely distributed through southeast Asia and the Indo-Australian archipelago; recorded from Java and Sumatra (Auffenberg 1980; Brown & Alcala 1978; De Rooij 1915; Whitten *et al.* 1984). It is known to feed on insects, spiders, smaller geckos, mice and small birds (Auffenberg 1980; Whitten *et al.* 1984) and is the world's largest gecko species (Goin *et al.* 1978). Auffenberg (1980) records *C. platyurus* and *Hemidactylus frenatus* as major prey items. The species is a common 'house gecko' (Brown & Alcala 1978; Whitten *et al.* 1984). Away from human habitation *G. gecko* primarily forages on large trees and shelters in tree hollows and cavities (Auffenberg 1980).

Rakata. First records: Jly 1982, film of 'Tokay Gekko' (Plage 1983); Zwarte Hoek, 28 Nov. 1982, one calling (I. W. B. Thornton). Additional records: Zwarte Hoek, 1983 (one I. W. B. Thornton), 1984 (20), 1985 (4), 1986 (5); West Ridge 250 m 1983 (one I. W. B. Thornton), 1984 (4).

Status. All records from Rakata from 1982 to 1986 are restricted to Zwarte Hoek and adjacent areas on the West Ridge to 250 m above sea level and the presence of adults and juveniles throughout this area shows a breeding population. The restricted distribution on Rakata is considered to show a recent dispersal to this area. The close association of *G. gecko* with human settlements and its large size shows that dispersal by human agency on a boat is most likely, but rafting in a large log or tree is also possible.

(*d*) *Gekko monarchus* (Dumeril & Bibron)

A medium-sized insectivore/carnivore (up to 95 mm snout–vent, 215 mm total length, De Rooij 1915) widely distributed through the Indo-Australian archipelago; recorded from Java and Sumatra and Sebesi in the Sunda Strait (Brown & Alcala 1978; De Rooij 1915; Whitten *et al.* 1984). It is known to feed on insects and smaller geckos (Whitten *et al.* 1984). Although De Rooij (1915) considered it to be a 'house-gecko', our observations in west Java did not confirm this and Brown & Alcala (1978) state that in the Philippines, *G. monarchus* is most common in forest and only rarely found around houses.

Rakata. First records: Zwarte Hoek 17–19 Sep. 1984, four collected, one observed; South Bay, 18 Sep. 1984, two observed. Additional records: Owl Bay, 1985 (3); Zwarte Hoek, 1986 (1).

Panjang. First record: Northwest cliff, observation bunker 14 Sep. 1984, one observed.

Status. The species was recorded from both sides of Rakata in 1984–1986 and the presence of adults and juveniles shows a well-established breeding population. The single sighting on Panjang in 1984 must be taken as an unconfirmed incidental record and not indicative of a resident breeding population. Dispersal may have been by human agency on a boat or, more likely, by rafting on a large log or tree. Sebesi is a possible source area.

(*e*) *Hemidactylus frenatus* Dumeril & Bibron

A small insectivore (up to 65 mm snout–vent, 134 mm total length, De Rooij 1915) this cosmopolitan species is very widely distributed through southeast Asia, the Indo-Australian archipelago and on many Pacific islands; recorded from Java and Sumatra (Auffenberg 1980; Brown & Alcala 1978; Cogger 1983; De Rooij 1915; Whitten *et al.* 1984). *H. frenatus* is

common over a large part of the tropics up to 500 m, it is probably the most abundant reptile in the lowlands of the larger Indo-Australian islands and is generally present in the very limited assemblage of species on the smaller islands (Auffenberg 1980; Brown & Alcala 1978). It is, without doubt, the commonest 'house gecko' in the tropical Indo-Australian region (Cogger 1983; Whitten *et al.* 1984).

Rakata. First record: 4–6 May 1908 (Jacobson 1909 as *Hemidactylus* spp.). Additional records: 1919 (1), 1928 (1, eggs) (Dammerman 1948); 1951 ('heard regularly') (Hoogerwerf 1953); Zwarte Hoek 1984 (7, several calling), 1986 (1); Owl Bay 1985 (14, 4 eggs), 1986 (many calling); South Bay 1985 (7, 8 eggs).

Sertung. First record: Apl. 1920, one collected (Dammerman 1948). Additional records: 1930; north spit 1930 (Dammerman 1948); north spit, 1984 (7, 4 eggs), 1985 (3, many calling); southeastern edge of north spit and forest south of spit 1985 (many calling); southeastern limit of north spit 1986 (4).

Panjang. First record: May 1908 (Jacobson 1909 as *Hemidactylus* spp.). Additional records: 1933 ('the well-known sound of the house gecko (*Hemidactylus*) was heard') (Dammerman 1948); northwest Foreland 1984 (2); northeast beach 1984 (one I. W. B. Thornton); northwest cliff observation area 1984 (one, D. Ewart & D. Walsh), 1986 (several calling); northeast beach 1985 (7, 8 eggs); west beach north of bat caves 1986 (1).

Anak Krakatau. First records: 7–13 Aug. 1982, one collected (Ibkar-Kramadibrata *et al.* 1986); 26 Oct.–15 Nov. 1982, one collected (Iwamoto 1986). Additional records: *Casuarina* area East Foreland 1984 (15), 1985 (31, 1 egg), 1986 (3); rim, outer cone 125 m 1985 (1); rim, inner cone 175 m 1985 (1) (N. Rosengren); *Casuarina* area North Foreland 1985 (15).

Status. The early records of *H. frenatus* from the Krakatau group (1908), the presence of breeding populations on Rakata, Sertung and Panjang by 1933 and the establishment of a breeding population on Anak Krakatau by 1982 combined with the abundance of specimens on all islands, makes this species (with *Varanus salvator*) one of the two most successful vertebrate colonists of the group. The abundance of *H. frenatus* in coastal areas, especially in debris in the supralittoral zone, would predispose the species to dispersal on ocean currents in driftwood and flotsam. However, the close association of *H. frenatus* with human settlements makes dispersal to the Krakatau group and between islands by human agency on boats the most likely mode of dispersal, and the species is often observed on boats and in cargo (Auffenberg 1980, Dammerman 1948; personal observation 1985, 1986).

The species is apparently very resilient to volcanic activity. Dammerman (1948) found *H. frenatus* under bark on *Casuarinas* killed by the August 1930 ash fall on Sertung and heard them calling on Panjang on 4 January 1933 after a heavy rain of volcanic ash from Anak Krakatau. Direct confirmation of this resilience came from the discovery on 20 Aug. of a specimen living among rocks at 175 m on top of the inner rim of the active cone of Anak Krakatau. Thus not only is *H. frenatus* predisposed to disperse to new volcanic islands, it is also well adapted to survive on them.

(*f*) *Hemiphyllodactylus typus* Bleeker

A very small insectivore (up to 44 mm snout–vent, 82 mm total length, De Rooij 1915) widely distributed through the western part of the Indo-Australian archipelago; recorded from Java and Sumatra (Auffenberg 1980; Brown & Alcala 1978; De Rooij 1915). The species occurs around houses but is predominantly found in the forest. Auffenberg (1980) records it as living up to 1300 m in Java and Sumatra, but is not common. Brown & Alcala (1978) also

record its abundance as low in the Philippines and comment that it is most commonly found in leaf axils of *Pandanus*, arboreal ferns or coconut palms or under bark on dead stumps.

Sertung. First record: forest southwest of north spit 18 Aug. 1985, one collected with two eggs.

Panjang. First record: forest northwest Foreland 26 Aug. 1985, four hatched eggs collected.

Status. The specimen collected from Sertung on 18 Aug. 1985 was under bark on a rotten tree stump with two very small unhatched eggs barely 5 mm long and 4 mm in diameter, much smaller than the eggs of other gecko species from the Krakataus. The record for Panjang is based on the discovery of four hatched eggs the same size as those on Sertung under bark on a rotten tree stump. It is considered that these records are indicative of breeding populations on both islands. Dispersal could have been by human agency, but is considered to have most likely been by rafting in a floating rotten log or possibly in *Pandanus* on a floating island.

