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Source: *Journal of Biogeography*, May, 1994, Vol. 21, No. 3 (May, 1994), pp. 245-258

Published by: Wiley

Stable URL: https://www.jstor.org/stable/2845528

Journal of Biogeography (1994) **21**, 245–258

The role of frugivorous bats and birds in the rebuilding of a tropical forest ecosystem, Krakatau, Indonesia

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Abstract. Krakatau provides a case study in tropical forest rebuilding following sterilization of the islands in 1883 by volcanic eruptions. On the basis of historical and recent records, the roles of frugivorous birds and bats in plant colonization and spread are assessed with reference to the interior forest communities. It is established that the islands are within the effective seed-transport range of members of both the avifauna and bat fauna and it is argued that it is parsimonious to assume a role for both taxa in introducing small-seeded species. For instance, the most successful genus of plant colonists, *Ficus* with twenty-four species, is attractive to both groups of dispersers. Larger seeds which cannot be ingested by bats must have been introduced by birds, with the exception of diplochorous, primarily sea-dispersed species (or human introductions). The largest-seeded partially-zoochorous species are bat-spread trees. Birds have a dispersal role for a more balanced range of plant growth forms than do bats, for which available records indicate a restriction largely to trees and shrubs.

Early this century savanna was predominant, but following the establishment of scattered patches of trees and shrubs, forest closure occurred very rapidly, almost exclusively involving zoochorous trees, notably *Ficus* spp. For the period 1883–1992 a total of 124 species of plants are identified as probably having been introduced endogenously by birds and bats and a further forty-nine partially zoochorous species have been recorded. Birds and bats are argued to have partially overlapping yet complementary roles as dispersers. The implications of these observations for restoration ecology and forest conservation are discussed.

Key words. Conservation biology, dispersal, frugivory, island ecology, plant colonization, succession, zoochory.

INTRODUCTION

The roles of phytophagous bats and birds in rebuilding disturbed tropical ecosystems have received surprisingly little attention (Snow, 1981; Marshall, 1983; Gautier-Hion *et al.*, 1985; Johnson *et al.*, 1985; Lambert, 1989a) despite their wider relevance for management and restoration ecology (Howe, 1984; Pannell, 1989). The Krakatau Islands, Indonesia, provide a rare research opportunity since the recolonization of the islands by plants and animals has been documented intermittently over the period since the sterilizing eruptions of 1883 (Ernst, 1908; Docters van Leeuwen, 1936; Dammerman, 1948; Whittaker, Bush & Richards, 1989; Zann, Male & Darjono, 1990a; Bush & Whittaker, 1991; Whittaker *et al.*, 1992a). The four islands of the group are separated from mainland source populations by significant distances of open sea, given which a distinction may be made between: (i) the long-distance dispersal of seeds to the islands; (ii) subsequent jump dispersal within the group; and (iii) local spread or scatter of seeds from bridgehead populations established within a locality. Not all frugivores will be successful in seed dissemination at all levels, just as certain animal-spread plants may not be dependent on zoochory for colonization.

In previous articles we have separated the primary dispersal types of the Krakatau flora, distinguishing between wind, sea, animal and human transport to the islands (eg. Whittaker *et al.*, 1989, 1992a; Whittaker & Bush, 1993, see also Whittaker & Jones, 1994), but we have not hitherto attempted to subdivide the zoochorous component of the flora. The potential for colonization through endogenous transport is primarily dependent on two factors. First, the carriage-time of the seed must be long enough to allow the island to be reached before regurgitation or defecation. This is of course related as much to the speed of flight and distance travelled as to the particular digestive characteristics of the species concerned. The retention time of a seed will depend upon both the frugivore and the seed type, which together determine whether the entire seed is passed intestinally or processed and then regurgitated. In turn, this

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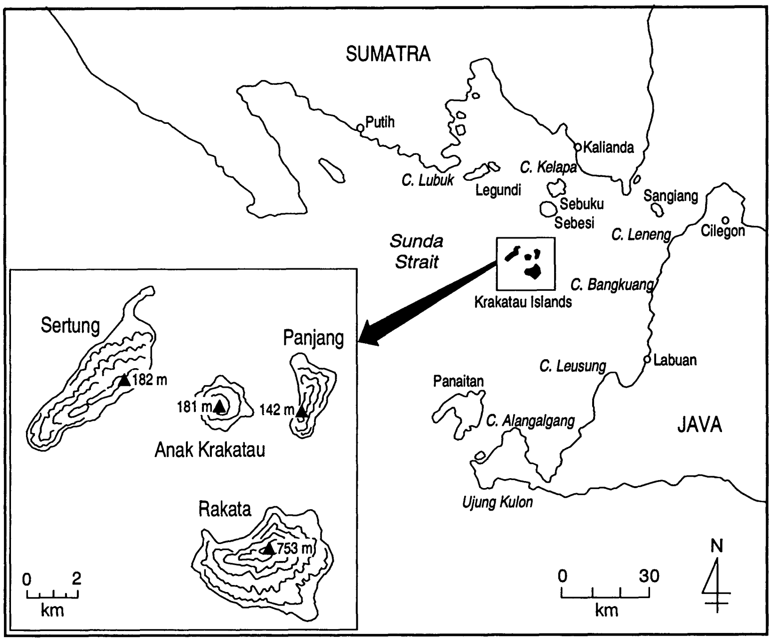

FIG. 1. Sunda Straits and the Krakatau islands (distances between selected named islands and points are given in Table 1).

will have bearing on the distance of seed-carriage since times to regurgitation of ballast are typically shorter than to defecation for any given species (Proctor, 1968; Johnson *et al.*, 1985). Second, the transported seed must be viable, i.e. have the potential for germination and establishment. Viability may be severely reduced after ingestion, in which case the frugivore may more meaningfully be termed a 'seed-predator' (Snow, 1981; Johnson *et al.*, 1985). In contrast, for certain species germination may actually be enhanced by gastrointestinal passage (Fleming & Heithaus, 1981). In many cases, however, seed viability will neither improve with frugivore handling nor suffer without (Howe & Smallwood, 1982).

Over the period 1919–1934, Docters van Leeuwen (1936) conducted a number of experiments and made detailed observations concerning the means of dispersal of plant species to Krakatau, differentiating wherever possible between bird- and bat-transport. We have collated both these early data and post-1934 plant data (Whittaker *et al.*, 1989; Partomihardjo, Mirmanto & Whittaker, 1992; Whittaker & Bush, 1993; and unpublished data) for which dispersal information has been derived from the literature and, to a lesser degree, from direct observation. Our aim in this contribution is to assess the differing roles and relative significance of bats and birds in forest ecosystem rebuilding on Krakatau. We go on to assess the significance of these data for tropical forest conservation and restoration.

STUDY AREA

The Krakatau group consist of three prehistoric islands (Rakata, Sertung and Panjang) arranged around a fourth much younger and volcanically active island (Anak Krakatau) that emerged from a submarine vent in 1930 (Fig. 1). The three older islands are covered in evergreen tropical humid forest while Anak Krakatau is sparsely vegetated and is characterised by ash and cinder fields. The islands are isolated from the nearest-points of mainland Java and Sumatra by approximately 40 km of sea, although the distance to neighbouring islands to the north is much less (Table 1).

