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A Preliminary Appraisal of the Braconid (Hymenoptera) Fauna of the Krakatau Islands, Indonesia, in 1984–1986, with Comments on the Colonizing Abilities of Parasitoid Modes

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Abstract One hundred and two species of Braconidae, comprising 15 subfamilies, were collected on the four Krakatau Islands in Sunda Strait, Indonesia, in general surveys made in 1984, 1985 and 1986, about a century after the devastating 1883 eruption. The braconid fauna of Anak Krakatau, which emerged from the submarine caldera of Krakatau in 1930 and suffered a self-devastating eruption in 1952, was distinct from that of the three older islands, whose biota dates from the 1883 eruption. Anak Krakatau's braconid fauna, evidently like that of the older islands between 1908 and 1933, was heavily biased towards koinobiont endoparasitoids of Lepidoptera, mostly of the braconid subfamilies Cheloninae, Microgastrinae and Rogadinae. In contrast, not one koinobiont endoparasitoid of the cyclorrhaphous Diptera, Coleoptera or Hemiptera was collected on Anak Krakatau, although 31 such species were collected on the three older islands. The differences between parasitoid modes that relate to colonizing ability are briefly considered and discussed.

Key words: Braconidae; Krakatau; recolonization; parasitoid community; tropical forest.

Introduction

The Krakatau Islands, in Sunda Strait, Indonesia, are about 44 kilometres from both the large islands Java and Sumatra, and some 12 kilometres from the nearest island in the strait, Sebesi. The biotas of the three peripheral islands of the group, Rakata (1,152 ha in area), Sertung (784 ha) and Panjang (272 ha) are believed to have been destroyed in the devastating 1883 eruption of the island of Krakatau, of which Rakata is the southern remnant (Fig. 1). These islands are thus about a century old biologically, although the subsequent development of new biotas on Sertung and Panjang has been affected by the continuing volcanic activity of Anak

