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Colonization of an island volcano, Long Island, Papua New Guinea, and an emergent island, Motmot, in its caldera lake. VI. The pioneer arthropod community of Motmot

John S. Edwards[1] and Ian W. B. Thornton[2] [1]*Department of Zoology, University of Washington, Seattle, WA 98195, USA, and* [2]*Department of Zoology, La Trobe University, Bundoora, 3083 Australia*

ABSTRACT

Aim To evaluate the arthropod community of Motmot in relation to primary colonization of young volcanic surfaces.

Location Motmot, an island in Lake Wisdom which occupies the caldera of Long Island, Papua New Guinea.

Methods Arthropod sampling by means of pitfall, water and tube traps, fallout collectors, and hand collecting.

Results At least thirty-five species of arthropod were collected in 6 days between 23 June and 3 July 1999. Lycosid spiders and ants dominated in all areas. The predator–scavenger arthropod population is largely or entirely dependent on allochthonous input of aquatic insects from the surrounding lake.

Main conclusions Major changes in the arthropod fauna since the pioneer surveys of Ball and his colleagues in the 1970s are the loss of a strand flotsam community as the island has eroded to form a predominantly cliffed coastline. Ant and spider diversity has increased. The current colonists include a number of widespread 'tramp' species *sensu* Diamond.

Keywords
Allochthonous arthropods, ants, arthropod colonists, organic fallout.

INTRODUCTION

The origin of communities is one of the most intriguing questions of ecology. How do pioneer plants and animals reach and become established on bare ground, and how are sustainable communities developed? Opportunities to study the natural assembly of communities *de novo* are rare. Long-term studies have been made of the recovery of communities following devastating volcanic eruptions (Thornton, 1996, 2000; Edwards, 2002) and of the origin and growth of biotas in two well known cases of the emergence of marine islands – Surtsey (Fridriksson, 1975) and Anak Krakatau (Thornton, 1996). Bassot & Ball (1972) and Ball & Glucksman (1975, 1981) made periodic studies on the pioneer biota of an emergent island, Motmot, in Long Island's freshwater caldera lake, Lake Wisdom. In 1999 we took the opportunity to extend the pioneer studies of Ball and his colleagues.

As a result of volcanic activity in Lake Wisdom between 1953 and 1955 an island emerged, which by 1982 had been reduced by wind and wave erosion to two small, low ash islets. Resumption of volcanic activity then formed the present island, Motmot (see Thornton, 2001), *c.* 600 sq.m. in area, with the summit *c.* 40 m above Lake Wisdom. Motmot is some 4–5 km from the nearest lake shore (Figs 1 and 2a).

The initial arthropod colonists of Motmot were monitored by Ball and colleagues (Bassot & Ball, 1972; Ball & Glucksman, 1975) (Table 1). In 1969 lycosid spiders were observed as well as odonates. In 1971 an earwig, two species of ant and an anthicid beetle were also present, as well as two species of chironomid Diptera. In the following years five more ant species were recorded together with several

Correspondence: John S. Edwards, Department of Zoology, University of Washington, Seattle WA 98105.
E-mail: hardsnow@u.washington.edu

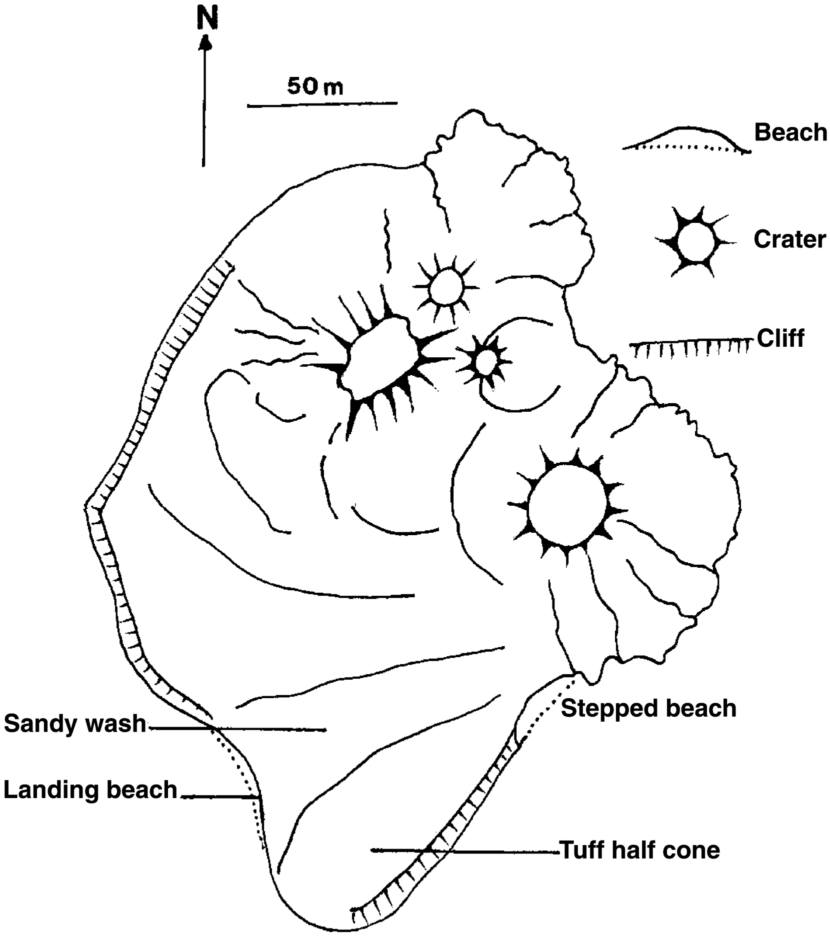

Figure 1 Sketch map of Motmot as of 1999.

more Diptera, an ephydrid shore fly, a muscid, a calliphorid and two more chironomids. Saldid bugs were present in strand debris and notonectids in the island's short-lived crater pond. Termites were seen flying on Motmot but they must have originated elsewhere.