FRUIT BATS OF KRAKATAU

In the old world tropics and sub-tropics, phytophagous bats are represented by the Megachiroptera (174 species), which are exclusive to these regions (Marshall, 1985). These bats interact with a wide variety of plant families and genera, feeding upon nectar, pollen, petals, bracts, fruits and leaves (Pijl, 1957; Marshall, 1985). In serving as pollinators and seed dispersers they may be highly significant to particular plant species (loc. cit., Fujita, 1991; Cox *et al.*, 1992).

The history of fruit bat colonization of Krakatau is documented by Tidemann *et al.* (1990) and Rawlinson *et al.* (1992), with important early accounts being provided by Docters van Leeuwen (1936) and Dammerman (1948). The first sightings of fruit bats were of *Cynopterus sphinx angulatus* on Rakata and Sertung in 1919. As bats were not recorded from a three day expedition in 1908, it is assumed that this species became resident after 1908 but before 1919 when they were quite common (Docters van Leeuwen, 1936; Dammerman, 1948). A second species, *C. horsfieldi*, was observed on Rakata in 1920 and on Sertung in 1930 but has not maintained its presence. In contrast, *C. sphinx* has been found on each subsequent survey and is known from all four islands (Rawlinson *et al.*, 1992). A colony of

TABLE 1. Inter-island and island-mainland distances (km) for the Krakatau Islands and selected points within the Sunda Strait region, Indonesia (refer to Fig. 1 for location of named points); initials S and J after place name refers to Sumatra and Java, respectively.

Name/abbreviation	R	S	P	A	Si	Su	C.K	L	C.Lb	Pt	C.A	C.Ls	Sn	C.B
Rakata														
Sertung	6													
Panjang	3	5												
Anak Krakatau	3	2	1.5											
Sebesi	17.5	12.5	12	14										
Sebuku	25.5	20.5	19.5	22.5	2									
Cape Kelapa, S	37.5	33.5	31.5	35	14.5	7								
Legundi	36.5	27	33	31.5	24	22	31.5							
Cape Lubuk, S	45	35.5	42	40.5	33.5	34	42.5	5						
Panaitan	44.5	47	50.5	50	65.5	73.5	85.5	75	79					
Cape Alangalang, J	53	58.5	60.5	60	75	83	93.5	89	95	9.5				
Cape Leusung, J	40.5	50.5	46.5	47.5	58	64	70.5	81.5	90	42.5	35			
Sangiang	45.5	48.5	42.5	46.5	34.5	33	12	59.5	72	88.5	90.5	57		
Cape Bangkuang, J	41	49	42.5	45	44	47.5	36	73	83	71	69.5	33	25	
Cape Leneng, J	51.4	57	50	54	45.5	45.5	26.5	72.5	84.5	89.5	89.5	54	10	20.5

a third fruit bat, *Rousettus amplexicaudatus*, was first recorded in a cave on Panjang in 1933. The next collections of bats were not made until 1974, when a third *Cynopterus, C. titthaecheilus*, was confirmed for Rakata. It has since been found on Sertung and Panjang also. The taxonomy of *Cynopterus* appears particularly uncertain and comparisons of Dammerman (1948), Hill (1983), Tidemann *et al.* (1990) and Rawlinson *et al.* (1992) suggest a number of different scenarios for colonization within this genus: of which we have simply followed the most recent view. A single record of the long-tongued fruit bat, *Macroglossus sobrinus*, was made in 1974 (Hill, 1983). Finally, a large colony of *Pteropus vampyrus*, the large Malayan flying fox, was found in 1985 on Sertung. It was apparently absent during the visit of Rawlinson *et al.* (1992) in 1986, but was seen again in 1989, when it consisted of well over 600 individuals (RJW, pers. obs.).

BATS AS DISPERSERS

Megachiroptera are known to feed upon fruits of 145 genera of plants, in many families, but most notably Palmae, Anacardiaceae and Sapotaceae (Marshall, 1985). *Ficus* species (Moraceae) have also been highlighted as having a major role in the diets of plant-feeding bats and birds in this region, and consequently have been termed 'keystone' plant resources (Marshall, 1985; Lambert, 1989b, 1991). Bat dispersed plants appear to be mostly trees in which sugary types of fruit predominate, rather than the oily fruits which are important to birds (Snow, 1981; Marshall, 1985). For instance, in the genus *Syzygium* (*Eugenia*), Ridley (1930) distinguished between bird-fruits that were small, juicy, colourful and produced low on the branches, and bat-fruits that were large, greenish and provided with a firm pericarp. In *Ficus*, a similar distinction can be made between cauliflorous species with large, dull 'bat-fruits' (e.g. *Ficus fistulosa*), and small, coloured figs that appear to be most suited to bird-dispersal. Ridley (1930) and Pijl (1957) also considered that hard-fleshed green drupes would seem to offer no attraction to birds or to mammals other than bats. The following characteristics have been identified as being typical properties of 'bat-fruit' (Pijl, 1957; Marshall, 1985):

colour, greenish or brownish, inconspicuous;
odour, unfresh, rancid or musty when ripe;
dimensions, can be up to a few centimetres, or so large that they cannot be transported by birds; some cannot be transported whole by bats either;
position, fruits borne away from foliage, e.g. on pendulous branches, on old open branches, in pagoda-shaped trees, or from trunks (cauliflory);
seed size, very small seeds may be ingested and therefore transported fairly long distances, larger seeds are not swallowed, but can be transported moderate distances;
nutrition, sugary rather than oil-rich.

Such generalizations may, however, represent a poor predictor of actual dispersal agents in a given field situation, as a high proportion of zoochorous plants are undoubtedly dispersed both by bats and birds (Marshall, 1985).

Two main categories of seed dispersal by bats can be identified: (i) the plucking of large-seeded fruits and the subsequent consumption of the fruit-flesh and discarding of the seed, generally at a nearby perching site, and (ii) the incidental ingestion of small seeds and their subsequent defecation or oral ejection (Pierson & Rainey, 1992). The former has been instrumental in the spread of the large-seeded *Terminalia catappa* on Krakatau (Docters van Leeuwen, 1936; Pijl, 1957). Little is known about the weight-threshold of Krakatau bats, although Pijl (1957) observed that *Cynopterus* sp. of about 30 g in weight could carry fruits of up to 75 g (but rarely further than 200 m), while *Pteropus vampyrus* of about 800 g could carry fruits of > 200 g. Plant colonization of the islands by this means is highly improbable. Further, very large fruits, such as *Mangifera* (Anacardiaceae) and *Carica* (Caricaceae), must generally be consumed *in situ* and are not dispersed effectively by bats (Marshall, 1985).

Since fruit-bats have narrow gullets (e.g. 2.0–2.5 mm in *Cynopterus*, Docters van Leeuwen, 1936), only the smallest seeds are dispersed following intestinal passage. Examples from among the Krakatau flora include *Cyrtandra sulcata*, *Ficus fistulosa*, *F. racemosa*, *Muntingia calabura* and *Piper aduncum*; seeds of each of which have been recovered from intestines or excrement of *Cynopterus* spp. (Docters van Leeuwen, 1935; Pijl, 1957). Similar observations have also been made in connection with the larger *Pteropus* (Pijl, 1957). The potential range of this mode of seed transport depends on the relationship between seed throughput time and speed of the bat. Fleming & Heithaus (1981) cite 15–20 min as the through-put time for the neotropical *Carollia perspicillata* (Phyllostomatidae) and Wolton *et al.* (1982) observed mean through-put times of 20–70 min for six species of Liberian Pteropodidae. In general, Wolton *et al.* (1982) found that through-put time increases with animal size, with the slowest passage being for a species (*Epomops buettifokeri*) of less than a fifth the weight of *Pteropus vampyrus*. On the basis of these data, *P. vampyrus* could be expected to reach Krakatau carrying a full seed load. Similarly, the *Cynopterus* species might be anticipated to have a mean through-put time of between 20 and 24 min, which would put them within range of seed sources (Table 1). Simple extrapolations made on the basis of weight and gut-length may, however, be misleading, for Tedman & Hall (1985) obtained *mean minimum* (our stress) food through-put times of 12–34 min for cultivated fruits fed to *Pteropus alecto* and *P. poliocephalus* and an inconsistent relationship between intestinal length and food transit time. What is more assured, however, is that seeds which are processed intestinally by large bats are likely to be carried further than those processed orally (Pijl, 1957; Marshall, 1985).