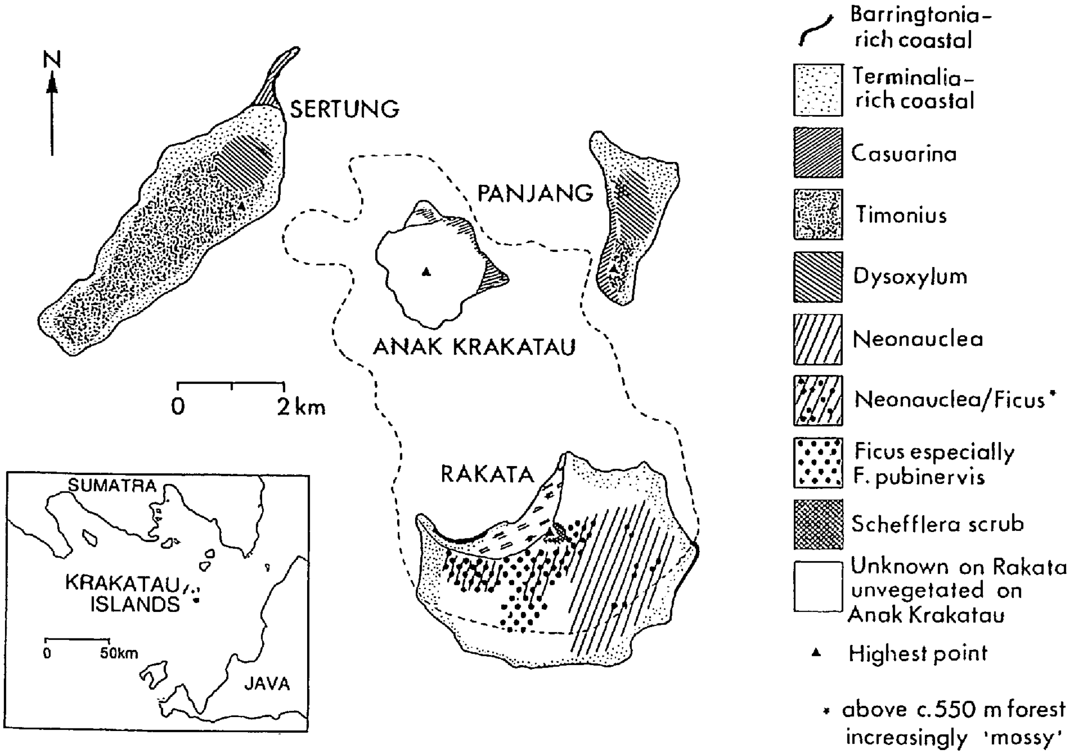

Fig. 1. The Krakatau Islands, showing major vegetation types, in 1984–1986. Dashed line indicates Krakatau Island prior to August 27th 1883. Modified from WHITTAKER *et al.*, 1989.

Krakatau; the reassembly of a biota on Rakata has been only slightly constrained, if at all, by this activity. Anak Krakatau emerged from Krakatau's submarine caldera in 1930, suffered self-devastating eruptions in 1952/1953 and erupts at intervals of about 4–5 years, the most recent eruption being in November 1992. The island is some 280 ha in area and 200 m high, although in the period 1984–1988 only about 17 ha had a cover of vegetation, the remainder being almost barren ash and lava fields.

In the period 1984–1986 Anak Krakatau's vegetation consisted of grasslands, *Saccharum*, *Imperata* and *Ischaemum*, and woodlands of the pioneer tree *Casuarina equisetifolia*, within which a few early successional forest trees such as *Ficus fulva* and *Ficus septica* had become established. In 1983 some 66 species of vascular plants were recorded on the island and in 1989 the total had increased to 94 species (PARTOMIHARDJO *et al.*, 1992). In contrast, the interior of Rakata was covered with mixed secondary forest dominated by *Neonauclea calycina* and species of *Ficus*, and the forests of Sertung and Panjang were dominated mainly by *Timonius compressicaulis* or *Dysoxylum gaudichaudianum* (TAGAWA *et al.*, 1985; WHITTAKER *et al.*, 1989). Well over 200 species of vascular plants were present on Rakata in the period 1984–1986 (BUSH & WHITTAKER, 1991).

The great majority of braconids comprises primary parasitoids of other insects, mainly immature endopterygotes. Of the insect groups for which collections have been worked up, THORNTON and NEW (1988) reported that about one third of the fauna of the archipelago was present on Anak Krakatau. Of those groups that include hosts of the archipelago's braconid fauna, Anak Krakatau carried 23 of the archipelago's 54 species of butterflies, 10 of the archipelago's 39 species of the seven dipteran families that had been reported upon by specialists, and 3 of the 16 species of Hemiptera found on the archipelago by YUKAWA and YAMANE (1985). Thus, of the known representatives of the orders of insects parasitised by the braconids reported upon here, Anak Krakatau carried about 33% of the archipelago's known fauna.

In this paper a preliminary determination is provided, by the first author, of the braconids collected in the period 1984–1986 on zoological expeditions (THORNTON & ROSENGREN, 1988) of La Trobe University and the Bogor Zoology Museum (a section of L.I.P.I.) led by the second author. The known braconid fauna of Anak Krakatau, which in 1984 was no more than about three decades old biologically, is compared to that of the three older islands of the archipelago, whose biological age was about 100 years. The relative success of braconids of various parasitoid modes in colonizing the young ecosystem developing on Anak Krakatau is considered and discussed.

Methods

Braconids were collected on the islands in the course of general zoological surveys (THORNTON & ROSENGREN, 1988) carried out in September 1984, August 1985 and September 1986, and were mostly acquired by sweeping, beating, and the use of MALAISE traps and light traps. One species was collected in a pitfall trap only (one specimen) and one species in a fruit-bait trap (two specimens) as well as in a light trap (Table 1).