Apart from the termites, and freshwater insects derived from the lake, the pioneer land arthropods – abundant lycosids and (later) earwigs, ants, and anthicid beetles – were scavengers and predators. As with other volcanoes (Thornton, 2000; Edwards, 2002), arthropods established populations long before the appearance of vegetation. In the absence of primary productivity these pioneer arthropods must have depended on imported organic material arriving at the site as flotsam and airborne fallout. A quarter of a century later, part of Motmot is sparsely vegetated but much of the volcanic surface remains bare. On these mineral surfaces arthropod populations typical of pioneer communities persist with relatively high biomass, based on allochthonous sources of organic input.

METHODS

We visited Motmot on 6 days between 23 June and 3 July 1999 (12 man-days collection) and spent one night on the island. Arthropods were sampled by passive and active collecting methods and rough estimates of numbers obtained.

Passive collecting was carried out using pitfall traps made from 7 cm diameter plastic cups containing water with detergent, crawl-in tube traps (Majer, 1978), and water traps (20 cm diameter white enamel dishes holding water with detergent and ringed with Vaseline). The warm wind rapidly dried water from the dish traps but the residual viscous

Figure 2 (a) Profile of Motmot from Lake Wisdom, looking east. The caldera wall of Long Island is visible above the low saddle mid right. (b) View toward the south ridge of Motmot from mid-island. A Zodiac boat is visible on the western shoreline of the sandy wash. (c) View to the north-east from the western margin of the sandy wash showing stable slopes with sedge vegetation in the middle distance, and *aa* beds beyond. (d) View of *aa* field looking east across Lake Wisdom to Long Island. (e) West coast of Motmot immediately north of the sandy wash showing shelving beach devoid of flotsam. (f) View to north-west showing summit crater with protected vegetation, and northern margin of Lake Wisdom. (g) Tetragnathid spider web on *aa* beds, with adult to left and immature to right. (h) Cyperus seed head covered with tetragnathid eggmasses embedded in silk. Coastline of Motmot.

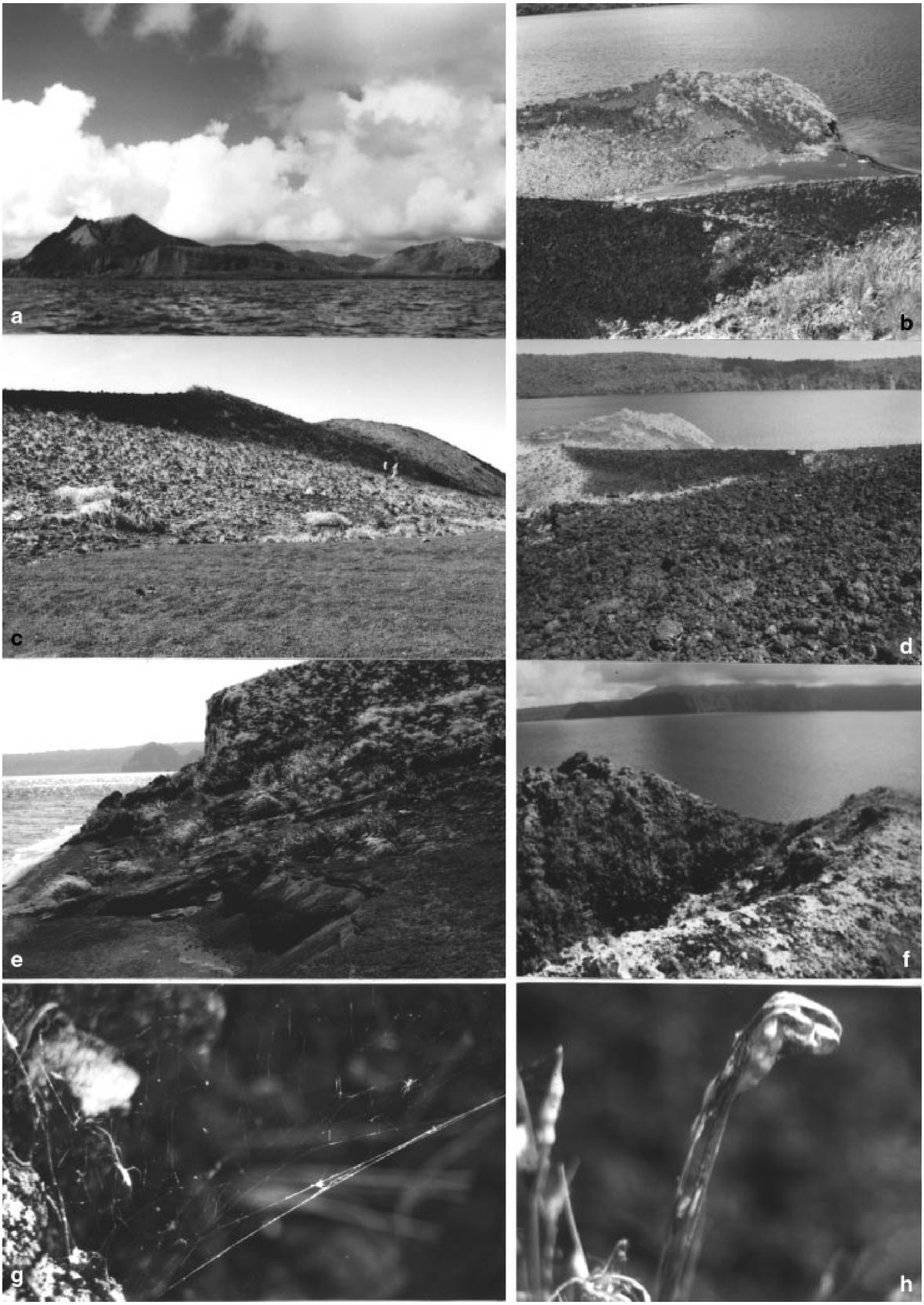
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Table 1 Arthropod records from Motmot based on records of Ball & Glucksman (1975) and the 1999 expedition