Resident populations of bats might initially be anticipated to be more important as agents of local spread of plants than of their colonization; however, fruit bats are known to travel considerable distances to feed. Marshall (1985) cites distances of 50 km and 25 km respectively for *Pteropus vampyrus* and *Rousettus amplexicaudatus*, while Dammerman (1948) suggests that the nightly range of *P. vampyrus* may be as great as 70 km. *Pteropus* have been

TABLE 2. Non-migrant resident avifauna known from Krakatau capable of endogenous seed transport, the survey period in which they were observed (after Thornton, Zann & Stephenson, 1990), and their typical food items (after MacKinnon, 1988). The 1908 survey was by Jacobson (1909), the 1919 survey by M. Bartels (Dammerman, 1922), 1934 refers to the 1932–34 survey by Dammerman (1948), 1952 to the 1951–52 survey by Hoogerwerf (1953), and 1986 to the 1984–86 survey by Zann *et al.* (1990a).

Family and species	Years of observation	Dietary components
Columbidae:		
Chalcophaps indica	1908	Fallen fruits & seeds, insects
Ducula aena	1986	Small berries, wild nutmegs, figs & other fruit
Ducula bicolor	1919, 1934, 1986	Fruits, eg. wild nutmegs, some figs
Geopelia striata	1919, 1952	Seeds & insects
Macropygia emiliana	1934, 1952, 1986	Seeds, berries & other small fruits
Ptilinopus melanospila	1952, 1986	Small fruits (esp. figs)
Treron vernans	1908, 1919, 1934, 1952, 1986	Small fruits (incl. figs & Melastoma), shoots
Corvidae:		
Corvus macrorhynchos	1908, 1919, 1934, 1952, 1986	Various fruits, invertebrates, carrion
Cuculidae:		
Eudynamys scolopacea	1919, 1934, 1952	Figs & berries, also insects
Dicaeidae:		
Dicaeum trigonostigma	1919, 1934, 1952, 1986	Berries, small figs, small insects
Nectarinidae:		
Aethopyga mystacalis	1952, 1986	Flowers, nectar, seeds, insects & spiders
Anthreptes malacensis	1919, 1934, 1952, 1986	Nectar, arthropods, & soft fruit
Oriolidae:		
Oriolus chinensis	1908, 1919, 1934, 1952, 1986	Figs, berries, other fruits, insects, caterpillars
Pycnonotidae:		
Pycnonotus aurigaster	1908	Berries & other small fruits, some insects
Pycnonotus goiavier	1908, 1919, 1934, 1952, 1986	Invertebrates, buds, small fruits, seeds
Pycnonotus plumosus	1952, 1986	Figs, berries, caterpillars, beetles, other insects
Rallidae:		
Amaurornis phoenicurus	1919, 1934, 1952, 1986	Invertebrates, small fish, rice, grass seed
Sturnidae:		
Aplonis panayensis	1919, 1934, 1952, 1986	Fruits (incl. figs), insects, caterpillars, spiders
Turdidae:		
Zoothera interpres	1986	Fruits, insects, worms, snails

observed to gather in large roosts on islands but fly to mainland sites in order to feed (Marshall, 1983). Dammerman (1922) has also recorded the reverse behaviour, Sumatran mainland populations flying to Sebesi (Fig. 1) to feed. *P. vampyrus* individuals roosting on Sertung in 1989 were observed by RJW to be heading away from the Krakatau group at dusk, many in the direction of Sebesi. Although the species was not recorded on Krakatau prior to the 1980s, earlier visits must have occurred, but simply went unobserved. The species is common on both sides of the Sunda Straits, and in the 1920s Dammerman (1948) noted individuals moving across the Sunda Straits, following trajectories that would take them close to or through the Krakatau group. Within mainland areas *Pteropus* is also known to be highly mobile, exhibiting movements that may represent non-seasonal nomadism rather than migration (Marshall, 1983). Such movements may be related to food availability and Tidemann *et al.* (1990) considered that this might explain the erratic nature of observations of *Pteropus vampyrus*, *Cynopterus* spp. and *Rousettus amplexicaudatus* on Krakatau.

FRUGIVOROUS BIRDS OF KRAKATAU

Zann *et al.* (1990a), record forty-five non-migrant land birds from Krakatau, of which thirty-six species were present between 1984 and 1986. A conservative estimate of the number capable of introducing diaspores endogenously is nineteen species (Table 2). Of this frugivorous and/or granivorous guild, six were recorded during Jacobsen's 3 days on the islands in 1908 (the first bird survey), the cumulative total rising to thirteen as a result of the second survey in 1919. These data suggest that important frugivorous birds, including fruit pigeons (Columbidae), bulbuls (*Pycnonotus*) and the glossy starling (*Aplonis panayensis*), became established on the islands at a slightly earlier stage than did the first frugivorous bats (see also: Docters van Leeuwen, 1936).

BIRDS AS DISPERSERS

'The pigeons and doves are the most important dispersers of seeds of any group of birds. They are voracious eaters of berries, drupes, and grain, and fly very

TABLE 3. Krakatau plant species: feeding and dispersal observations related to particular bird species of Krakatau. Source for a–e = Docters van Leeuwen (1936); a, feeding observed on Krakatau; b, feeding observed in aviary; c, observed in gizzard, crop or intestine; d, eaten (source unspecified); e, observed growing in nest; f, inferred as being eaten from observation of Ridley (1930); g, observed in stomach contents by Zann *et al.* (1990b); h, feeding observed on Krakatau (Whittaker & Turner, 1994); i, Ridley (1930).

Frugivore	Plant eaten	Plant family	Source
Aplonis panayensis	*Pipturus argenteus*	Urticaceae	a
	Homalanthus populneus	Euphorbiaceae	e
	Morinda citrifolia	Rubiaceae	e
	Scaevola taccada	Goodeniaceae	b
	Tinospora glabra	Menispermaceae	a
	Leucosyke capitellata	Urticaceae	a
	Cayratia trifolia	Vitaceae	a
	Dysoxylum gaudichaudianum	Meliaceae	h
Corvus macrorhynchos	*Carica papaya*	Caricaceae	c
	Ficus spp.	Moraceae	i
Pycnonotus aurigaster	*Cayratia trifolia*	Vitaceae	a
	Solanum torvum	Solanaceae	d
	Pipturus argenteus	Urticaceae	a
	Leucosyke capitellata	Urticaceae	a
Pycnonotus goiavier	*Cassytha filiformis*	Lauraceae	g
	Dysoxylum gaudichaudianum	Meliaceae	h
	Melastoma polyanthum	Melastomataceae	i
	Clidemia hirta	Melastomataceae	i
	Ficus benjamina	Moraceae	i
	Passiflora foetida	Passifloraceae	i
Pycnonotus spp.	*Mussaenda frondosa*	Rubiaceae	b
	Scaevola taccada	Goodeniaceae	b
	Melastoma polyanthum	Melastomataceae	i
Fruit-pigeons	*Scaevola taccada*	Goodeniaceae	d
	Cassytha filiformis	Lauraceae	c
	Oncosperma tigillarium	Palmae	f
Ducula aenea	*Dysoxylum gaudichaudianum*	Meliaceae	h
Ptilinopus melanospila	*Dysoxylum gaudichaudianum*	Meliaceae	h
Treron vernans	*Bridelia stipularis*	Euphorbiaceae	f
	Ficus benjamina	Moraceae	i
	Ficus retusa	Moraceae	i
	Oncosperma tigillarium	Palmae	i
Sturnus contra (non-resident)	*Mussaenda frondosa*	Rubiaceae	b

long distances, not only over land, but far over the sea, and they move very fast, so that they can disperse seeds swallowed at a very great distance from the spot from which they took them.' H. N. Ridley (1930, p. 497).