(*g*) *Lepidodactylus lugubris* (Dumeril & Bibron)

A small insectivore (up to 45 mm snout–vent, 106 mm total length, De Rooij 1915) very widely distributed through southeast Asia, the Indo-Australian archipelago and the tropical islands of Oceania to the western coasts of Panama and Columbia; recorded from Sebesi in Sunda Strait in 1922 and Java in 1934, but apparently not yet formally recorded from Sumatra (Dammerman 1948; Whitten *et al.* 1984). *L. lugubris* is a 'house gecko' (Cogger 1983; Dammerman 1948; De Rooij 1915). The species is coastal and normally collected from buildings, rocks and the trunks and crowns of mangrove trees, palms and other vegetation near the shore, but occasionally up to elevations of about 300 m (Auffenberg 1980; Brown & Alcala 1978; Cogger 1983).

Rakata. First record: Apl. 1920 'already abundant' (Dammerman 1948). Additional records: 1933, 1934 ('fairly numerous') (Dammerman 1948).

Sertung. First record: Oct. 1921 (Dammerman 1948). Additional records: 1933 ('fairly numerous') (Dammerman 1948).

Panjang. First record: Nov. 1932 (Dammerman 1948).

Status. The records of *L. lugubris* for Rakata, Sertung and Panjang from 1920 to 1933 as 'fairly numerous' and 'already abundant' (Dammerman 1948) show that breeding populations had become established on these islands by that time. The failure to locate specimens in 1951 (Hoogerwerf 1953), 1982 (Yukawa *et al.* 1983, 1984; Iwamoto 1986; Ibkar-Kramadibrata *et al.* 1986), 1984, 1985 and 1986 on any of the Krakatau islands suggests that the species is now extinct or only present in low numbers.

From the accounts by Brown & Alcala (1978) and Cogger (1983) it appears that *L. lugubris* favours very open coastal habitats. The extinction or severe loss in status of this species on Rakata, Sertung and Panjang probably resulted from the very substantial loss of open coastal habitat through continual coastal erosion and canopy closure of the developing rainforest since the mid 1930s (see below). Dispersal of *L. lugubris* could have been by human agency on boats or by rafting on driftwood or flotsam. The species is associated with human settlements and is readily transported by ship (Dammerman 1948). It is considered that dispersal to the Krakatau group and between the islands was primarily by human agency on boats.

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Family Scincidae

(*h*) *Emoia atrocostata* (Lesson)

A medium-sized insectivore (up to 96 mm snout–vent, 254 mm total length, De Rooij 1915) widely distributed through the Indo-Australian archipelago to north Australia and islands in the east Pacific; recorded from Java and some islands off Sumatra, but apparently not yet formally recorded from Sumatra itself (Cogger 1983; Dammerman 1948; De Rooij 1915). The species is restricted to coastal lowland forests, mangroves, scrubs, grasslands and beaches and is especially abundant in mangroves and in the littoral and supralittoral zones of rocky foreshores in the flotsam and debris washed up on the shore (Cogger 1983; Dammerman 1948). On Sertung, Dammerman (1948) noted that *E. atrocostata* was 'confined to the seashore between high- and low-water marks' and he recorded it as a very common component of the beach fauna and typical of the *pes-caprae* formation community.

Sertung. First record: Dec. 1919, 'fairly abundant' (Dammerman 1948 as *Lygosoma atrocostatum*). Additional records: 1920, 1933 ('very common on the beaches') as *Lygosoma atrocostatum* (Dammerman 1948).

Status. Dammerman (1948) recorded *E. atrocostata* for the first time from the north spit of Sertung in 'December 1919 and at that time fairly abundant' and noted it was 'still numerous in 1933', so it is obvious that a breeding population had been established. The species was not recorded for Sertung in 1951 (Hoogerwerf 1953) or 1982 (Yukawa *et al.* 1983, 1984; Iwamoto 1986). In 1984, 1985 and 1986 the north spit and the entire littoral and supralittoral zones of the north coast were carefully and repeatedly searched but no traces of *E. atrocostata* were found and it seems certain that the species is now extinct. Dispersal could have been by human agency on a boat or by rafting on driftwood or flotsam. Dammerman (1948) notes that *E. atrocostata* is closely associated with driftwood in the supralittoral zone and concludes the species dispersed to the Krakataus by chance in driftwood, which helps explain why the species only became established on Sertung. Chance dispersal by ocean currents on driftwood or flotsam is considered the most likely means by which *E. atrocostata* reached Sertung.

(*i*) *Mabuya multifasciata* (Kuhl)

A medium-sized omnivore (up to 130 mm snout–vent, 350 mm total length, De Rooij 1915) one of the most widely distributed lizard species of the Indo-Australian archipelago; recorded from Java and Sumatra (Dammerman 1948; De Rooij 1915). Whitten *et al.* (1984) describe it as a common skink in Sumatra, especially in mangrove forests, whereas Dammerman (1948) considers it to be one of the most common skinks, found everywhere in Java. In 1984, 1985 and 1986 it was observed to be in high density in west Java, especially in the coastal areas around Carita and Labuan.

Rakata. First record: southeast side, Jly. 1924, 'large numbers' (Dammerman 1948). Additional records: southeast side 1928, 1932, 1933; Zwarte Hoek 1933 ('one specimen observed') (Dammerman 1948); southeast side and other places 1951 ('extremely numerous...particularly...in the southeast...also observed in many other places. The species seems to occur throughout the island') (Hoogerwerf 1953); 1982 (film of 'golden skink') (Plage 1983); 1982 ('observed to live at a high density') (Yukawa *et al.* 1983, 1984); 1982 (four, many observed, 'density 24 per ha† in forest') (Iwamoto 1986); Zwarte Hoek 1984 (18,

† 1 hectare = 10^4 m^2.

many observed); West Ridge 200 m 1984 (5); West Ridge 250 m 1984 (20); peak 777 m 1984 (5); South Bay 1984 (17), 1985 (two, many observed); Owl Bay 1984 (3), 1985 (5, many observed), 1986 (many adults and juveniles observed); southeast point, Handl's Bay 1985 (one, many observed).

Status. Breeding populations throughout Rakata. Dammerman (1948) considers the time of arrival of this species on Rakata can be dated fairly precisely; in July 1924 these skinks suddenly appeared in large numbers on the southeastern side of the island where so much collecting had been done as late as January 1922. It is also possible to partially document the spread of *M. multifasciata* across Rakata from the southeast. Dammerman (1948) records observing a skink at Zwarte Hoek in January 1933 that looked like a *Mabuya* so the species had apparently spread to the other side of the island by that time. In 1951 Hoogerwerf (1953) recorded the species seemed to occur throughout the island and in 1982 the species was observed to occur at a high density throughout Rakata with an average of 24 ha^{-1} over a 2 km transect (Iwamoto 1986). In 1984, 1985 and 1986 the species was observed to live at medium to high density from the coast to the peak (777 m). These observations represent a significant population expansion since 1933 when Dammerman (1948) recorded *M. multifasciata* as 'typical of the beach fauna *pes-caprae* formation' and noted that the species 'may also be found inland'.

Dispersal to Rakata could have been by human agency on a boat or by rafting by ocean currents on driftwood or flotsam. Dammerman (1948) favoured accidental dispersal on driftwood or flotsam, however the density of *M. multifasciata* around coastal settlements on west Java would make it a prime candidate for dispersal by boat. In addition Handl established a small settlement on southeast Rakata from 1917 to 1921 (Dammerman 1948) and southeast Rakata was a favoured camp site for expeditions from 1919 to 1934. Thus we consider that dispersal by human agency on a boat was the most likely means by which *M. multifasciata* reached Rakata between January 1922 and July 1924.

Family Varanidae

(*j*) *Varanus salvator* (Laurenti)

A very large carnivore and carrion feeder (up to 1040 mm snout–vent, 2360 mm total length, De Rooij 1915) very widely distributed through southeast Asia and the Indo-Australian archipelago; recorded from Java, Sumatra and Sebesi in the Sunda Strait (Cogger 1983; Dammerman 1948; De Rooij 1915). The species is semi-aquatic and is normally found in vegetated areas around estuaries, rivers or swamps where it feeds opportunistically on live prey (crabs, reptiles, birds and mammals) or carrion (Auffenberg 1980; Cogger 1983). A detailed study by Iwamoto (1986) found that *V. salvator* feeds principally on three species of omnivorous terrestrial crabs (*Gecarcoidea natalis*, *Metasesarma aubryi* and *Ocypode kuhli*) on the Krakataus. In 1984 adult specimens were observed raiding three *Chelonia mydas* egg nests at Turtle Beach on Rakata and eating the eggs. *V. salvator* has no close association with human settlements, but will forage around them for food.