	1969	1971	1972	1999	
Arachnida					
Araneae					
Lycosidae					
?*Varacosa tanna* (Strand)*	x	x	x		
'*Trochosa*' *papakula* (Strand)*				x	
Tetragnathidae					
Tetragnatha mandibulata Walckenaer				x	
Tetragnatha nitens Audouin				x	
Salticidae One species indet.				x	
Araneidae					
Neoscona sp. indet.				x	
Pseudoscorpionida					
One species, indet.				x	
Insecta					
Odonata					
Xiphiagrion cyanomelas Selys	x			x	
Orthetrum sabina (Drury)				x	AK**
Pantala flavescens (Fabricius)				x	K, AK
Tramea liberata (Lieftinck)	x	x	x	x	
Orthoptera					
Gryllidae					
Teleogryllus oceanicus Le Guillou				x	
Acrididae					
Acridid, immature, sp. indet.				x	
Isoptera					
Nasutitermes novarum-hebridarum (Holmgren)			x		Mass flight
Dermaptera					
Labidura sp. indet.	x	x	x		AK
Labidura riparia (Pallas)				x	
Hemiptera					
Saldidae sp. indet.			x		Strand
Berytidae sp. indet.				x	
Coccidae sp. indet.				x	
Coleoptera					
Carabidae sp. indet.			x		Strand
Anthicidae					
Anthicus sp.		x		x	
Staphylinidae, sp. indet.		x			Strand
Tenebrionidae					
Gonocephalum sp.				x	
Coccinellidae 2 spp.				x	
Trichoptera					
Triplectides helvolus Morse & Neboiss				x	
Lepidoptera					
Hesperidae					
Parnara sp. indet.				x	
Sesiidae sp. indet				x	
Diptera					
Chironomidae					
Polypedilum sp. A		x	x		
Poypedilum sp. B			x		
Polypedilum nubifer (Sknse)				x	
Chironomus sp.		x	x	x	
Cryptochironomus griseidorsum Kieffer			x?		
Ablabesmyia hilli Freeman			x		
Ablabesmyia sp.				x	
Cricotopus sp.			x	x	
Metriocnema sp.			x?		
Dicrotendipes sp.			x?		

Table 1 *continued*

	1969	1971	1972	1999	
Cecidomyidae sp. indet.				x	
Ephydridae					
Hecomede persimils Hendel			x		Strand
Muscidae					
Musca vetustisima Walker			x		
Calliphoridae					
Lucilia papuensis Macq.			x		Flotsam
Hymenoptera					
Formicidae					
Paratrechina ?bourbonica (Forel)		x	x		
Paratrechina sp.				x	
Hyponeura ?biroi (Emery)		x			
Cardiocondyla ?nuda (Mayr)			x		
Cardiocondyla sp.				x	
Trachymesopus darwini (Forel)			x		Strand
Brachymyrmex sp.			x		Strand
Technomyrmex albipes (Fr. Smith)			x		Strand
Technomyrmex sp.			x	x	Alates only '99
Camponotus sp.			x	x	Alates only "99
Anoplolepis gracilipes (Smith)				x	K, AK
Tetramorium sp.				x	
?*Monomorium* sp.				x	
Pheidole sp.				x	

*The lycosid names *Varacosa tanna* and '*Trochosa*' *papakula* may denote the same species. '*Trochosa*' is used in quotes to denote provisional name, the entire Pacific lycosid fauna requiring re-evaluation (Cor Vink, pers. comm.).
**K signifies also found on Krakatau. AK signifies also found on Anak Krakatau.