Remarkably few specific data are available linking Krakatau plant species to Krakatau birds (Table 3), and although a more exhaustive literature search may have revealed more, these data simply establish the possibility of a dispersal role of some sort. In extreme cases, initial colonization is more parsimoniously explained by sea-transport (compare Tables 3 and 4). Fruits that are most attractive to birds are typically small, red or purple in colour, lack seed protection, or are dehiscent with arillate seeds (Gautier-Hion *et al.*, 1985). Certain frugivore species, by virtue of their population number and/or their ability to disperse viable seed, will contribute disproportionately to the plant community. One species which is likely to have had an importance not reflected in Table 3 is the large fruit-pigeon *Ducula bicolor*, which has been described as roaming in large flocks between off-shore islands in the region (Dammerman, 1948) and which was observed to be present on Krakatau in large numbers in 1919–1920 (Dammerman, 1922). Wyatt-Smith (1953) considered the same species to have been largely responsible for the introduction of the fifty-one bird-dispersed plant species he recorded from Jarak Island in the Straits of Malacca.

Few data are available concerning seed-retention times of Krakatau bird species. Docters van Leeuwen (1936, p. 222) stated that the digestive process in *Ducula* takes 7.5 h, but he did not elaborate on the derivation of this estimate. A study of Malaysian populations of two species established figures of 4–12 h for throughput of fig seeds by the ground-foraging emerald dove (*Chalcophaps indica*) and 0.5–4 h by the omnivorous black-naped oriole (*Oriolus chinensis*) (Lambert, 1989a). This study also provides values for non-Krakatau species of shared genera: *Treron, Ptilinopus* (both pigeons) and *Pycnonotus* (bulbuls). The pigeons retained seeds for tens of minutes through to several hours, the bulbuls for 5–41 min. Elsewhere, studies

TABLE 4. Diplochorous species of Krakatau involving secondary endogenous transport by birds and/or bats, having colonized by sea or human agencies. Principal sources for attribution: Ridley (1930), Docters van Leeuwen (1935, 1936), Pijl (1957), Marshall (1985), Fujita (1991), Cox *et al.* (1992).

Diplochorous mode	Species	Family	Growth form
Sea-colonist, bat-spread			
	Gluta renghas	Anacardiaceae	Small tree
	Spondias mombin	Anacardiaceae	Small tree
	Terminalia catappa	Combretaceae	Med/Large tree
	Cycas rumphii	Cycadaceae	Single stem to 1.6 m
	Cerbera manghas	Apocynaceae	Small tree
	Ochrasia oppositifolia	Apocynaceae	Small tree
	Calophyllum inophyllum	Guttiferae	Large tree
	Hernandia peltata	Hernandiaceae	Medium tree
	Erythrina fusca	Leguminosae	Medium tree
	Erythrina variegata	Leguminosae	Medium tree
	Mucuna acuminata	Leguminosae	Liane
	Pandanus tectorius	Pandanaceae	Shrub
	Guettarda speciosa	Rubiaceae	Small tree
	Morinda citrifolia	Rubiaceae	Small tree
Sea-colonist, bat- or bird-spread			
	Ximenia americana	Olacaceae	Shrub
	Passiflora foetida	Passifloraceae	Climbing herb
	Premna corymbosa	Verbenaceae	Shrub
	Vitex paniculata	Verbenaceae	Shrub
Sea-colonist, bird-spread			
	Scaevola taccada	Goodeniaceae	Shrub
	Cassytha filiformis	Lauraceae	Parasitic trailer
	Adenanthera pavonia	Leguminosae	Large Tree
	Sterculia foetida	Sterculiaceae	Medium tree
	Tacca leontopetaloides	Taccaceae	Herb
	Cayratia trifolia	Vitaceae	Small liane
Human-introductions, can be fed on by bats			
	Mangifera indica	Anacardiaceae	Small tree
	Annona muricata	Annonaceae	Small tree
	Durio zibethinus	Bombacaceae	Large tree
	Ananas comusus	Bromeliaceae	Herb
	Cynometra cauliflora?	Leguminosae	Small tree
	Tamarindus indica	Leguminosae	Medium tree
	Artocarpus altilis	Moraceae	Small tree
	Artocarpus heterophyllus	Moraceae	Medium tree
	Musa paradisiaca	Musaceae	Large herb
	Citrus sp.	Rutaceae	Small tree
Human-introductions, can be fed on by bats & birds			
	Phoenix sp.	Palmae	Medium tree
	Lycopersicon lycopersicum	Solanaceae	Herb
Human-introductions, can be spread by birds			
	Cucurbita moschata	Cucurbitaceae	Trailing herb
	Gnetum gnemon	Gnetaceae	Small tree
	Capsicum frutescens	Solanaceae	Herb

Table includes species for which this pattern has been established on Krakatau or elsewhere, but excludes a small number of species which may be diplochorous but for which initial introduction to Krakatau has been attributed to animals, e.g. *Flagellaria indica* (liane, Flagellariaceae) is supposedly diplochorous, but was first found on Krakatau at an altitude of > 10 m in 1924, and has therefore been categorized simply as zoochorous in this study. The *Cynometra* may have been *C. ramiflora* (a thalassochore), but the specimen concerned died before it could be determined.

of two other Columbidae have produced estimates of up to 24 h for seeds of < 2.0 mg in weight (Proctor, 1968). Given the relatively short distances between Krakatau and source areas (Fig. 1, Table 1), and especially when considering the possibility that the islands of Sebuku and Sebesi to the north may act as 'stepping-stones' from mainland Sumatra (a cumulative inter-island distance of 21 km), it seems that only the shortest regurgitation- or defecation-times will impede seed-carriage to the islands. Docters van Leeuwen (1936) observed that many birds fly at around 50 km h^{-1}, with doves flying at around 80 km h^{-1}, and he estimated that they could therefore reach Krakatau from

Sebesi in 15–30 min, and from Java or Sumatra in 30–60 min (see also Dammerman, 1948).