The intensity of collecting on the various islands by these methods was somewhat uneven during the surveys (Table 1), MALAISE traps and light traps being employed almost exclusively on Rakata and Anak Krakatau. These two islands also received the most attention by sweeping and beating, which was carried out roughly according to island area except that the very small vegetated area of Anak Krakatau meant that intensity of sweeping and beating was greatest on this island. Although 24 days of the MALAISE trapping on Anak Krakatau were either on the barren western lava fields, the active crater, or the barren outer rim, traps were set in vegetation for a total of 28 days, comparable to the 33 days of MALAISE trapping on Rakata.

Since there are no reliable taxonomic revisions for most Oriental Region braconid genera, most of the determinations are to generic level only, with recognition often to morphospecies. The species totals may thus require correction in the

Table 1. Relative extent of sweeping and beating (S, in collector-hours), MALAISE trapping (M, 24-hours periods) and light trapping (L, evenings) on the Krakatau islands during the 1984, 1985 and 1986 expeditions, with the number of individuals and species of braconids collected by these methods. Species collected are not additive, several species being collected by more than one method; one species included in the right hand column was collected only in a pit-fall trap on Anak Krakatau. ( )=vegetated area.

Island	Area (km^2)	Height (m)	Collecting extent			Individuals			Species			Total species
			S	M	L	S	M	L	S	M	L	
Rakata	11.5	800	97	33	17	58	23	5	37	7	5	47
Sertung	7.8	182	34	2	1	57	2	0	36	2	0	37
Panjang	2.7	142	38	0	1	75	0	0	36	0	0	36
Anak Krakatau	2.8 (0.2)	200	44	52	7	21	58	18	10	8	3	18
Total all islands			213	87	26	211	83	23	88	15	8	102

future, although any such change is likely to be small and unlikely to affect the main conclusions offered here. A series of voucher specimens will be deposited in the Bogor Zoology Museum, Indonesia, and a parallel series will be deposited in the National Institute of Agro-Environmental Sciences, Tsukuba, Japan.

Results

A total of 102 recognisable braconid species, of 15 subfamilies, was found in the collection of 211 specimens (Table 2).

The division of parasitoids into idiobionts and koinobionts was suggested by HAESELBARTH (1979) and supported by ASKEW and SHAW (1986). Idiobionts are mainly ectoparasitoids and kill or paralyse the host when they oviposit, preventing further movement or development. Koinobionts, most of which are endoparasitoids, allow the host to develop, feed and move, often regulating its development. The species collected on the Krakataus were placed into idiobiont ectoparasitoid and koinobiont endoparasitoid categories according to their usual host insects (Table 2), following, for example, QUICKE and VAN ACHTERBERG (1990). Five groups resulted, and are indicated by letter codes opposite subfamilies and species in Table 2.

The extent of faunal overlap between pairs of islands is illustrated in Fig. 2. Similarity between individual island faunas was measured by using both the SORENSEN and NOMURA-SIMPSON coefficients of similarity; these are shown in Table 3.

Apart from the rather low NOMURA-SIMPSON coefficient for the Rakata-Panjang comparison, both coefficients are generally lower for comparisons involving Anak

Table 2. Braconidae collected on the various Krakatau Islands, 1983–1986 with their parasitoid category*. Abbreviations: KCH, KD and KL — koinobionts of Coleoptera or Hemiptera; cyclorrhaphous Diptera; and Lepidoptera; respecively. ICLD and IL — idiobionts of Coleoptera, Lepidoptera or, rarely, Diptera; and of Lepidoptera; respectively. Anak K. — Anak Krakatau.