detergent retained specimens. These traps were set out for 10 days on the 'sandy wash', a low flat saddle towards the south of the island (Fig. 1). Fallout collectors, modified from those used on Mount St Helens (Edwards, 1986, 1988), using a monolayer of cemented, grey-painted table tennis balls instead of golf balls, were also deployed on the slopes to the north of the sandy wash. Eight 0.1 m fallout collectors were exposed for 10 days on upper east-facing slopes during a period when light to moderate winds from the east predominated. A Malaise trap was set up and operated for 7 days on the upper bench of a stepped beach to the east of the saddle in order to sample material arriving from Lake Wisdom and Long Island some 5 km distant. An aerial insect net was set vertically against the prevailing wind at 1.5 m above ground on the north coast during one night to sample aquatic insects emerging from the lake. Arthropods were also collected from vegetation by beating, sweeping and netting. Undersides of rocks were hand searched. Visual estimates of the numbers of lycosid spiders were made by eye-shine spotlighting at night. An estimate of the numbers of insects in the lower 6 m of the air column was obtained by counting the numbers passing through a vertical headlight beam in a given time.

RESULTS

Four distinct habitats are recognized for the purposes of evaluating arthropod communities: 1. sandy wash saddle; 2. stabilized slopes to the north of the saddle; 3. open *aa* lava fields; and 4. sheltered vegetation, as in the summit crater 'ravine'.

Resident arthropods

Sandy wash (Fig. 2b,c)

A low flat saddle between the sharply rising south ridge (Fig. 2a) and the gentler slopes to the north was covered with sand and grit and devoid of vegetation except at the margins. During the entire period of the expedition moderate to strong winds from the east raked the saddle. Pitfall and tube traps were established in this area. Large numbers of a large lycosid spider '*Trochosa*' *papakula* (Strand) were taken in pitfall traps, together with some ants of two species *Anoplolepis gracilipes* (Smith), and a *Tetramorium* species, while tube traps took large numbers of *A. gracilipes*. A sense of the abundance of this ant comes from counts from tube traps set on the wash (Table 2).

The nest site/s of these ants was not found, but none of the tube traps was thought to be set close to a nest; visual estimates of ant density in the vicinity of the traps appeared to be typical of the entire wash area. A second ant, a *Tetramorium* species was present in small numbers together with *A. gracilipes*.

Both pitfall and tube traps took two species of Coleoptera, the tenebrionid *Gonocephalum* sp., a scavenger that was

Table 2 Tube trap captures of the ant *Anoplolepis gracilipes* on the sandy wash

25–27 June	
Tube no. 1	415
Tube no. 2	720
Tube no. 3	39
2–3 July	
Tube no. 1	1638
Tube no. 2	456
Tube no. 3	40

also taken in pitfalls on the western shore of Lake Wisdom, and an anthicid, *Anthicus* sp.

A fringe of *Cyperus* sedges on the south-western margin of the saddle supported a population of crickets (*Teleogryllus oceanicus* Le Guillou). One female tetragnathid spider *Tetragnatha mandibulata* Walckenaer, was taken during extensive sweep-netting of the sedges fringing the saddle. On neither the steeply shelving landing beach to the west, the 'stepped beach' to the east of the wash, nor on any other part of Motmot's coastline (e.g. Fig. 2e) was there stranded organic flotsam that might shelter arthropod assemblages.

Stable slopes to the north of the saddle (Fig. 2c,e)

The complex surface of this mid-region of the island was composed of exposed lava, and encrusted tephra bearing sparse but variable herbaceous vegetation, mainly sedges. Pitfall traps in this area took large numbers of the lycosid '*T*'. *papakula* and relatively small numbers of the ant *A. gracilipes*. A second species of tetragnathid spider on Motmot, *Tetragnatha nitens* Audouin, was prominent throughout this area, especially in association with vegetation, where silken egg batches were fixed to the tips of sedge leaves and orb webs were spun on the rocky surface (Fig. 2h). An araneid spider *Neoscona* sp. also occurred in low numbers on vegetation in this area. One early instar acridid nymph was taken in a fallout sampler, and numerous faecal pellets that appeared to be of acridid origin also accumulated in fallout collectors, but no live late instar or adult acridids were seen during our time on Motmot.

Open aa lava fields (Fig. 2b,d)

The substrate did not allow pitfall traps to be deployed in this area, but nocturnal observations of eyeshine from headlights indicated the presence of numerous '*T.' papakula.* Counts were made of the lycosids, using their conspicuous eyeshine, on *aa* surfaces overnight on 2–3 July. On scree slopes above the north-west shore, counts at 7.00 PM gave a mean spider density of 13.1/sq.m. ($n = 11$). The same area counted at midnight gave a mean of 13.0 ($n = 10$). Counts made on level *aa* lava nearby between midnight and 1 AM gave a mean of 5.5 spiders/sq.m. ($n = 10$). With a mean adult weight of *c.* 0.5 g the biomass of lycosids on the scree slopes thus amounted to *c.* 6.5 g/sq.m. While not as numerous as the lycosid, webs of the tetragnathid *T. nitens* were widespread and evident on all *aa* lava areas (Fig. 2g). Raised structures, especially dead trees and sedge stems, were festooned with web (Fig. 2h). Tetragnathids moved up into these raised sites at night and retreated to the ground at dawn.