Rakata. First record: 1889 'gigantic lizards (of the genus *Varanus*)' (Selenka & Selenka 1905; Dammerman 1948). Additional records: 1908 ('*Varanus*' spec. very numerous on shore') (Jacobson 1909); 1919, 1920, 1924, 1933, Zwarte Hoek; 1924, 1933, east coast 1933 (Dammerman 1948); southeast ('large numbers'), Zwarte Hoek 1951 (Hoogerwerf 1953); 1982, (film of 'water monitor') (Plage 1983); 1982 (specimens observed) (Yukawa *et al.* 1983, 1984); coastal areas and forests 2 km inland 1982 (specimens observed) (Iwamoto 1986);

peak, 777 m, 1983 (one, I. W. B. Thornton); Zwarte Hoek 1984 (seven, two hatchlings); West Ridge 450 m 1984 (1); South Bay 1984 (4), 1985 (2); Owl Bay 1986 (1).

Sertung. First record: August 1930 (Dammerman 1948). Additional records: 1933, North Sertung 1920, 1929 ('common') (Dammerman 1948); coastal areas and inland forest 1982 (specimens observed) (Yukawa *et al.* 1983, 1984); coastal areas and coastal forest 1982 (two, others observed) (Iwamoto 1986); north spit west side 1984 (1); north spit, 1984 (one, one hatchling), 1985 (6); north spit north end 1985 (many tracks observed); north spit West Beach 1985 (10 tracks); north spit, east side to spring 1985 (many tracks); southeast coast forest gully 1986 (one, I. W. B. Thornton).

Panjang. First record: Aug.1896–Jan.1897 'some monitors (observed by) Muller' (Dammerman 1948). Additional records: 1908 (young specimen collected from sea) (Jacobson 1909); 1982 (several observed) (Yukawa *et al.* 1983, 1984); coastal areas and coastal forests 1982 (several observed) (Iwamoto 1986); 1982 (several observed) (Ibkar-Kramadibrata 1986); North Beach 1984 (four, one hatchling), 1985 (two, three tracks), 1986 (2); northeast Beach 1985 (5); West Beach 1985 (one, many tracks).

Anak Krakatau. First records: Jly. 1982 film of 'water monitor' (Plage 1983); Jly., Aug., Oct., Nov. 1982 specimens observed (Yukawa *et al.* 1983, 1984); coastal areas 26 Oct.–15 Nov. 1982 several observed (Iwamoto 1986); 7–13 Aug. 1982, two collected (Ibkar-Kramadibrata 1986). Additional records: *Casuarina* forest East Foreland 1984 (four, two hatchlings, four tracks), 1985 (seven, five hatchlings, 19 tracks), 1986 (2); ash bed above lava flow 1984 (1); South Beach near lava flow 1984 (4); north point, 1985 (four tracks); southeast Beach 1986 (one, I. W. B. Thornton).

Status. Breeding populations on all islands. The species was recorded from Rakata in 1889 and was almost certainly the first terrestrial vertebrate to colonize the islands after August 1883 (Dammerman 1948). Evidence in Dammerman (1948) shows that breeding populations were established on Rakata and Sertung by 1908 and on Panjang by 1920 and became so numerous that in May 1929 people from Sebesi and Sebku were observed capturing these reptiles on the Krakataus in order to sell the skins. In 1948 Dammerman nominated *V. salvator* as 'still the most common reptile on the islands' and noted that although it utilized many habitats it was mostly a coastal inhabitant that fed chiefly on crabs. The heavy dependence of *V. salvator* on crabs noted by Dammerman (1948) was confirmed in 1982 by the Kagoshima University – L.I.P.I. expedition (Yukawa *et al.* 1983, 1984; Iwamoto 1986). The early arrival of *V. salvator* on the Krakatau group (1889), the presence of breeding populations on Rakata and Panjang by 1908, Sertung by 1920 and Anak Krakatau by 1982 combined with the abundance of specimens on all islands makes this species (with *H. frenatus*) one of the two most successful vertebrate colonists of the Krakatau group. As with *C. porosus*, *V. salvator* is a very active swimmer known to readily cross ocean barriers and it appears certain that the early dispersal of *V. salvator* to the Krakatau group and between the islands was by active swimming (Dammerman 1948). As the species inhabits Sebesi (as with *P. reticulatus* and *C. paradisi*) this is the most probable source area.

Dammerman (1948) also notes the species is very resilient to volcanic activity. He records that after a series of eruptions on Anak Krakatau in July and August 1930 accompanied by heavy ash falls on Sertung '...where the denuded trees around the lagoon on the north spit (of Sertung) suggested a winter landscape...a monitor lizard walked along its banks'. Thus, as

with *H. frenatus*, not only is *V. salvator* predisposed to disperse to new volcanic islands, it is also well adapted to survive on them.

(*k*) *Unverified record of lizard species*

Ernst (1908) in his account of revegetation on the Krakataus provides an additional lizard species record that cannot be verified.

Rakata. 1894. Ernst (1908) when discussing observations of *V. salvator* on 26 Apr. 1906 comments 'The fact that Selenka (1) and Sluiter found two specimens of *Calotes jubatus* (Agamidae) in 1894 renders it probable that other lizards, in addition to *Varanus*, occur on the island.'

Ernst's footnote (1) refers to Selenka and Selenka (1905) and 'a communication by letter from Professor Sluiter of Amsterdam'. Selenka records 'gigantic lizards' but makes no reference to *C. jubatus* and the communication by Sluiter is unavailable. Presumably, the specific reference was in the letter by Sluiter, however, as the record cannot be verified in any way, it is not further discussed in this paper.

Suborder Serpentes
Family Boidae

(*l*) *Python reticulatus* (Schneider)

A very large carnivore (up to 7.25 m and possibly 10 m in length, see, for example, De Rooij (1917); van Hoesel (1959); Pope (1961)) widely distributed through southeast Asia and the Indo-Australian archipelago; recorded from Java, Sumatra and Sebesi in the Sunda Strait (Dammerman 1948; De Rooij 1917). *P. reticulatus* is reputed to be the world's second largest snake (Goin *et al.* 1978) and, despite its size, inhabits areas around human settlements (Pope 1961). Regarded as a common snake living in the neighbourhood of water, *P. reticulatus* preys on live animals, principally rats and birds, but very large pythons may take monkeys, geese, pigs, deer and goats (De Rooij 1915; van Hoesel 1959). Pope (1961) records that egg clutch sizes range from 15 to 103 and average 48 with sexual maturity being attained at 3 m length 4–5 years after hatching.

Rakata. First record: Sep. 1908 photo caption 'big boa constrictor found by Brun' (Dammerman 1948). Additional records: 1919, 1922 (one, two juveniles), 1924 ('fairly numerous... two collected, both males, one of 3.63 m, the other 2.94 m'), 1933 (Dammerman 1948); Zwarte Hoek 1951 (1) (Hoogerwerf 1953); 1982 (film of 'python') (Plage 1983); 1982 ('information on its existence') (Yukawa *et al.* 1983, 1984); 1982 ('reports from Indonesian fishermen') (Iwamoto 1986).

Sertung. First record: Oct. 1921 (Dammerman 1948). Additional records: 1933 (Dammerman 1948); 1977 ('observed by Indonesian botanist') (Iwamoto 1986); 1982 ('information on its existence') (Yukawa *et al.* 1983, 1984); 1982 ('reports from Indonesian fishermen') (Iwamoto, 1986); north spit 1984 (one, 4 m long) (Achmad Saim); 400 m west of PHPA post 1987 (one, 3–4 m long observed by Ulas Ferdous) (I. W. B. Thornton, Feb. 1988).

Panjang. First record: 1928–1931 'pythons often seen... by members of Volcanological Survey' (Dammerman 1948). Additional records: 1982 (one, large adult photographed under log) (Ibkar Kramadibrata 1986, plate 9*b*); Northeast Beach 1985 (track of large adult photographed).