Parasitoid mode	Subfamily-Species	Rakata	Sertung	Panjang	Anak K.
	Doryctinae				
	Allorhogas pallidiceps (PERKINS)		1♀		
	Doryctes sp. 1		1♀		
	Doryctes sp. 2		1♂	2♂	
	Ecphylus sp.	2♀	5♀	1♀ 1♂	
	Heterospilus sp. 1		1♀		
	Heterospilus sp. 2		(1♀)		
	Heterospilus sp. 3	1♂			
ICLD	*Rhaconotus signipennis* (WALKER)	2♀ 2♂	3♀ 5♂	8♀ 10♂	
	Rhaconotus sp. (nr. *testaceus* (SZÉPL.))	3♀ 4♂	2♂		3♀ 1♂
	Spathius capys NIXON			3♀	
	Spathius psammathe NIXON			1♀	
	Spathius sp. 1 (nr. *bion* NIXON)	1♀	2♀(1♀)		
	Spathius sp. 2			1♀ 2♂	
	Spathius sp. 3			1♀	
	Spathius sp. 4 (nr. *dolon* NIXON)			1♀	
	Gen. sp. (Doryctini)		1♂	1♂	
	Braconinae				
KL	*Aspidobracon noyesi* VAN ACHTERBERG	(1♀)			
ICLD	*Bracon* sp. 1		1♀		
ICLD	*Bracon* sp. 2 (nr. *asphondyliae* (WATANABE))	1♀ 1♂	1♀ 2♂		
ICLD	*Bracon* sp. 3			1♀	
ICLD	*Bracon* sp. 4	1♂			3♂
ICLD	*Campyloneurus* sp.			1♀	
ICLD	*Esengoides* sp. 1 (nr. *fulvus* QUICKE)	1♀			
ICLD	*Esengoides* sp. 2		1♀	1♀	
ICLD	*Spinadesha* sp.		2♂		
IL	*Tropobracon shoenobii* (VIERECK)	1♀			
ILLD	Gen. sp. (Braconini)			1♂	
	Exothecinae				
	Acanthormius? *iriomotensis* WATANABE	1♀			
	Acanthormius sp.	2♀			
	Aulosaphes psychidivorus NIXON	[1♀]			
	Aulosaphes? *unicolor* (ASHMEAD)			2♀	
	Aulosaphes sp.			1♀	
IL	*Hormius* sp. 1		1♂		
	Hormius sp. 2				[1♂]
	Hormius sp. 3		1♂		
	Parahormius sp. 1	2♀			
	Parahormius sp. 2				3♂
	Parahormius sp. 3	[1♂]			

Table 2. (Continued.)

Parasitoid mode	Subfamily-Species	Rakata	Sertung	Panjang	Anak K.
	Rogadinae				
	Aleiodes sp. 1			1♀	1♀ [1♀ 14♂]
	Aleiodes sp. 2	1♀[1♀]			
KL	*Aleiodes* sp. 3				1♂
	Aleiodes sp. 4				{1♀}
	Clinocentrus sp.	(2♀)			
	Opiinae				
	Bitomus hemicoriaceus (FISCHER)		1♂	1♀	
	Opius tamurensis Fischer	1♀			
	Opius sp. 1 (nr. *fulvifacies* FISCHER)			3♀ 1♂	
	Opius sp. 2	2♂		1♀	
KD	*Opius* sp. 3		1♀		
	Opius sp. 4		1♂		
	Opius sp. 5	1♀			
	Opius sp. 6 (nr. *penetrator* FISCHER)		1♂		
	Opius sp. 7	2♂			
	Orientopius sp.	1♂			
	Alysiinae				
	Asobara sp. 1	1♀	2♀ 3♂		
	Asobara sp. 2	1♀			
	Asobara sp. 3		1♀		
	Asobara sp. 4 (nr. *orientalis* VIERECK)	[1♀] ⟨2♀⟩			
	Aspilota sp. 1	1♀			
KD	*Aspilota* sp. 2	1♀			
	Cratospila sp.	(1♀)	2♀	1♀	
	Dinotrema sp.			1♀	
	Heratemis sp. (not *filosa* WALKER)		1♂	1♀ 2♂	
	Idiasta sp.	1♂			
	Phasmalysia sp.	1♂	1♂	1♀	
	Gen. sp. (Alysiini)	1♂	1♂		
	Aphidiinae				
KCH	? *Lipolexis* sp.		1♂		
	Helconinae				
	Diospilus sp.			1♂	
KCH	*Eubazus* (*Calyptus*) sp.	1♂			
	Schizoprymnus sp. (nr. *tortilis* PAPP)			1♀	
	Blacinae				
KCH	*Blacus* (*Tarpheion*) sp.		1♂		
	Euphorinae				
	Cosmophorus sp.	1♂	1♂	6♂	
	? *Cryptoxilos* sp.	1♀			
KCH	*Leiophron* sp. 1			1♂	
	Leiophron sp. 2	1♂			