Sheltered vegetation (Fig. 2f)

There was little evidence of overt phytophagous activity on foliage of trees and shrubs in sheltered localities such as the summit crater, or on trees and ferns in open unprotected areas along the shore of the island, but crickets were observed in the ravine, where their skeletonized remains, presumably the work of omnipresent scavenging ants, were found under rocks. Coccids were present on some fig trees and on stems of the prostrate creeper *Tylophora flexuosa* R. Br. together with black fungi associated with honeydew deposits. Ants (*A. gracilipes*) attended coccids on some figs, and on convolvulus. Sweep-net samples taken in the vegetation of the summit crater yielded two species of tetragnathids, *T. nitens,* and *T. mandibulata,* several immature specimens of one species of an ant-mimic salticid spider, an immature pseudoscorpion, two species of coccinellid, one corylophid beetle and an anthocorid bug.

Allochthonous arthropods

The three major potential sources of imported organic material to Motmot are adult aquatic insects from the lake, material carried on the wind from Long Island, and organic flotsam stranded on Motmot's shores. Steady winds from the east were characteristic of the entire period of our visit. Given the wind speeds (estimated to range between 2 and 10 m s^{-1} and the fauna of Motmot, it is unlikely that catches in the Malaise trap, other than worker ants and some spiders, were from Motmot itself. The catch from 23 to 27 June, for example is shown in Table 3.

The diversity of arrivals in this trap contrasts with comparable data for a Malaise trap set up during the same time interval on the margin of Lake Wisdom, where in addition to taxa taken on Motmot numerous muscoid, brachyceran and nematoceran Diptera, vespoids and parasitic Hymenoptera were taken. A tetragnathid spider, *Tetragnatha ceylonica* Cambridge, taken in the Lake Wisdom Malaise trap was not found on Motmot.

A second approach to the estimation of the arrival of allochthonous arthropods involved the use of water traps placed on *aa* lava surfaces in areas devoid of vegetation. Summed results from six plate water traps exposed for 7 days are as follows (Table 4):

Table 3 Malaise trap captures on Motmot 23–27 June 1999

Thirtyone worker ants (thirty *A. gracilipes,* one *Tetramorium* sp.)
Ten lycosids (immature, presumably '*T.' papakula*)
Ten chironomids (at least four spp., predominantly *Polypedilum nubifer*)
Five caddis fly (*Triplectides helvolus* Morse & Neboiss)
One damsel fly (*Xiphiagrion cyanomelas* Selys 1876)
One skipper (*Parnara* sp.)

Table 4 Summed captures of six plate water traps exposed for seven days 22–28 June 1999 on areas of lava devoid of vegetation on Motmot

Ninetythree chironomids
Fortyone worker ants (*A. gracilipes*)
Ten lycosids (immature and adult '*Trochosa*' *papakula*)
Three moths (one noctuid, two sessiids)
Three scoliid wasps
Three caddisfly (*Triplectides helvolus*)
Two muscoid Diptera
One berytid bug

In the dry fallout collectors plant fragments and seeds of composites amounting to 20 mg predominated in the fallout material, while arthropod fragments, including exuviae of lycosid and tetragnathid spiders, ant bodies and other unidentified cuticular fragments amounting to 3 mg, and one feather accumulated. No specimens attributable to import from Long island arrived in the fallout collectors during the relatively brief period of exposure.

Observations on aquatic insects on Motmot

Damselflies and chironomids were commonly noted in the webs of tetragnathid spiders, especially on the *aa* lava flows. At one site on the low cliffs on the north-west, large numbers of dragonflies, *Pantala flavescens* (Fabricius), had emerged, as evidenced by a count of 125 last instar nymphal exuviae in 1 sq. m of the surface of a low cliff about 1.5 m above lake level. Ants (*A. gracilipes*) were observed attacking the dragonflies during the moult to adult. Intersegmental membranes were lacerated and fluid taken from the wounds, ultimately leaving only the partially inflated, empty cuticle.

Adult caddisflies, *Triplectides helvolus* Morse & Neboiss, were rising in numbers from Lake Wisdom from just prior to dusk until at least 8.00 PM. They were present in all trap catches and were seen to be carried on shore by brisk winds.

Chironomids of at least four species dominated by *Polypedilum nubifer* (Skuse) and with one species each of the genera *Chironomus*, *Cricotopus*, and *Ablabesmyia*, were ubiquitous in trap catches and in spider webs. An insect net set to face the wind overnight on the north-west cliffs captured seventy four individuals, almost all of which entered the net between 5.30 and 9 AM, when dense swarms were evident elsewhere in sheltered sites. Counts of chironomids observed passing through a vertical headlight beam per minute at 8 PM were 14, 11 and 20. At 9 PM the counts were 4, 6 and 4, while at midnight the count was zero. Flight resumed immediately before dawn but ambient light levels rendered this counting method ineffective.

Coastline fauna (Fig. 2e)

As noted above, the shoreline during our visits was essentially devoid of littoral debris and thus of the fauna normally associated with this material. An earwig species, *Labidura riparia* (Pallas) was restricted in distribution to a small area at the shoreline on the west (windward) coast under wet rocks and an ant, *Pheidole* sp. was taken locally on the west coast shoreline.

Comparison of ant diversity on Motmot and adjacent Long Island

The diversity of the ant fauna of Motmot and the adjacent Long Island shore of Lake Wisdom is shown in Table 5.