Dispersal will only be successful if seed viability is maintained. Little is documented about this aspect of seed ecology for south-east Asian frugivores, although Lambert's (1989a) study of Malaysian lowland forest pigeons again provides some insights. He observed that *Chalcophaps indica* ground up all but a few ingested fig seeds, while *Treron* spp. left very few such seeds intact in faecal material. In contrast, *Ptilinopus jambu* (*P. melanospila* is the Krakatau species) defecated all seeds intact. The key features appear to be that *Treron* and *Chalcophaps* have grit-containing muscular gizzards, while *Ptilinopus* and *Ducula* species tend to have thinner-walled gizzards and do not use grit. Zann *et al.* (1990b) found seed of *Cassytha filiformis* (Lauraceae) and a grass in the stomach contents of *Pycnonotus goiavier* (the yellow-vented bulbul) on Anak Krakatau, but the viability of these seeds was not assessed. Docters van Leeuwen (1936) successfully germinated seeds from intestinal samples of *Aplonis panayensis*, describing it as among the most effective agents of plant dispersal (p. 230). He concluded that it is possible to separate fruit eaters which do not destroy seeds from the granivores (cited above) which do.

SUCCESSION OF BAT- AND BIRD-SPREAD PLANTS IN THE INTERIOR

Historical patterns of vegetation succession on Krakatau are described in Ernst (1908), Docters van Leeuwen (1936) and Whittaker *et al.* (1989), from which the following is largely drawn. The first vascular plant species collected on Krakatau in 1886 were all either sea or wind dispersed. And, of the forty-two vascular plant species found by 1897, Docters van Leeuwen (1936) attributed only six to zoochory: *Ficus fulva*, *F. hispida*, *F. padana*, *F. septica*, *Macaranga tanarius*, and *Melastoma affine*. All are small trees, except *Melastoma affine* which is a shrub, and although colonization may have been effected by birds, all but *Macaranga tanarius* have also been noted as bat-spread.

By 1906 the development of vegetation on Krakatau had proceeded rapidly and a belt of strand-forest had formed parallel to the shore on the south side of Rakata, characterized by the non-zoochorous *Casuarina equisetifolia*. Inland, a dense savanna had developed in which isolated trees and shrubs were seen on the low-lying ground which rises gradually to the base of the conical mountain; in some of the ravines half-way up they formed patches of forest, reappearing as scattered plants on the higher ridges and on the peak (Ernst, 1908). It is not clear how many zoochorous species were already fruiting, but specific mention was made of two figs, *Ficus fulva* and *F. fistulosa*, the creeper *Tricosanthes bracteata*, and the sea-colonist but bird-spread *Scaevola taccada* (Ernst, 1908).

The true endozoochorous element *c.* 1906–1908 included: two herbs, *Costus speciosus* and *Tricosanthes bracteata*; the shrubs *Cyrtandra sulcata, Ficus hirta, F. montana, Lantana camara, Leea aequata, Leucosyke capitellata, Melastoma affine* and *Pothomorphe subpeltata*; the small trees *Carica papaya, Ficus fistulosa, F. fulva, F. hispida, F. padana, F. septica, Gluta renghas, Homolanthus populneus, Macaranga tanarius, Mallotus multiglandulosa, Pipturus argenteus* and *Trema orientalis*; and one large tree, *Artocarpus elasticus* (after Whittaker *et al.*, 1989). It was Ernst's (1908) opinion that frugivorous birds were responsible for all these arrivals, yet the possibility of introductions by visiting bats cannot be discounted. The fig trees are each now known to be bat-spread, and several may have been introduced in substantial numbers, judging by the early accounts. More recently Tidemann *et al.* (1990) attributed *Ficus* seedlings found in several places on bare lava on Anak Krakatau in 1985 to the movements of bats over the island. Pijl (1957) has argued that low-growing shrubs and herbs are likely to be bird- rather than bat-spread and from our data-base of 1883–1992 records this seems to be the case for the Krakatau flora (below). It is interesting, therefore, that the above list contains only two herbs and indeed that tree species outnumber shrubs. The strand flora contained a number of typical diplochorous species, e.g. *Calophyllum inophyllum, Morinda citrifolia* and *Terminalia catappa*, each sea-colonists but often bat-spread. However, at this stage they had not, apparently, spread far from the strand-line. The shrub *Pluchea indica* and the tree *Neonauclea calycina* were the only arboreal species recorded by 1908 which we have classified as wind-colonists (but see below), demonstrating the overwhelming importance of zoochory to the development of interior forest cover.

Saccharum grasslands remained the predominant cover of inland areas until *c.* 1919, but within this grass-steppe there were many variably-sized patches of trees that were gradually coallescing and shading out the grassland. Docters van Leeuwen (1936) commented that within the woodland patches '... *everywhere one could see* Saccharum *plants standing or lying half-dead or dead in the shade of the groves* ...' and '... *It is remarkable that these are all species of trees with fruits eaten by birds and bats, and the seeds of which are spread endozoically. Principally, they are* Macaranga, Pipturus, *and a few species of* Ficus.' (p. 448). The process of forest closure had proceeded to varying degrees in different parts of the islands, but was more or less complete by the end of the 1920s.

RELATIVE CONTRIBUTION OF BATS AND BIRDS TO THE FLORA OF KRAKATAU

> 'An obvious modification for dispersal may not predict the actual process' Howe & Smallwood (1982, p. 203).

As the adaptations of plants to bird- and bat-dispersal are commonly non-discriminatory (above), a definitive assessment of the roles of birds and bats in re-colonization is not feasible. Our best-estimates for the zoochorous flora up to and including our (unpublished) 1992 survey data are given in Table 5. The figures include some species for which recent records are lacking and which may therefore be extinct on the islands (cf. Whittaker *et al.*, 1989). We attribute the colonization of 124 species to endogenous transport by birds and/or bats. The small exochorous bird-

TABLE 5. Number of plant species found on Krakatau between 1886 and 1992, for which birds and bats have a dispersal role. The data set includes all four Krakatau islands and all records (i.e. including some species which have not maintained a presence). Evidence of dispersal is strong in some cases but largely inferential in others: these values are thus provisional.

Dispersal mode	No. species
Endochorous introduction (bird and/or bat)	124
Exochorous introduction (bird)	10
Human introduction, endochorous spread (bird and/or bat)	15
Sea-colonist, endochorous-spread	24
Total zoochorous introduction and/or spread	173
Of the 124 species introduced endogenously:	
Either bird or bat-colonist	43
Bird colonist, bat-spread	31
Bird-dispersal	50

carried element (ten species) is largely made up of grasses and composites, but may include one tree, *Alstonia scholaris*, which is, however, also wind-dispersed (cf. Ridley, 1930). Information concerning the distribution of colonizing populations has to a considerable extent enabled the separation of bird/bat colonists from human introductions and sea-transport, where otherwise ambiguity may have arisen (Docters van Leeuwen, 1936; Whittaker *et al.*, 1989; Partomihardjo *et al.*, 1992). In Table 5, the total zoochorous count of 173 species was derived by adding those species which have been (or are likely to be) spread by animals subsequent to colonization to those introduced by zoochorous means. It represents 42% of the total flowering plant flora.