Status. Breeding populations on Rakata, Sertung and Panjang. *P. reticulatus* reached Rakata by 1908, Sertung by 1921 and Panjang by 1928 and information provided by Dammerman (1948) shows that breeding populations had been established on all three islands by 1933. Dammerman (1948) considered that there was a correlation between python numbers and the arrival and spread of rats on Rakata after 1918 and on Panjang before 1928. In the case of Rakata he noted that the house rat (*R. rattus*) was introduced in 1918 and it increased rapidly, and coincidentally python numbers started to increase from 1919 until they were 'fairly numerous' in 1924. Dammerman contends the new arrival had a distinct effect on python numbers and this is possible as the data provided by Pope (1961) for *P. reticulatus* demonstrates six years (1918–1924) is adequate time for a significant population response. Even one large gravid female could establish a substantial population in five years, provided abundant prey were available.

It is considered that breeding populations of *P. reticulatus* are still extant on Rakata, Sertung and Panjang despite the fact that the various expeditions of 1982, 1984, 1985 and 1986 yielded only direct evidence in the form of sightings for single specimens on Rataka (1982), Sertung (1984) and Panjang (1982), plus additional indirect evidence covering the period 1977–1987. The reticulate python, being a very large snake, can range widely in search of prey (Dammerman 1948) and voluntarily enters long periods of fasting. Pope (1961) records captive specimens provided with food fasting for periods of up to 679 days and states that large specimens could easily survive without feeding for two and a half years. Unlike the smaller reptiles of the Krakatau group, reticulate pythons would not be expected to exhibit continuous activity and they probably range over large areas. The low number of direct sightings over the period 1982–1986 is attributable more to the low probability of locating active pythons than to small populations. These observations are confirmed by Dammerman (1948) who commented on the fact that although members of the Volcanological Survey sometimes saw large numbers of pythons on Panjang over the period 1928–1931, at other times none were to be found and none were directly observed by the scientific expeditions from 1919–1933.

On the Krakatau group Dammerman (1948) recorded *P. reticulatus* as an inhabitant of grass jungle and virgin forest but noted it was not specially connected with them and that it was 'equally at home in open, almost treeless country'. Dispersal to the Krakatau group and between the islands is most likely to have been by active swimming as proposed by Dammerman (1948). *P. reticulatus* (like *V. salvator* and *C. paradisi*) is known to inhabit Sebesi, and Dammerman (1948) proposes this as the probable source area, pointing out the relatively short distances involved, 7.5 miles (12 km) from the nearest point of Sebesi to the nearest point of Sertung.

Family Colubridae

(*m*) *Chrysopelea paradisi* Boie

A medium-sized carnivore (up to 810 mm snout–vent, 1120 mm total length, De Rooij 1917; van Hoesel 1959), widely distributed through southeast Asia and the Indo-Australian archipelago; recorded from Java, Sumatra and Sebesi in Sunda Strait (Dammerman 1948; De Rooij 1917). *C. paradisi* is principally an arboreal species that can flatten and hollow the whole length of the body to facilitate gliding from tree to tree. Van Hoesel (1959) considers it to be 'the unrivalled glider among all snakes' and commented that they were very abundant in Java in the vast teak forests. The principal prey items are geckos, but frogs, small birds and bats are also taken (De Rooij 1917; van Hoesel 1959).

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Rakata. First record: Jly 1982 film of 'flying snake' (see below) (Plage 1983); Jly., Aug., Oct., Nov. 1982, one collected (Yukawa *et al.* 1983, 1984); 26 Oct.–15 Nov. 1982, one collected, 'a TV cameraman from Germany caught one on Rakata Besar and gave it to me' (see above) (Iwamoto 1986). Additional records: West Ridge 360 m 1984 (one, M. Bush & P. Vaughan); South Bay 1985 (1).

Sertung. First record: Oct., Nov. 1982, one observed 'fighting with a small two-banded monitor' (Yukawa *et al.* 1983, 1984); 26 Oct.–15 Nov. 1982 'Dr Yukawa...observed a paradise tree snake fighting with a young monitor lizard (*V. salvator*)...on Sertung' (Iwamoto 1986). Additional records: north spit, 1984 (5); north spit east side, 1984 (1, I. W. B. Thornton); Spring Beach 200 m southeast of north spit 1984 (1); northern point of north spit 1985 (1).

Panjang. First record: 7–13 Jly. 1982, one collected on *Hibiscus tiliaceus* and photographed (Ibkar-Kramadibrata *et al.* 1986, plate 9*a*). Additional record: northeast Beach 1985 (1).

Anak Krakatau. First record: landing beach East Foreland 10 Sep. 1984, one sloughed skin collected. Additional records: *Casuarina* forest East Foreland, 1985 (2), 1986 (1).

Status. Breeding populations now present on all islands. Although *C. paradisi* was first recorded from Rakata, Sertung and Panjang in 1982 and from Anak Krakatau in 1984, the fact that by those dates there were breeding populations on all islands shows that they arrived on the Krakatau group much earlier. The record of an unidentified snake on Panjang in January 1933 (Dammerman 1948) may possibly be attributable to *C. paradisi* (see below). On the Krakatau islands the species was most commonly observed in *Casuarina* forests on the coast and several specimens were located on the ground foraging through debris in the supralittoral zone. *C. paradisi* is one of only three vertebrate species (with *H. frenatus* and *V. salvator*) to have established breeding populations on all four islands of the Krakatau group.

The occurrence of *C. paradisi* in the supralittoral zone would appear to predispose it to dispersal on ocean currents in driftwood and flotsam or to dispersal by human agency on boats. However, the species is essentially arboreal and only intermittently forages in the supralittoral zone making these modes of dispersal less probable. *C. paradisi* is a swift moving active hunter (as exemplified by its gliding habits) and a very efficient and active swimmer. It is considered most likely that dispersal to the Krakatau group and between the islands was by active swimming. *C. paradisi* is known to inhabit Sebesi so (as with *V. salvator* and *P. reticulatus*) this is the probable source area.

Family Typhlopidae

(*n*) *Ramphotyphlops braminus* (Daudin)

This very small insectivore (up to 175 mm total length, De Rooij 1917), reputed to be the smallest and most widespread snake in the world (van Hoesel 1959), ranges from Madagascar and southern Africa through Iran, South East Asia, the Indo-Australian archipelago into the Pacific and through Oceania to southern Japan and Mexico; recorded from Java and Sumatra (Cogger 1983; De Rooij 1917; van Hoesel 1959). *R. braminus* is a burrowing species common in forest areas usually in the upper 15 cm of soil and feeds principally on termites, but may take other small insects (Auffenberg 1980; van Hoesel 1959). All known specimens are female and the species reproduces parthenogenetically (Cogger 1983; Goin *et al.* 1978). Two to seven eggs may be laid, the average being three (Auffenberg 1980; van Hoesel 1959).

Sertung. First record: forest 1.5 km southwest of spit 11 Sep. 1984, two collected, one laid three eggs.

Status. The two specimens collected on Sertung 11 Sep. 1984 were found in rotten logs in forest. Both were females, one having a total length of 160 mm and the other 148 mm. The larger specimen laid three eggs after capture. It is considered that a breeding population has been established. *R. braminus* is one of the best colonizers of tropical ocean islands and Dammerman (1948) notes that it has even managed to travel the 900 km to the Cocos–Keeling islands. The very small size, parthenogenetic mode of reproduction and habits of *R. braminus* predispose it to disperse across oceans and adapt it for colonizing islands.

Human agency is normally accepted as the primary method of dispersal of the species (Cogger 1983). Dammerman (1948) specifically commented on the absence of blind snakes (family Typhlopidae) from the Krakatau islands (p. 20) and predicted typhlopid species would eventually arrive. The discovery of two specimens on Sertung in rotten logs, shows the species could readily disperse in driftwood, and this is considered to be the most likely way *R. braminus* reached the Krakatau group.

(*o*) *Records of unidentified snakes*

Dammerman (1948) and Iwamoto (1986) each record unidentified snakes. Both records are based on incidental sightings and neither includes sufficient data for more than informal speculation on their identity.

Rakata. 26 Oct.–15 Nov. 1982. Iwamoto (1986) 'Another species of snake was observed in the forest (140 m in altitude) on Rakata Besar. This was a slender snake about 1.5 m in length, which moved very quickly, and was neither python nor paradise tree snake'. Although this brief account does not explain why the snake could not have been *C. paradisi*, it should be noted that Iwamoto, a herpetologist, had at the time already seen a specimen of *C. paradisi* from Rakata (see above).