DISCUSSION

Trophic relationships

Despite the passage of several decades and the emergence of scattered vegetation on Motmot (Harrison *et al.,* 2001), the arthropod fauna remains essentially a primary colonist, early successional one, although now with greater diversity (Table 1). Like those of the blast zone of Mount St Helens (Edwards & Sugg, 1993; Sugg & Edwards, 1998), barren ash and lava areas on Anak Krakatau (New & Thornton, 1988; Thornton *et al.,* 1988) and young pahoehoe lava flows on the island of Hawaii (Howarth, 1979), the Motmot arthropod fauna is dependent on allochthonous input and largely independent of primary productivity. The major resource during the period of our study was the chironomid

Table 5 Comparison of 1999 ant fauna on Motmot and on adjoining western lakeside fringe of Lake Wisdom, Long Island

	Motmot	Long Island
Anoplolepis gracilipes (F. Smith)	w, (?qa)	
Camponotus quadriceps (F. Smith)	qa	w, qa
Camponotus novaehollandiae Mayr, s.lat		w
Cardiocondyla minutior Forel	w, qd	w
Iridomyrmex sp. (*anceps* group)	w	w
Monomorium sp.A	w	
Odontomachus simillimus (F. Smith)		w
Paratrechina sp.A	w	w
Pheidole sp.A	w, s	w
Polyrhachis (*Chariomyrma*) gab Forel		w
Polyrhachis (*Hedomyrma*) sp		w
Polyrhachis (*Cyrtomyrma*) sp.		w
Rhytidiponera araneoides (Le Guillou)		w
Tetramorium sp.A	w, qd	w
Tetramorium sp.B		w
Turneria dahlii Forel		w
Worker species diversity	7	14
A. gracilipes	m	m
Camponotus sp.	qa	qa
Formicinae sp.		m
Leptogenys sp.A.		m
Technomyrmex albipes (F. Smith)	aq	
Turneria dahlii		qa
Total species diversity	11	19

a: alate; d: dealate; m: male; q: queen; s: soldier; w: worker.
Workers, implying established resident colonies, are listed first in alphabetical order. Alates follow.

P. nubifer, with the caddis *T. helvolus* probably second in biomass, both of them derived from the surrounding lake.

At present the food chains on Motmot are short. The top arthropod with the highest biomass, a lycosid spider, is nocturnally active and thus not exposed to bird predation. It is surprising that no reptile which might exploit this potentially rich resource, e.g. a geckonid, has yet become established on Motmot. The rufous night heron, *Nyctycorax caledonicus* (Gmelin) a crepuscular and night feeder on arthropods, was seen by us on Motmot in 1999. This heron's feeding range surely extends beyond Motmot, but it is possible that it takes Motmot lycosids. In contrast to the lycosid, the large tetragnathid spiders are conspicuous by day and are seemingly open to bird predation, but no such behaviour was observed during our time on the island.

Sources of the arthropod community

Most members of Motmot's arthropod community are opportunistic species with wide tropical distributions. Although the necessary distributional data for the Bismarks are not available, the species have characteristics indicating that they are the arthropod analogues of Diamond's high class tramp species (Diamond, 1974, 1975).

The dragonfly *P. flavescens* is a circumtropical, strongly flying and wide ranging libellulid, a fugitive species that colonizes rain pools throughout the tropics (D. Paulson, pers. comm.). This species has great powers of over sea dispersal. It has reached oceanic islands (e.g. Cocos-Keeling, Easter, Hawaii and Canton Islands) that are at least 1000 km from the nearest land (van Zwaluwenberg, 1942). Mass flights 480 km from land over the Indian Ocean have been reported and it was one of the early arrivals on Krakatau, after the eruption (Dammerman, 1948).

The anthicid beetle found in 1999 is probably the same species, *Anthicus oceanicus* Laf., found on many islands under washed-up seaweed, and is probably a scavenger. *Anthicus oceanicus* was present on Krakatau by 1921, 38 years after the eruption, and was on the beach of Anak Krakatau when the island was first visited 6 months after its emergence (Bristowe, 1931; Reimoser, 1934).

The carnivorous earwig *Labidura riparia* (Pallas) is common on marine shorelines and to a lesser extent on sandy river strands around the world (Fabian Haas, pers. comm.). It does not fly and presumably reached both Long Island and Motmot by rafting. *Labidura* earwigs had been noted as conspicuous members of the early colonist fauna but in 1971 they were found only under rocks near the beach. In the following year the earwig was almost ubiquitous but by 1976 its numbers had again fallen and it occupied a much reduced area (Ball & Glucksman, 1975, 1981). In 1999 *L. riparia* was very rare and localized; despite extensive search the species was found at only one site in the littoral under damp stones on the westernmost point of the island, a site likeliest to receive rafted materials from the windward rim of Lake Wisdom. The absence of shoreline accumulations of organic material on any of the shelving beaches on Motmot means that a prime habitat for Dermaptera, and other scavenging arthropods was absent. Observations on earwig density on five occasions since Motmot's origin may indicate wide population fluctuations of an opportunistic species dependent on the availability of stranded organic material. Alternatively, earwig distribution on Motmot now may reflect outcompetition by ants and the specimens we found may have represented a periodically replaced meta-population. The cricket *Teleogryllus oceanicus*, which was not previously observed on Motmot but which now occurs throughout vegetated areas is widely distributed throughout Australia and the Pacific.