Of the endozoochorous colonists of 1883–1934, only *Piper blumei* was identified by Docters van Leeuwen (1936) as probably introduced by bat- rather than bird-transport. This may have been an over-cautious estimate. On account of their small seeds and on the basis of evidence of bat-dispersal in a variety of studies (e.g. Marshall, 1985), other species of the 1883–1992 flora that are sensible candidates for colonization by bat-transport include: *Cyrtandra sulcata, Melastoma malabathricum, Piper aduncum, Pipturus argenteus, Solanum melongena, S. torvum, S. verbascifolium, Muntingia calabura*, and *Ficus* species. *Cyrtandra sulcata* was the first arboreal dominant of upland Rakata, forming in the early 1920s an almost monotypic stand above about 400 m ASL. It clearly attracted the first 'resident' fruit bats, *Cynopterus sphinx*, as its seeds and those of *Ficus* spp. were found in bat-splatters in the upper reaches of the island (Docters van Leeuwen, 1936). Its actual means of introduction is, however, uncertain since its seeds were also discovered in bird-droppings (loc. cit.). To date twenty-four species of *Ficus* have been confirmed from Krakatau, of which thirteen (*F. ampelas, F. benjamina, F. callosa, F. elastica, F. fistulosa, F. fulva, F. hispida, F. racemosa, F. retusa, F. ribes, F. septica, F. tinctoria* and *F. variegata*) have been shown to be spread by bats (Docters van Leeuwen, 1935, 1936; Pijl, 1957; Fujita, 1991). While some species may possess apparent adaptations to one agency, it is probable that most of the twenty-four *Ficus* species are in fact spread intestinally by both bats and birds. Indeed, Lambert (1989b) found in his study of Malaysian figs that some of the largest concentrations of feeding birds were actually associated with four 'bat-syndrome' species, each with dull coloured, cauliflorous figs. We are thus unable to produce a listing of zoochorous colonists which could *only* have been introduced by bats. However, from careful study of literature and herbarium material we identify a total of forty-three species which could reasonably be either bat or bird transported colonists (Table 5). This total includes a few erect herbs, twelve shrubs and twenty-five tree species. Over half of the forty-three species are figs, ranging from small shrubs such as *Ficus montana*, to large forest trees such as the stranglers *F. elastica* and *F. retusa*. Indeed, there are nine figs classed as large trees (defined here as >30 m at maturity), from only seventeen primarily zoochorous trees which typically reach this stature (see discussion). One interesting recent addition to the 'bird or bat' group is the exotic tree *Muntingia calabura* (planted in gardens in W. Java) discovered on Sertung in 1989 and known to be bat-spread.

There are a further thirty-one species which we have identified as almost certainly bird-introduced colonists which may be spread locally by bats (Table 5). Most of these species are relatively large-seeded and have probably been carried to the islands by one of the large *Ducula* species, for example: *Buchanania arborescens* (Anacardiaceae), *Canarium hirsutum* (Burseraceae), *Tricosanthes bracteata* (Cucurbitaceae), *Maranthes corymbosum* (Chrysobalanaceae), two *Bridelia* spp. (Euphorbiaceae), two *Dysoxylum* spp. (Meliaceae), *Melia azedarch* (Meliaceae), three *Calamus* spp. (Palmae/Aracaceae), *Erioglossum edule* (Sapindaceae), and *Lantana camara* (Verbenaceae). This is an ecologically diverse group, spread across nineteen families and includes small to large trees, rattans and other climbers. Moreover, it includes a few of the more abundant tree species, in particular *Dysoxylum gaudichaudianum, Buchanania arborescens* and *Bridelia monoica*. *D. gaudichaudianum* is one of the most important canopy trees, dominating large areas on Sertung and Panjang (Bush *et al.*, 1992). It is known to be spread by several bird species (Table 3) and, although direct evidence is lacking there is circumstantial evidence that it could also be bat-spread (Whittaker & Turner, 1994). Following disturbance of the Krakatau forests by volcanism in *c.* 1930–35 and 1952–53, *D. gaudichaudianum* and the bird-dispersed *Timonius compressicaulis* were the two species that spread most successfully into the damaged areas, achieving a remarkable dominance of the resulting low diversity canopies (Whittaker *et al.*, 1989; Bush *et al.*, 1992).

We have isolated fifty endozoochorous species for which there is as yet no evidence for bat involvement in dispersal. They include prostrate and climbing herbs, shrubs, lianes, and small, medium and large trees. Several of the members of this group are important constituents of the forests of Krakatau. There is some concentration in particular families within this list. Notable arboreal families in this category include: (i) five Euphorbiaceae, e.g. the once abundant early successional *Macaranga tanarius* and *Homolanthus populneus*; (ii) six Rubiaceae, e.g. *Tarenna* spp. and the abundant *Timonius compressicaulis*; (iii) three Urticaceae, notably *Leucosyke capitellata* and *Villebrunea rubescens* which have been significant understorey components for over 60 years; (iv) two Myristicaceae, the recently discovered *Knema cinerea* (large tree, found in 1989), and *Horsfieldia glabra* (unconfirmed, 1992); and (v) three Araliaceae, *Arthropyllum javanicum* (frequent in parts of lowland Rakata), *Polyscias nodosa* and *Schefflera polybotrya* (a characteristic component of the summit cloud forest on Rakata). Other species which are notable as widespread (but not canopy) components of the forests on each of the older islands are *Trema orientale* (Ulmaceae), *Leea sambucina* (Vitaceae) and *Ardisia humilis* (Myrsinaceae). The group also contains three species of trailing Cucurbitaceae and four trailing or climbing members of the Menispermaceae, plus several of the larger and more significant vine species: *Smilax zeylanica* (Smilacaceae), *Tetrastigma lanceolarium* (Vitaceae), and *Eleagnus latifolia* (Elaeagnaceae) (see also Bush, Whittaker & Partomihardjo, in press).

DIPLOCHOROUS SPECIES SPREAD BY ANIMALS

Many plant species have an established ability to disperse by two different dispersal modes, i.e. they are diplochorous (Ridley, 1930; Pijl, 1982). The commonest pattern of diplochory with respect to Krakatau is undoubtedly thalassochorous colonization (i.e. sea-transport), followed by establishment in the strand flora and subsequent spread of locally produced seed inland by animals (Table 4). In contrast to the zoochorous colonists, there is a clearly distinguishable bat-spread component. This subset is typified by *Terminalia catappa*, the fruit of which is a large dull-green drupe that is not dispersed (even locally) by birds.

The 'sea-colonist bat-spread' group (Table 4) are mostly trees and include no herbaceous plants. *Cycas rumphii* has never been recorded far inland and, on the older islands at least, *Pandanus tectorius* is also restricted to locations at or very close to the strand line. However, other species have commonly been found inland and two large trees, *Terminalia catappa* and *Calophyllum inophyllum*, are significant canopy species in the near-coastal forests. Both are found in lowland Rakata and along the central ridges of Panjang and Sertung. *Mucuna acuminata* was recorded up to 300 m altitude on Rakata by Docters van Leeuwen (1936), making it the highest ranging species of this set and the only Legume to penetrate any distance into the interior. In contrast, the sea-colonist and possibly bird-spread species include only two trees, *Sterculia foetida*, known from Panjang and Sertung and, *Adenanthera pavonica*, known from a single record from Sertung in 1982 (Table 4). Despite this group contributing much less to forest canopies, they all maintain populations to this day and can thus be judged successful colonists. Three species of the sea-colonist diplochorous set have not been recorded since 1934, the potentially bat-spread species *Erythrina fusca*, *Ochrasia oppositifolia* and *Spondias mombin*.