Panjang. 4 January 1933. Dammerman (1948) 'A second species of snake was noticed on Lang Island... but we did not succeed in identifying it' '... In January 1933... we were warned in the evening of the 4th that in one of the sheds a snake was present. On our arrival we saw the creature just making its escape between the floor and the wall of bamboo; by its small size and dark appearance we could be quite sure that it was not a young python.'

Two facts emerge from this account. First, the snake was not a python, and secondly, its size and dark colour do not preclude *C. paradisi*. However, the sighting cannot be taken, even tentatively, as a record of the species for Panjang for 1933. The sheds mentioned were those of the Volcanological Survey, on Panjang at that time to monitor the activity of Anak Krakatau, and the snake could have arrived with supplies for the group.

Class Mammalia
Order Rodentia
Family Muridae

(*p*) *Rattus rattus* (Linnaeus)

A medium-sized terrestrial omnivore (up to 196 mm head–body, 387 mm total length, Dammerman 1948) very closely associated with human settlements, *R. rattus* has been dispersed around the world by human agency principally on boats; recorded from Java and Sumatra and Sebesi in the Sunda Strait area (Dammerman 1948; Whitten *et al.* 1984). A study by Iwamoto (1986) on Rakata in 1982 revealed the diet is essentially plant matter, with fruit comprising 81.0% of stomach contents on average.

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Rakata. First record: southeast corner, 1918 'rats appeared...a great nuisance' (Dammerman 1938 and 1948). Additional records: southeast Handl's Bay, 1919 ('rats trapped...a nuisance'), 1920 ('rats trapped'), 1929 ('rats trapped again'), 1933 ('rats in fairly large numbers...plentiful'), 1934 ('rats again abundant'); northwest, near Zwarte Hoek 1920 ('single specimen trapped') (Dammerman 1948); southeast 1951 (14) (Hoogerwerf 1953); 1982 ('many collected and many observed...density 65 per ha') (Yukawa *et al.* 1983, 1984); 1982 (24, many observed, density in grid BQ per 65.3 ha, density in grid Bq 31.3 per ha) (Iwamoto 1986); Owl Bay, 1982 (many observed, I. W. B. Thornton), 1984 (several observed), 1985 (two, many observed); Zwarte Hoek 1984 (one, many observed); peak, 777 m 1984 (several observed); West Ridge 250 m 1984 (many observed); South Bay 1984 (many observed), 1985 (two, many observed.)

Anak Krakatau. First record: *Casuarina* forest East Foreland 22 Aug. 1985, one specimen accidentally trapped in bucket half-filled with water, collected by I. W. B. Thornton.

Status. Jacobson (1909) encountered no rats during his three-day stay on Rakata in 1908 and Dammerman (1948) states that there were no rats on Rakata in 1917, according to Handl who settled there in that year. Handl recorded their appearance in the southeast corner of the island in 1918 (Dammerman 1948) and noted that 'soon afterwards they were in sufficient numbers to be a great nuisance'. Dammerman (1948) was certain that *R. rattus* arrived by human agency with Handl's group and it seems clear that this was the case. Large numbers of *R. rattus* were observed and trapped by Dammerman (1948) on the southeast of Rakata in 1919, 1920, 1929 and 1933, but he failed to observe or trap specimens there in 1924 and attributed this phenomenon to a temporary population decline caused by the rapid increase in *Python reticulatus* numbers with consequent heavy predation (see above under *P. reticulatus*).

In 1920 Dammerman (1948) trapped a single specimen of *R. rattus* on the other side of Rakata at Zwarte Hoek but he was unable to observe or trap any more specimens at this spot up to 1933. He concluded that this incidental record represented a second introduction of *R. rattus* to the island. By 1982 *R. rattus* had successfully colonized the whole island.

The single specimen collected on Anak Krakatau in August 1985 is an incidental record and does not indicate a breeding population. Several days before the collection of this specimen a boat anchored adjacent to the Eastern Foreland and a large party of tourists came ashore and set up camp for two nights. Shortly after they departed the rat, a sub-adult, was trapped. It is almost certain that this specimen was introduced when the tourists equipment and food was

Table 1. Results of trapping on Rakata and Anak Krakatau, 1985

(Traps were Elliott metal folding, baited with fresh peanuts; trapping success relates to *Rattus rattus*.)

locality	dates	number of traps set	rats trapped	trapping success (%)
Rakata				
Owl Bay	22, 23, 24 Aug. 1985	75	2	2.7
South Bay	25, 26 Aug. 1985	50	2	4.0
		125	*4*	*3.2*
Anak Krakatau				
in *Casuarina* East Foreland	13, 14, 17 Aug. 1985	75	0	0.0
gully edge, South lava flow	15, 19 Aug. 1985	50	0	0.0
South lava flow	21 Aug. 1985	25	0	0.0
		150	*0*	*0.0*

brought ashore. No rats were encountered by our 1986 expedition, which concentrated on Anak Krakatau. The results of our trapping on Rakata and Anak Krakatau are shown in table 1.

The method of dispersal of *R. rattus* to Rakata was discussed extensively by Dammerman (1948) who concluded that the founders of the *R. rattus* population on Rakata reached the Krakatau group by human agency on boats.

(*q*) *Rattus tiomanicus* (Miller)

A medium-sized terrestrial omnivore (up to 187 mm head–body, 403 mm total length) widely distributed through the Indo-Australian archipelago (Dammerman 1948); recorded from Java and Sumatra (Dammerman 1948; Whitten *et al.* 1984). Although the species is common in natural ecosystems throughout its range, it also inhabits agricultural regions and coconut plantations (Whitten *et al.* 1984). Studies on Sertung and Panjang in 1982 (Iwamoto 1986) revealed that (as with *R. rattus*) the diet is essentially plant matter with fruit comprising 77.5% (Sertung) and 70.8% (Panjang) of stomach contents on average.

Sertung. First record: Jly., Aug., Oct., Nov., 1982 'many collected and observed, density high, 108 per ha' (Yukawa *et al.* 1983, 1984); 26 Oct.–15 Nov. 1982, 56 trapped, many observed, 'density in grid SQ 108.2 per ha, density in grid Sq 76.7 per ha' (Iwamoto 1986). Additional records: north spit and southwestern end of north spit 1984 (many observed); southern end of north spit in forest 1985 (10, many observed); forest near spring northeast Sertung 1985 (5).

Panjang. First record: 1928 'rats very common...prior to volcanological survey' (Dammerman 1938, 1948 as *Rattus rattus jalorensis*). Additional records: 1928 ('extremely common...using five traps caught 49 specimens in one night'), 1932 ('extremely common'), 1933 ('extremely common') (Dammerman 1948); 1982 (22, many observed, 'density 65 per ha') (Ibkar-Kramadibrata *et al.* 1986); 1982 ('many collected and observed, density very high, 328 per ha') (Yukawa *et al.* 1983, 1984); 1982 (37, many observed, 'density in grid KQ 281.6 per ha') (Iwamoto 1986); northwest cliff observation area, 1984 (many observed), 1985 (three, many observed); north Beach 1983 (3); east Beach and North Foreland 1985 (many observed); north Beach 1985 (several observed).

Status. Breeding populations on Sertung and Panjang. A Topographical Survey team spent 5 months on Panjang from 1896 to January 1897 and they encountered no rats during their stay (Dammerman 1948). However, the 1928–1931 Volcanological Survey team found rats to be extremely numerous on arrival in 1928 so a breeding population was established well before this date. Dammerman (1948) thinks it is possible the species was introduced during the 1896–1897 Topographical Survey and stresses that rats were definitely absent until 1896.

R. tiomanicus has remained abundant on Panjang since the first formal record in 1928. Dammerman (1948) noted 'every time we visited the island this rat was extremely abundant and at night an annoyance' and the species was recorded as very abundant in 1982 (Yukawa *et al.* 1983; 1984; Iwamoto 1986; Ibkar-Kramadibrata *et al.* 1986), 1984 and 1985.