The lycosid spider *'T.' papakula*, previously referred to as *Varacosa papakula*, as in Ball & Glucksman (1975), is part of an undescribed genus found throughout the Pacific (Cor Vink, pers. comm.). *'Trochosa' papakula* is a widespread species known from the Moluccas and Aru Island in Indonesia, and elsewhere in New Guinea. Lycosid spiders were also part of the pioneer fauna of Anak Krakatau (New & Thornton, 1988) and pahoehoe lava flows on the island of Hawaii (Howarth, 1979), but were not found on the historical lava fields in the Canary Islands (Ashmole & Ashmole, 1988). In the biotic recovery of the blast zone on Mount St Helens after the 1980 eruption, lycosids were the first spider colonists of barren sites (Crawford *et al.,* 1995). Two species of tetragnathid spider occur on Motmot and a third, *T. ceylonica* Cambridge, was taken on Long Island. Two species of this genus were taken by the first spider specialist to visit Krakatau after the eruption (Bristowe, 1931; Reimoser, 1934). Long distance dispersal of *Tetragnatha* juveniles is well established, 101 of 105 spiders collected 400 km from land in tow nets in the East China Sea were of this genus (Okuma & Kisimoto, 1981).

The caddis *T. helvolus* is a northern Australian species and has not previously been recorded from the New Guinea region (W. Mey, pers. comm.). The skipper butterfly *Parnara* sp. belongs to a speciose genus, which includes active migrants that are widespread pests of sugarcane and rice fields; at least one species is known to have mass long-distance flights. One of the chironomids, *Cryptochironomus griseodozum*, is also a denizen of rice fields. The most numerous chironomid during our visit, *Polypedium nubifer,* is a very widely distributed species known from the Mediterranean region to mid-Australia, and is a nuisance species in Australia and Hawaii.

The history of ant colonization on Motmot is rendered somewhat problematic by the uncertainty of nomenclature, but a clear trend is evident (Table 5). In 1969 no ants were observed; in 1971 two species were recorded, and five more species were found later in the same decade. In 1999 we found seven colonist species, based on the presence of workers, only one of which had been recorded earlier, with four potential immigrants, based on the capture of alates only. In contrast, twelve resident species of worker ant and four as alates only were taken on Long Island close to the shoreline of Lake Wisdom.

Motmot's commonest ant in 1999 had not been observed previously on the island but had become dominant by the time of our visit. *Anoplolepis gracilipes* (formerly *A. longipes*) is widely spread by human activity in tropical areas of

Africa, Asia and the Australian region, but in continental Australia it has been found only on the coast of the Gove Peninsula, Northern Territory (Shattuck, 1999). It nests primarily in soil but may be arboreal. It is a general predator on a wide range of arthropods and is known to tend homopterans for honeydew. In some situations it has invaded dwellings and become a pest of domestic animals, but in others is regarded as beneficial and actively encouraged, having been recommended as part of integrated pest management programmes (Shattuck, 1999). Greenslade (1971) observed that when *A. gracilipes* flourished in coconut plantations in the Solomon Islands, species diversity declined sharply, but when *A. gracilipes* declined diversity increased. It may be that the low arthropod species diversity on Motmot is at least in part because of the dominance of *A. gracilipes*. This species was the most widely spread and abundant ant on the Krakatau Islands when the first zoologists visited them in 1908, 25 years after the eruption (Jacobson, 1909).

We found no carabid beetles on Motmot despite extensive searching. Only one carabid specimen was taken on Motmot in 1972 (Ball & Glucksman, 1975). Nor were carabids important in the early community on Anak Krakatau. It is notable that carabids, which play important pioneer roles in cold temperate regions (e.g. Edwards, 2001), do not occupy this niche in the tropics.

In conclusion, the present arthropod fauna of Motmot, like that of other young tropical islands, is composed largely of widely distributed species which are the arthropod analogues of Diamond's 'tramp species'.

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REFERENCES

Ashmole, M.J. & Ashmole, N.P. (1988) Arthropod communities supported by biological fallout on recent lava flows in the Canary Islands. *Entomologia Scandinavica*, **332** (Suppl.), 67–88.

Ball, E.E. & Glucksman, J. (1975) Biological colonisation of Motmot, a recently created tropical island. *Proceedings of the Royal Society of London, Series B*, **190**, 421–442.

Ball, E.E. & Glucksman, J. (1981) Biological colonization of a newly created volcanic island and limnological studies on New Guinea lakes, 1972–78. *National Geographic Society Research Reports*, **13**, 89–97.

Bassot, J.M. & Ball, E.E. (1972) Biological colonization of recently created islands in Lake Wisdom, Long Island, Papua New Guinea, with observations on the fauna of the lake. *Proceedings of the Papua New Guinea Science Society*, **23**, 26–35.

Bristowe, W.S. (1931) A preliminary note on the spiders of Krakatau. *Proceedings of the Zoological Society of London*, **1931**, 1387–1400.

Crawford, R.L., Sugg, P.M. & Edwards, J.S. (1995) Spider arrival and primary establishment on terrain depopulated by volcanic eruption at Mount St Helens, Washington. *American Midland Naturalist*, **133**, 60–75.