A further identifiable sub-set is those species which have been introduced to the islands by humans, but which can subsequently be spread endogenously by birds and/or bats. Of the fifteen species, three, *Cucurbita moschata*, *Phoenix* sp. and *Tamarindus indica* were discovered as individuals on Anak Krakatau as recently as 1989; and three, *Annona muricata*, *Cynometra cauliflora* and *Artocarpus heterophyllus* (Jak fruit) were discovered respectively in 1989, 1989 and 1992 near a well-used landing point on Rakata. None has yet had time to spread, and indeed *C. cauliflora*, which was found as a seedling in the camp-site area (Owl Bay) in 1989 (Whittaker *et al.*, 1992a), did not survive to 1992. *Durio zibethinus* and *Citrus* sp. were each known from only a single specimen in the 1920s. *Artocarpus altilis (incisa)* (Bread fruit) was planted on Sertung, but was killed in the eruptions of 1952. *Ananas comusus* and *Musa paradisiaca* have been introduced at least twice, but have not succeeded in spreading. In addition, some cultivars, e.g. of *A. comosus*, *Musa paradisiaca* and *Artocarpus altilis* are infertile. It therefore seems likely that failure to establish breeding populations rather than dispersal limitations *in situ* lies behind the failure of these species. Only three species can be judged to be long-term sucesses: *Mangifera indica*, a typical bat-fruit introduced c. 1916; *Capsicum frutescens*, which is presumed to be bird-spread; and *Gnetum gnemon*, which is the most successful in this group, having spread in northern Sertung and parts of Rakata and Panjang (presumably aided by birds), after first being found in association with a temporary settlement on Rakata in 1919 (Docters van Leeuwen, 1936).

ANEMOCHOROUS TREES OF THE INTERIOR

The significance of zoochorous or partially zoochorous trees can be underlined with reference to non-zoochorous trees of the interior forests, i.e. essentially the anemochorous species (Table 6). Krakatau forests contain very few such species despite there being numerous ferns and wind-dispersed herbaceous plants (mostly graminoids and orchids). Indeed, of the eight species listed in Table 6, one is a very uncertain record, and two could perhaps have been introduced by animals. *Alstonia scholaris*, a much earlier colonist than indicated by its first record (when found as large trees) is a possible candidate for exogenous transport by birds (above). *Neonauclea calycina* occurs on all four islands and has been the most important canopy tree on Rakata since the mid-1920s. We have previously assumed that it is solely wind-dispersed. However, there are records of bats feeding on fruit of members of the closely related genus *Nauclea* in both S.E. Asia (also birds) and Africa (Ridley, 1930; Marshall, 1985). The fruit of *Neonauclea calycina* is a globular capsule of about 0.8–1.0 cm diameter, with tiny seeds arranged on *c.* 1 cm long stalks around the outside. The fruits are dull brown and are borne at the end of shoots on the outside of the foliage. We speculate that, although primarily wind-dispersed, the fruit may perhaps be attractive to frugivores and in particular to bats. The seeds are certainly small enough to be swallowed if

TABLE 6. Anemochorous tree colonists of Krakatau, i.e. those species for which wind transport is thought to have been the means of initial colonization.

Species	Family	Years	Islands
Neonauclea calycina	Rubiaceae	1908–1992	RSPA (Sb)
Radermachera glandulosa	Bignoniaceae	1919–1992	RPA (Sb)
Vernonia arborea	Compositae	1922–1992	R (Sb)
Nauclea excelsa ??	Rubiaceae	1934	R
Alstonia scholaris	Apocynaceae	1979–1992	RS (Sb)
Bombax ceiba	Bombacaceae	1983	S
Crypteronia paniculata	Crypteroniaceae	1983–1992	R
Pterospermum javanicum	Sterculiaceae	1992	R (Sb)

The years given are the earliest and most recent records on Krakatau. Islands: R, Rakata; S, Sertung; P, Panjang; A, Anak; Sb, Sebesi in 1921 or 1989. The record for *N. excelsa* is very uncertain and it is perhaps best discounted. NB. *Crypteronia paniculata* was erroneously indicated to be zoochorous by Whittaker *et al.*, 1992a (Table 1).

taken into the mouth by a bat. The most recent addition to the anemochorous set is the large tree *Pterospermum javanicum* Jungh., found as a young specimen of 5 m height in 1992 (T. Partomihardjo, pers. comm.). The fruit of this species is described as gradually narrowed towards the base, slightly five-angular, 5–13 cm long, with the seed (including the wing) being 3–5 cm long and resembling that of the European sycamore (Corner, 1988). It thus has the appearance of a typical wind-scattered seed which, due to size, might be assumed to have effective dispersal over only short distances in normal weather conditions. Its arrival on Krakatau is thus notable. The source for this as for several other anemochorous species, may well have been Sebesi (Table 1)—despite the large-scale conversion of that island to plantation—as it was found there in 1921 (Docters van Leeuwen, 1923). *Crypteronia paniculata* is another large canopy tree which produces winged-seeds, at 2.5 mm long considerably smaller than those of *P. javanicum*: it is found in both mature and secondary forests throughout the region (Beusekom-Osinga, 1977). Although first recorded in 1983 we have observed scattered large specimens, indicating a far earlier colonization date.

In addition to the species in Table 6, other species may be wind-spread as a secondary means of dispersal. For instance, *Casuarina equisetifolia* and *Melochia umbellata* are both viewed as probable sea-colonist but wind-spread species, and in places *C. equisetifolia* has been a component in near-coastal forests and scattered further inland, especially on precipitous slopes.

BATS AND BIRDS AS POLLINATORS

In addition to dispersing plants, birds and bats may have other important roles that are critical to the long-term success of plant species, particularly as pollinators. As exemplars, bats are known to utilize pollen or nectar of the following sea-colonist Krakatau species: *Barringtonia asiatica*, *Cocos nucifera*, *Erythrina orientalis*, *Guettarda speciosa*, *Mucuna gigantea*, *Oroxylum indicum* (also wind-spread); and the following bird-colonist Krakatau species: *Freycinetia* sp. and *Trema orientale* (Ridley, 1930; Docters van Leeuwen, 1936; Marshall, 1983; Fujita, 1991; Cox *et al.*, 1992). Among Krakatau's birds, two species that may contribute significantly to the spread and regeneration of certain plants are the sunbirds *Aethopyga mystacalis* and *Anthreptes malacensis* (Nectarinidae). Both are nectar-feeders, typically utilizing small, orange or red, trumpet-flowers and acting as pollinating agents for species such as *Loranthus* (no Krakatau records), *Hibiscus* (*H. tiliaceus* the Krakatau species) and *Musa acuminata* (MacKinnon, 1988). A thorough assessment of the significance of birds and bats in pollination awaits further analysis (e.g. Bush, Whittaker & Partomihardjo, in press) but the existence of these relationships clearly carries implications for a wider role in ecosystem functioning than simply that of disperser (cf. Cox *et al.*, 1992; Elmqvist *et al.*, 1992).

DISCUSSION

The patterns established here, although site specific, may serve to inform discussion of the role of dispersers in forest maintenance and restoration. A distinction can be drawn between quality and quantity of dispersal (Marshall, 1983; after Janzen, 1971). Quality can be defined by the distance transported, the suitability of the site for escape from predation and for establishment and by the amount of damage done to the propagule by the disperser. For the successful introduction of a plant species to an isolated site, such as Krakatau, it may be necessary for a large number of seeds to be deposited. Many seeds must either fail to find the quality of site they require or, are predated; and even when establishment occurs, it must happen several times for an adequate population base to establish itself. Given which, the sequence of colonization and succession of forest on Krakatau constitutes exceptional evidence for the abilities of birds and bats to found new rain forest communities in isolated conditions. The early arboreal species of the interior were noted as almost exclusively animal-introduced or animal-spread species. The conversion of the majority of the land area to forest by the end of the 1920s is remarkably early considering the limited extent of forest species as of 1906–08, and the few bird and bat species recorded in the surveys of 1906–08 and 1919 (above).