There appears to have been a long time-lag between the first record for Panjang (1928) and Sertung (1982). Dammerman (1948) recorded that there were no rats on Sertung in 1921 and that in 1933 Sertung was 'still very poor in mammals...and rats have so far never been met. During each visit to the island numerous rat traps were set but not rat was ever caught'. *R. tiomanicus*, then, became established on Sertung some time between 1933 and 1982. However, the timing cannot be further estimated as the island was visited by scientists only once between

these dates in October 1951 by the ornithologist Hoogerwerf (1953) and he did not stay on the island overnight. Yukawa *et al.* (1983, 1984) and Iwamoto (1986) record that there are morphological differences between the Sertung and Panjang populations. For this reason they consider the Sertung population represents a new introduction to the Krakatau group ('probably by fishermen from Sumatra'), rather than the result of dispersal from Panjang.

Dammerman (1948) noted the species occurred abundantly in all habitats on Panjang and commented that it was not a true 'tree rat' as tall trees were still absent in 1934. In 1984 and 1985 the species was found to be abundant in all habitats on Sertung and Panjang including the closed forests. The results of our trapping on Sertung and Panjang are shown in table 2.

Table 2. Results of trapping on Sertung and Panjang, 1985

(Traps and bait as in table 1; trapping success relates to *Rattus tiomanicus*.)

locality	dates	number of traps set	rats trapped	trapping success (%)
Sertung				
bluff track, southwest end of north spit	18 Aug. 1985	15	10	66.7
forest near spring, northeast Sertung	18 Aug. 1985	10	5	50.0
		25	*15*	*60.0*
Panjang				
observation area, on northwest cliff	16 Aug. 1985	15	3	20.0
north beach	16 Aug. 1985	10	3	30.0
		25	*6*	*24.0*

The dispersal of *R. tiomanicus* to Panjang was discussed in detail by Dammerman (1948) who considered dispersal by active swimming from Sebesi or through human agency before concluding that dispersal to Panjang was by human agency on a boat. In support of this, Yukawa *et al.* (1983, 1984) and Iwamoto (1986) consider that the failure of *R. tiomanicus* to disperse from Panjang to Sertung up to 1933 shows that active dispersal is unlikely. Furthermore, these authors consider that the morphological differences between the Sertung and Panjang populations show that the Sertung population represents a second introduction to the Krakatau group by human agency. As with *R. rattus* on Rakata, it is considered most likely that *R. tiomanicus* has dispersed to Sertung and Panjang by human agency on boats.

(*r*) *Incidental records of domestic mammals*

Rakata. Dammerman records the sighting of a small black dog (*Canis familiaris*) in December 1933 and April 1934 on the southeast coast of Rakata at a spot 'where fisherman sometimes pass the night and have dug a well' (? Owl Bay).

Panjang. On 14 September 1984, a pig (*Sus scrofa*) was seen 500 m east of the northwest coast of Panjang by P. J. Vaughan, and scrapes and footprints were seen round the observation post area on top of the northwest cliff. In 1985 scrapes and footprints were again seen in the observation post area and abundant footprints were seen in gullies in the forest of the central area of the island. Pigs were not noted by the 1982 I.T.B. Expedition (Ibkar-Kramadibrata 1986), which stayed on Panjang for three days in July, nor by the Kagoshima University – L.I.P.I. Expedition which spent nine days there in September–October of the same year (Yukawa *et al.* 1983, 1984; Iwamoto 1986). Only one specimen has ever been seen, and there is no evidence as yet of a breeding population.

Anak Krakatau. An Associated Press report by Ingo Hertel in 1978 states that a mystic and

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his cat (*Felis catus*) took up residence on Anak Krakatau in July of that year but were both removed by the authorities (I. W. B. Thornton, February 1988). In August 1985 Indonesian fishermen tethered a goat (*Capra hircus*) ashore on Anak Krakatau in preparation for dispatch and consumption on a festival day.

The above records are regarded as isolated introductions by human agency and not as attempts to start breeding populations. They are not discussed further in this paper.

3. Discussion

Fifteen vertebrate species have been recorded from the Krakatau group since 1883. Two of the species records (*Crocodylus porosus* and *Cosymbotus platyurus*) are only incidental so thirteen species have managed to colonize one or more of the islands in the first 100 years. The species records are summarized in table 3. The data provided above gives some insight into the colonization and dispersal patterns and ecological relationships of these vertebrate species. To fully interpret these data, however, more information on the biological and geological evolution of the islands is required and some understanding of the impact of human activity in the region is necessary. The discussion is intended to achieve these ends.

Table 3. Records of terrestrial vertebrates on islands of the Krakataus from 1883 to 1986 in chronological order

	status										status	first
	1889	1896–97	1908	1919–24	1928–34	1934	1951	1977	1982	1984–86	1986	record
Reptilia												
Varanus salvator	R	P	RP	RS	RS	B	R	—	RSPA	RSPA	B	1889
Hemidactylus frenatus	—	—	RP	RS	RSP	B	R	—	A	RSPA	B	1908
Python reticulatis	—	—	R	RS	RSP	B	R	S	P	SP	B	1908
Emoia atrocostata	—	—	—	S	S	B	—	—	—	—	E	1919
Lepidodactylus lugubris	—	—	—	RS	RSP	B	—	—	—	—	E	1920
Crocodylus porosus	—	—	—	S	—	I	—	—	—	?R	I	1924
Mabuya multifasciata	—	—	—	R	R	B	R	—	R	R	B	1924
Cosymbotus platyurus	—	—	—	—	R	I	—	—	—	—	I	1928
Gekko gecko	—	—	—	—	—	—	—	—	R	R	B	1982
Chrysopelea paradisi	—	—	—	—	—	—	—	—	RSP	RSPA	B	1982
Gekko monarchus	—	—	—	—	—	—	—	—	—	R, ?P	B	1984
Ramphotyphlops braminus	—	—	—	—	—	—	—	—	—	S	B	1984
Hemiphyllodactylus typus	—	—	—	—	—	—	—	—	—	SP	B	1985
Total reptiles extant	—	—	—	—	—	6	—	—	—	—	9	—
Mammalia												
Rattus rattus	—	—	—	R	R	B	R	—	R	R, ?A	B	1918
Rattus tiomanicus	—	—	—	—	P	B	?P	—	SP	SP	B	1928
Total mammals extant	—	—	—	—	—	2	—	—	—	—	2	—
Total vertebrates extant	—	—	—	—	—	8	—	—	—	—	11	—

R, Rakata; S, Sertung; P, Panjang; A, Anak Krakatau; B, breeding population; E, now extinct; I, incidental record. Records to 1934 from Dammerman (1948); 1951, Hoogerwerf (1953); 1977 and 1982, Plage (1983); Iwamoto (1986); Ibkar-Kramadibrata *et al.* (1986) and Thornton (personal communication).

(*a*) *Eruption of Krakatau, August* 1883 *and the new forms of Rakata, Sertung and Panjang*

It is necessary to summarize the physical impact that the cataclysmic eruption of 1883 had on the islands of Rakata, Sertung and Panjang to appreciate how dynamic the subsequent physical changes to these islands have been. Simkin & Fiske (1983) provide a very detailed account from which the following major points emerge. On 26th Aug. 1883 a cataclysmic volcanic eruption commenced on the island of Krakatau. This eruption ejected more than 18 km^3 of hot volcanic ash and pumice which were deposited across the Sunda Strait area. The eruption culminated on the 27th August with the subsidence of the northern two-thirds of the island into the evacuated magma chamber. Over this period several major tsunamis were initiated that devastated the adjacent coastal areas in the Sunda Strait.

(*b*) *Coastal erosion of Rakata, Sertung and Panjang* 1883–1983

According to Simkin & Fiske (1983), after the eruption, 68% of Krakatau had been destroyed, its area had been reduced from 33.5 km^2 to 15.3 km^2 and the remnant island Rakata was created. The ash and pumice ejected formed a layer 60–80 m thick over the southern slopes of Rakata and over the adjacent islands of Sertung and Panjang. As a consequence the areas of these latter two islands increased, Sertung by 218% from 3.7 km^2 to 11.8 km^2 and Panjang by 10% from 2.9 km^2 to 3.2 km^2. The volcanic activity and deep hot ash layers effectively sterilized all the islands. Thus at the end of the eruption, the Krakatau group comprised Rakata covered on the south side by deep ash that extended well out to sea forming an extensive ash beach, and Sertung and Panjang that were both covered by deep ash layers that also extended well out to sea and formed extensive gently sloping ash beaches.