Dammerman, K.W. (1948) The fauna of Krakatau 1883–1933. *Koniklije Nederlandsche Akademie Van Wetenschappen, Afdeling Natuurkunde*, **II**, 1–594.

Diamond, J.M. (1974) Colonization of exploded volcanic islands by birds: the supertramp strategy. *Science*, **184**, 803–806.

Diamond, J.M. (1975) Assembly of species communities. *Ecology and evolution of communities* (eds M.L. Cody and J.M. Diamond), pp. 342–444. Harvard University Press, Boston, MA, USA.

Edwards, J.S. (1986) Derelicts of dispersal: arthropod fallout on Pacific Northwest volcanoes. *Insect flight: dispersal and migration* (ed. W. Danthanarayana), pp. 196–203. Springer Verlag, New York.

Edwards, J.S. (1988) Life in the allobiosphere. *Trends in Ecology and Evolution*, **3**, 111–114.

Edwards, J.S. (2002) Animals and volcanoes: survival and revival. *Volcanoes and the environment* (eds J. Marti and G.L. Ernst). Cambridge University Press, Cambridge, UK (in press).

Edwards, J.S. & Sugg, P.M. (1993) Arthropod fallout as a resource in the colonization of Mount St Helens. *Ecology*, **74**, 954–958.

Fridriksson, S. (1975) *Surtsey. Evolution of life on a volcanic island*. Butterworths, London.

Greenslade, P.J.M. (1971) Interspecific competition and frequency changes among ants in Solomon Islands coconut plantations. *Journal of Applied Ecology*, **8**, 323–352.

Harrison, R.D., Yamuna, R. & Thornton, I.W.B. (2001) Colonization of an island volcano, Long Island, Papua New Guinea, and an emergent island, Motmot, in its caldera lake. II. The vascular flora. *Journal of Biogeography*, **28**, 1311–1337.

Howarth, F.G. (1979) Neogeoaeolian habitats on new lava flows on Hawaii Island: an ecosystem supported by windborne debris. *Pacific Insects*, **20**, 133–144.

Jacobson, E.R. (1909) Die nieuwe fauna van Krakatau. *Jaarslag Van Den Topographischen Dienst in Nederlandsch-Indie*, **4**, 192–262.

Majer, J.D. (1978) An improved pitfall trap for sampling ants and other epigaeic invertebrates. *Journal of the Australian Entomological Society*, **17**, 261–262.

New, T.R. & Thornton, I.W.B. (1988) A pre-vegetation population of crickets subsisting on allochthonous aeolian debris on Anak Krakatau. *Philosophical Transactions of the Royal Society of London, Series B*, **322**, 481–485.

Okuma, D. & Kisimoto, R. (1981) Air borne spiders collected over the east China sea. *Japanese Journal of Applied Entomology and Zoology*, **25**, 296–298.

Reimoser, E. (1934) The spiders of Krakatau. With introductory notes by W.S. Bristowe. *Proceedings of the Zoological Society of London*, **1934**, 11–18.

Shattuck, S.O. (1999) *Australian ants: their biology and identification*. CSIRO Publishing, Australia.

Sugg, P.M. & Edwards, J.S. (1998) Pioneer aeolian community development on pyroclastic flows after the eruption of Mount St Helens. *Arctic and Alpine Research*, **30**, 400–407.

Thornton, I.W.B. (1996) *Krakatau. The destruction and re-assembly of an island ecosystem*. Harvard University Press, Boston, MA.

Thornton, I.W.B. (2000) The ecology of volcanoes: recovery and reassembly of living communities. *Encyclopedia of volcanoes* (ed. H. Sigurdsson), pp. 1057–1081. Academic Press, NY.

Thornton, I.W.B. (2001) Colonization of an island volcano, Long Island, Papua New Guinea, and an emergent island, Motmot, in its caldera lake. I. General introduction. *Journal of Biogeography*, **28**, 1299–1310.

Thornton, I.W.B., New, T.R., McLaren, D.A., Sudarman, H.K. & Vaughan, P.J. (1988) Airborne arthropod fall-out on Anak Krakatau and a possible pre-vegetation pioneer community. *Philosophical Transactions of the Royal Society of London Series B*, **322**, 471–479.

van Zwaluwenberg, R.H. (1942) Notes on the temporary establishment of insect and plant species on Canton island. *Hawaii Planters' Record*, **46**, 49–52.

BIOSKETCHES

John S. Edwards is Professor of Zoology Emeritus at the University of Washington, Seattle, USA. His research interests have been divided between neural development and regeneration in insects, and the ecology of arthropods in alpine and volcanic habitats.

Ian W. B. Thornton is Professor Emeritus in Zoology at La Trobe University, Melbourne, Australia. His research interests are in the assembly of communities on pristine isolates. Over a period of two decades he has worked on aspects of colonization on the Krakatau Islands, Indonesia, and is leader of the Long Island research team. Studies of the recolonization of Mount St. Helens, Washington State, after the 1980 eruption by Edwards' group, and on the colonization of Anak Krakatau by Thornton's group, have shown the importance of wind-borne allochthonous arthropods in primary colonization and in nutrient transport.