In terms of species number, the figs have been the most successful genus, not only of the zoochorous sub-set, but of the entire flora, a reflection of the evolutionary investment in their dispersal system (cf. Marshall, 1983). Seventeen of the twenty-four species were present within 40 years of sterilization, when they constituted 63% of the true zoochorous tree flora, including all six large species (> 30 m at maturity) then present (Whittaker & Bush, 1993). Today they provide a canopy component within all major forest types identified by Whittaker *et al.* (1989) and in places the major canopy constituents, e.g. in the *Ficus pubinervis*/*Neonauclea calycina* stands of W. Rakata. In turn they almost certainly constitute in sum a critical resource for frugivorous birds and bats, with a highly significant role in the food webs of these forests (cf. Howe, 1984; Compton, Ross & Thornton, 1994).

The extent to which bats have been responsible for introductions to the group is unquantifiable. From our consideration of potential seed dispersal distances it seems parsimonius to assume that they have had a role, but only in respect to small seeded species. As an apparent instance of inter-island transport, Tidemann *et al.* (1990) working on Anak Krakatau in 1984 failed to notice any fruiting figs in the small woodland area, yet they netted *Cynopterus sphinx* which both regurgitated and defecated fig seeds. The flight behaviour of bats on Krakatau, as evidenced by a variety of observations, especially of droppings (Docters van Leeuwen, 1936; Tidemann *et al.*, 1990), appears to result in the scattering of significant quantities of small seeds in relatively open, even barren, habitats. Given the apparent success of predators in picking-off colonizing frugivorous pigeons on Anak Krakatau in the 1980s (Zann & Darjono, 1992) it may well be that night-flying bats are more significant in seeding open habitats than are day-flying birds (cf. Fenton & Fleming, 1976; Fujita & Tuttle, 1991; Gorchov *et al.*, 1993). It was also notable that the spread of at least one large-seeded tree, *Terminalia catappa*, into the interior of the older Krakatau islands correlated with the arrival of 'resident' bat populations (Pijl, 1957). Nonetheless, in the sense simply of the number of colonists contributed, birds have had the greater role, while at the outset they also appear to have founded 'resident' populations of dispersers, crucial for intra-island dispersal, in advance of the bats.

The first woodlands on Krakatau were those fringing the strand-lines, as the colonization of sea-dispersed species was a relatively swift process. They included several diplochorous species (e.g. *Calophyllum inophyllum*, *Terminalia catappa*, *Scaevola taccada*, *Cassytha filiformis*), which together with early colonizing figs and other zoochores, may have had a vital role in attracting birds and bats to the islands, thereby rapidly advancing colonization and spread of arboreal species. This general point has been made before (cf. Thornton, 1984; Whittaker *et al.*, 1989), but the particular significance of diplochorous species is worth highlighting. In terms of establishing and maintaining large populations, the most successful plants have almost by definition been early successional species, which in mainland situations might be expected to survive as mobile early successional players, e.g. *Neonauclea calycina*, *Macaranga tanarius*, *Ficus fulva*, *Timonius compressicaulis*. Their ability to maintain large populations into the future will presumably depend on the disturbance regime of the islands and to some extent on what other tree species can colonize (Bush *et al.*, 1992; Whittaker, Walden & Hill, 1992b). The majority of true zoochorous species on Krakatau are capable of being spread, at least locally, by both birds and bats, and in this sense have generalist strategies. Although distinctions may be drawn between members of the tree flora as to successional stage, with some fairly large trees having colonized, as a whole the flora remains characteristic of early successional forest (Whittaker *et al.*, 1992a). The islands remain deficient in large-seeded arboreal species dispersed by animals other than birds, i.e. including large-seeded bat dispersed species. For example, the Annonaceae is a family containing a number of bat-spread species which, with one human-introduced species of tree, is under-represented on Krakatau (cf. Bush, Whittaker & Partomihardjo, in press). There are also few species of large seeded, wind-scattered forest trees, which typify many mature forests in the region (Ashton, 1982; Howe & Smallwood, 1982); although we have yet to assess the degree of this deficiency in relation to a variety of nearby mainland sites (work in progress). Our surveys between 1979 and 1992 (with colleagues from Herbarium Bogoriense), have produced four large anemochorous tree species (Table 6), yet their diaspore sizes are not comparable with, for instance, those of the Dipterocarpaceae which dominate many forests canopies in Sumatra (see Ashton, 1982).

Forest diversification on Krakatau is clearly constrained by the isolation of the site and by the effective barring of terrestrial dispersal agents from a role as introducers of plant species. The limited data available on the role of particular bird and bat species as dispersers does not suggest a unique or irreplaceable role for any single animal (cf. Howe, 1984). However, we believe that the largest pigeons, *Ducula* spp. (Table 2), may be particularly significant in terms of both an ability to transport the largest-seeded of the zoochorous colonists and of their established inter-island mobility (cf. Ridley, 1930). Equally, the known mobility of populations of certain fruit bats, especially the large *Pteropus vampyrus*, points to a role in introducing small-seeded plants far greater than indicated by the exceedingly sparse survey data for bats. From our data, birds appear to disperse plants of a more balanced assortment of growth-forms than bats, but not all of the plant species which can be bat-spread. More tentatively, we raise the hypothesis that birds and bats differ in their tendencies to disperse seed into open habitats. We conclude that the roles of birds and bats as groups, although clearly overlapping, are in some important ways complementary.

On the basis of the above considerations we would support the views promulgated by Pannell (1989) and Cox *et al.* (1992) that maintenance and restoration of forest in the region can benefit by encouraging the activities of birds and bats, and indeed other dispersers and pollinators. On the basis of the empirical evidence from Krakatau, we postulate that the best way to rebuild a forest cover quickly might be to plant small pockets of fruit-bearing trees and shrubs within an area of degraded grassland, using species selected to attract a variety of different dispersal agents (see also Estrada, Coates-Estrada & Meritt, 1993; Gorchov *et al.* 1993; Guervara & Laborde, 1993). Such a policy could, in this regard at least, be a fairly cheap and simple solution, involving minimal infrastructure. However, implementation of such practices would raise numerous other practical and political problems. Fire management and other management practices may also be necessary, such as protection for populations of the dispersal agents themselves (Howe, 1984; Fujita & Tuttle, 1991). Finally, if high forest biodiversity is to be maintained, in many tropical regions it must be achieved within the framework of a fragmented forest system (Estrada *et al.*, 1993). This study, by demonstrating the significance of these animals in transporting seeds between sites, thus also supports their significance for population interchange between forest patches, while at the same time highlighting some of the constraints on effective population interchange which isolation confers.

ACKNOWLEDGMENTS

The funding for this project was provided by the ODA Forest Research Programme (R4739). Additional support for fieldwork in 1992 was provided by Earthwatch Europe. We thank all those who participated in and/or supported the 1992 expedition, in particular T. Partomihardjo, M. B. Bush, and our colleagues in Herbarium Bogoriense, LIPI and PHPA (Labuan). This is Krakatau Research Project Publication No. 42, and Royal Society South-East Asian Rain Forest Research Programme Publication No. A/088.

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ADDENDUM

From examination of seeds on Krakatau in 1994, *Oroxylum indicum* (Bignoniaceae) Rakata 1989–1993, which had not previously been included in the data discussed in this paper, should be added to the list of anemochorous trees (Table 6). In common with some of the other species in this category it must have colonized the island many years ago.