Since August 1883 the ash layers on southern Rakata, Sertung and Panjang have been heavily eroded by rain and especially by wave action (Bird & Rosengren 1983, 1984; Rosengren 1985). Marine erosion has eaten into the ash layers replacing the post-eruption coastline of extensive ash beaches with steep cliffs and bluffs in many places (Bird & Rosengren 1983).

Marine erosion has been very severe on Sertung. Suwardi & Rosengren (1983) map the progressive changes from 1883 to 1946, and maps provided by Bird & Rosengren (1984) and Rosengren (1985) reveal that by 1983 the Island's area had been reduced by about one half. On Sertung only about 10% of the coast (mainly on north spit) is now sandy beach, the west coast being high marine cliffs and bluffs, and the east coast high marine cliffs and steep forested slopes, whereas the south coast comprises high marine cliffs with hanging ravines. For Panjang about 10% of the coast is sandy beach (mainly in the northwest, north and northeast) whereas for Rakata about 5% of the coast is sandy beach (mainly in the southeast and at Zwarte Hoek). For these two latter islands, the remaining coasts are marine cliffs, bluffs and steep forested slopes. The limited extent of sandy beaches as the result of marine erosion is ecologically very important for two reasons. First, it has severely restricted the open coastal ecosystems and habitats and secondly, it has progressively limited the opportunity for dispersal of vertebrates on driftwood and flotsam that must wash ashore in a safe area for successful invasion.

(*c*) *Ecological succession on Rakata, Sertung and Panjang and canopy closure*

The successional changes up to 1983 are reviewed by Kartawinta (1983). The bare ash slopes of Rakata, Sertung and Panjang gave way to open coastal *pes-caprae* formations and pioneer grass communities at higher altitudes by 1897. Coastal *Barringtonia* and *Casuarina* forests

were established by 1906 but *pes-caprae* persisted on the beaches. Canopy closure commenced by 1932 with the development of *Macaranga-Ficus* forests up to 500 m and *Neonauclea* forests above 500 m. By 1951 canopy closure was widespread with mature *Barringtonia* forests in coastal areas and mature *Neonauclea* forests occupying the middle and upper altitudinal regions. Thus after the 1930s open habitats were progressively lost away from coastal areas by canopy closure and over the same period the open coastal habitats have been progressively lost by marine erosion. These processes would impact severely on vertebrates such as *Lepidodactylus lugubris* and *Emoia atrocostata* which favour open coastal zones.

(*d*) *Development of Anak Krakatau* 1930–1983

The appearance and development of Anak Krakatau has been reviewed by De Neve (1953, 1980, 1983), Siswowidjojo (1985) and Sudradjat (1983) from which the following brief outline has been derived. Submarine activity was first noticed in December 1927 and increased in 1929 but a permanent island was not established until August 1930 after a series of eruptions commencing in July. Sudradjat (1983) shows how episodes of volcanic activity since 1930 have periodically increased the size of Anak Krakatau. Of particular importance was a large eruption on 10–11 October 1952 that deposited a layer of ash 3 m thick over Anak Krakatau and covered Sertung and Panjang with ash 0.5–1.0 m deep, and another strong eruption on 20–23 September 1953 also caused damage to Sertung and Panjang (De Neve 1953, 1980, 1983; Siswowidjojo 1985). In 1961–1963 the first lava was extruded and since then substantial flows of lava in the southwest have consolidated the coast in that area (Siswowidjojo 1985).

The appearance and development of Anak Krakatau since August 1930 has added a new dimension to studies in the Krakatau group as it has presented the opportunity to document the development of a new terrestrial ecosystem at the same time that Rakata, Sertung and Panjang are at more advanced successional stages.

(*e*) *Destruction of vegetation on Sertung, Panjang and Anak Krakatau by major eruptions in* 1930, 1932, 1952 *and* 1953

Dammerman (1937, 1948) recorded that very heavy eruptions of Anak Krakatau in July and August 1930 just before establishment of the permanent island, covered the northern part of Sertung to the lagoon on the north spit with a layer of fine ash that defoliated trees and killed the undergrowth 'in a strip of land about four kilometres in breadth'. Dammerman (1937) noted that there was a clear line of demarcation, mixed forests being badly affected by the 'ash-tornado' whereas north of the lagoon the *Casuarina* forests of the north spit 'remained practically undisturbed'. Dammerman (1948) also recorded that an eruption of Anak Krakatau from 14 November to 27 December 1932 deposited a 'rain of ash' on Panjang, damaged vegetation and produced a barren landscape.

The eruption on 10–11 October 1952 had much more serious effects and is singled out as of particular significance by De Neve (1953, 1983), Hoogerwerf (1953), Partomihardjo (1983), Siswowidjojo (1985) and Van Borssum Waalkes (1954, 1960). Eye witness accounts of the damage are available in De Neve (1953) and Van Borssum Waalkes (1954, 1960). De Neve (1953, 1983) records that after this eruption Anak Krakatau was covered with black ash to a depth of 3 m and that the vegetation on the island was destroyed, whereas Sertung and Panjang were covered with ash 0.5–1.5 m deep that had 'practically destroyed the whole vegetation' on Sertung and 'ninety percent' on Panjang. He states, however, that there was

'no trace of ash or destruction of vegetation' on Rakata. Van Borssum Waalkes (1954) account agrees with that of De Neve, he notes the eruption was severe and an inspection on 16 November 1952 revealed that the vegetation on Anak Krakatau was destroyed, that Sertung was desolate and burnt with tremendous damage to the north spit, and that Panjang was desolate and burnt except in the south and east. Like De Neve, he stated there was no trace of damage to Rakata. Van Borssum Waalkes (1960) provided a more detailed account that repeated the earlier information, but added that on the north end of Sertung, trees were defoliated and scorched and on the north spit the *Casuarinas* were stripped bare to the main trunk.

Of particular importance were Van Borssum Waalkes' (1960) observations of the surface layer on Sertung: 'Most striking was the ground cover (which) was covered almost everywhere with a more or less thick layer of wet, blackish ash at most about 1.5 m thick. The shrubs, the stripped off branches and young *Casuarina* trees were also covered here and there with thick clots of this ash'. He also noted that on Anak Krakatau there was 'black ash several metres thick' and that the vegetation was destroyed. Partomihardjo (1983) when discussing the plant succession on Anak Krakatau records the eruption of October 1952 as having totally destroyed the terrestrial vegetation.

De Neve (1953, 1983) and Siswowidjojo (1985) also record the Anak Krakatau eruption on 20–23 September 1953 as significant for Sertung and Panjang. De Neve (1953) noted it was a violent eruption that destroyed vegetation on the half of Sertung facing towards Anak Krakatau to its highest point and also on the southernmost tip of Panjang.

(*f*) *Surface currents in the Sunda Strait*

Surface currents are very important in assisting the dispersal of actively swimming vertebrates or of driftwood and flotsam carrying individuals or eggs. Birowo & Uktolseja (1983) provide valuable information on the surface currents in Sunda Strait. According to these authors the surface currents exhibit annual variations. The direction of flow is mostly from the Java Sea to the Indian Ocean with maximum speeds in the August–December monsoon period. Specifically, they record that '...for the greater part of the year the flow is (to the) south-west...but in November the direction is reversed and the flow is north-east'. They also record that from April to November 'the velocity is 0.38–0.65 m/sec.' (1.37–2.34 km/hr) while from December to March 'velocity rarely exceeds 0.25 m/sec.' (0.9 km/h). In general these conditions would favour ocean dispersal from Sebesi or Sumatra to the Krakatau group. As Sebesi is only 12 km from the Krakataus, animals dispersing by sea from Sebesi could make the journey in 5–9 h from April to November.

(*g*) *Extent of fishing boat activity in the Sunda Strait*

Dispersal by human agency on boats appears to have been very significant in the colonization of the Krakatau group by vertebrates. The Sunda Strait is an important fishing zone for Indonesia and there are major fishing industries in the Lampung area of Sumatra and at Labuan, Carita and Sukanagara in west Java that utilize the area around the Krakataus. Although there are no data available for Lampung, Utzurrum (1983) has published a detailed study for Labuan, Carita and Sukanagara that shows the extent of boat movements in west Java.

Utzurrum (1983) records that in 1981 there were 3402 fishermen living in these three

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villages operating 616 fishing boats of which 95 % had a displacement of less than 3 t. In eleven months of that year (data for April were not available) 13487 boat landings were recorded by the fish auction at Labuan, an average of 1226 per month or 40 per day. The monthly figures varied seasonally from 371 (12 per day) in January during the west monsoon season (wet) to 2124 (68 per day) in July during the east monsoon season (dry). In 1984, 1985 and 1986 we noted that on most days about 10 fishing boats would arrive in the Krakatau group and almost inevitably the fishermen would go ashore on one of the islands. As Utzurrum's (1983) data only cover Labuan, it can be seen that there could be opportunities for vertebrates to reach the Krakataus by human agency on a daily basis.

In 1984 and 1985 the operations of the fishing industry at Carita and Labuan were observed to see if reptiles or mammals had any real chance of boarding boats directly or indirectly. At the outset it was observed that it is common practice to stack cargo and luggage on the beach, normally in the supralittoral zone, so transport indirectly in cargo could easily occur. It is also common practice to bring fishing boats up the rivers and tie them up next to houses so species of 'house geckos' or domestic rats could easily board boats directly. Finally it is common practice to pull smaller boats out of the water for safety and beach them in the supralittoral zone and the same is done to larger boats in need of repair. In these ways supralittoral and coastal species (like *H. frenatus*) could also board boats directly. Thus vertebrate species common around fishing villages must have a high probability of dispersal by boat.

(*h*) *The first* 50 *years of colonization* 1883–1933

Dammerman's 1948 Monograph '*The fauna of Krakatau 1883–1933*' records that 10 terrestrial vertebrate species (eight reptiles and two mammals) are known to have reached the islands in the first 50 years. Of these ten species records, two were only incidental (*Crocodylus porosus* on Sertung and *Cosymbotus platyurus* on Rakata), therefore eight vertebrate species managed to establish breeding populations and successfully colonize the Krakatau group over this period (table 3).

Four species, *Hemidactylus frenatus*, *Lepidodactylus lugubris*, *Varanus salvator* and *Python reticulatus* managed to establish breeding populations on Rakata, Sertung and Panjang between 1883 and 1933. These species were therefore the most successful colonists of the generally open early successional habitats. The remaining four species each managed to establish breeding populations on only one island, *Mabuya multifasciata* and *Rattus rattus* on Rakata, *Emoia atrocostata* on Sertung and *Rattus tiomanicus* on Panjang. The lower rate of colonization for the latter four species shows a lower ability to disperse between the islands compared with the former four species.

(*i*) *The second* 50 *years of colonization* 1933–1983

The data provided above show 12 terrestrial vertebrate species (10 reptiles and two mammals) from the islands over the period 1982–1986. One of these species records (*Crocodylus porosus* on Rakata) is incidental and therefore eleven species had breeding populations at the end of 100 years (table 3).

Three species, *Hemidactylus frenatus*, *Varanus salvator* and *Chrysopelea paradisi* had established breeding populations on Rakata, Sertung, Panjang and Anak Krakatau and a fourth, *Python reticulatus*, was absent only from Anak Krakatau. These four species, then, are the most successful colonists at the end of 100 years after canopy closure has occurred on Rakata,

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Sertung and Panjang. *Lepidodactylus lugubris*, a very successful colonist in the first 50 years, appears to have become extinct through habitat loss (see below) and *Chrysopelea paradisi* has arrived in this second period.

Of the remaining seven species, two, *Hemiphyllodactylus typus* and *Rattus tiomanicus* have established breeding populations on Sertung and Panjang, four species, *Gekko gecko*, *G. monarchus*, *Mabuya multifasciata* and *Rattus rattus* have breeding populations only on Rakata and one, *Ramphotyphlops braminus*, has a breeding population only on Sertung. Four of these species, *H. typus*, *G. gecko*, *G. monarchus* and *R. braminus* have arrived in the Krakatau group since 1933 and one species *E. atrocostata* previously restricted to Sertung, has become extinct probably as a result of habitat destruction in 1952 (see below). The lower rate of colonization of these seven species with more limited distributions in the Krakatau group shows a lower ability to disperse between the islands when compared with the four more widely distributed species.

Since 1934, five new species have established breeding populations on the Krakatau Group and one, *C. paradisi* has been highly successful as it is now found on all four islands. One of the new species, *H. typus*, has established breeding populations on Sertung and Panjang, two, *G. gecko* and *G. monarchus*, are restricted to Rakata and one, *R. braminus*, is restricted to Sertung. For these latter four species, their more restricted distributions may show recent arrival rather than poor powers of inter-island dispersal and this applies particularly to *G. gecko* which is, at the moment, restricted to the Zwarte Hoek area on Rakata that suggests a very recent arrival.

Two species, *Lepidodactylus lugubris* and *Emoia atrocostata* have apparently become extinct since 1933. In the case of *L. lugubris* it had established breeding populations on Rakata, Sertung and Panjang but it is a species that favours open coastal habitats which have been severely reduced on these islands over the last 50 years through the twin processes of canopy closure and continuing coastal erosion (see above). Habitat loss is considered to be the cause of these extinctions. *E. atrocostata* had established a viable population on Sertung by 1933 but it was always restricted to the supralittoral zone of the north spit. This area was devastated by the deposition of hot ash during the severe October 1952 eruption of Anak Krakatau (see above) and habitat destruction at that time was almost certainly the cause of the extinction.

Although Anak Krakatau has existed as an island since 1930, its present terrestrial ecosystem has been subjected to periodic destruction during eruptions. The developing biota appears to have been totally destroyed in the October 1952 eruption (see above) and most probably has been affected severely several times since then. Nevertheless, three reptile species, *H. frenatus*, *V. salvator* and *C. paradisi*, have managed to establish breeding populations and they are obviously very successful early colonists of volcanic islands in the area.

(*j*) *Dispersal patterns*

The data provided above show that of the 15 terrestrial vertebrate species that have been recorded from the Krakatau group since 1883, four (27%) *C. porosus*, *V. salvator*, *P. reticulatus* and *C. paradisi*, are thought most likely to have dispersed to the islands by active swimming; four (27%) *G. monarchus*, *H. typus*, *E. atrocostata* and *R. braminus* are thought most likely to have dispersed by rafting on driftwood or flotsam; and seven (46%) *C. platyurus*, *G. gecko*, *H. frenatus*, *L. lugubris*, *M. multifasciata*, *R. rattus* and *R. tiomanicus*, are thought most likely to have dispersed by human agency on boats. Thus a high percentage (46%) of vertebrate species could have reached the Krakatau group on boats, which is to be expected, given the density of boat traffic (see above).

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(*k*) *Ecological relationships*

Of the thirteen vertebrate species that have established breeding populations on the Krakatau group since 1883, five (38.5%) *H. frenatus*, *H. typus*, *L. lugubris*, *E. atrocostata* and *R. braminus* are insectivores; five (38.5%) *G. gecko*, *G. monarchus*, *V. salvator*, *P. reticulatus* and *C. paradisi* are carnivores; and three (23%) *M. multifasciata*, *R. rattus* and *R. tiomanicus* are omnivores. The high overall percentage of insectivores and carnivores (77%) is a reflection of the availability of food sources during the early stages of succession. The two extinctions from the Krakatau group (*L. lugubris* and *E. atrocostata*) are both insectivores.

(*l*) *Conclusion*

The terrestrial vertebrate fauna of the Krakatau group over the first 100 years comprises species that are very widely distributed in the tropics, especially in the Indo-Australian archipelago. In many cases the species recorded are common in the vicinity of human settlements and are pre-adapted to dispersal by human agency and transport by boat is thought to have been very significant. Although Rakata, Sertung and Panjang have now developed closed forests, the opportunities for forest-inhabiting terrestrial vertebrate species to disperse in driftwood is reducing as coastal erosion proceeds and the areas of sandy beach (best suited to stranding of driftwood) are becoming more limited. Although there are many common coastal Javan and Sumatran species still absent from the Krakataus the very limited extent of coastal habitat on Rakata, Sertung and Panjang may prevent their establishment even if they are transported by boat. Anak Krakatau, however, has extensive stretches of sandy and gravelly beach so, barring further major eruptions like that of October 1952, this island would be the most likely site for new arrivals and colonizations in the future.

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