Table 2. (Continued.)

Parasitoid mode	Subfamily-Species	Rakata	Sertung	Panjang	Anak K.
	Macrocentrinae				
KL	*Macrocentrus* sp. (nr. *persephone* NIXON)	1 ♀			
	Agathidinae				
	Bassus similis (BHAT & GUPTA)				(1 ♀)
KL	*Cremnops atricornis* (SMITH)				1 ♀
	Cheloninae				
	Chelonus (*Microchelonus*) sp. 1	(3 ♀)			
	Chelonus (*Microchelonus*) sp. 2			1 ♀	
	Chelonus (*Microchelonus*) sp. 3			1 ♀	(1 ♀)
	Phanerotoma sp. 1	(1 ♀)			(17+)
KL	*Phanerotoma* sp. 2	2 ♀		2 ♀ 3 ♂	3 ♀(28 ♀)
	Phanerotoma sp. 3	[1 ♀]			
	Phanerotoma sp. 4				1 ♀
	Phanerotomella sp. (nr. *namkyensis* SIGWALT)		1 A	1 ♂	(5 ♀)[2 ♀]
	Microgastrinae				
	Apanteles? *cypris* NIXON				(1 ♀)
	Apanteles? *dissimile* NIXON			1 ♂	
	Apanteles? *elagabalus* NIXON	2 ♀ 4 ♂ (6 ♀ 8 ♂)	1 ♂	1 ♂	(1 ♂)
	Apanteles sp. 1	1 ♂			
	Apanteles sp. 2		1 ♂		
	Apanteles sp. 3		1 ♂		
	Apanteles sp. 4 (nr. *vacillans* NIXON)		1 ♂		
KL	*Choeras* sp. 1		1 ♂	2 ♂	
	Choeras sp. 2	1 ♂			
	Cotesia sp.		1 ♀		
	Diolcogaster sp. (*xanthapis*-group)			1 ♂	
	Glyptapanteles sp. 1 (*octonarius*-group)				1 ♀ (1 ♀ 3 ♂)
	Glyptapanteles sp. 2 (*octonarius*-group)	1 ♀			
	Glyptapanteles sp. 3 (*octonarius*-group)	(1 ♀)			
	Glyptapanteles sp. 4 (*siderion*-group)	1 ♂		1 ♂	
	Snellenius sp.				1 ♀ 1 ♂
	Miracinae				
KL	*Mirax*? *irruptor* PAPP	1 ♂	1 ♀		
Total number of species		47	37	36	18
Total number of species in the survey=102					

* No. of catches in MALAISE traps ( ), in light traps [ ], in fruit-bait traps < > and in pit-falls { }, otherwise (no brackets) by sweeping or beating.

Table 3. SORENSEN's quotions of similarity (QS, upper triangle) and NOMURA-SIMPSON's coefficients of similarity (NSC, lower triangle, in italics) between braconid fauna of the Krakatau islands.

	Rakata	Sertung	Panjang	Anak Krakatau
Rakata	—	0.286	0.217	0.154
Sertung	*0.324*	—	0.356	0.109
Panjang	*0.250*	*0.361*	—	0.185
Anak Krakatau	*0.278*	*0.167*	*0.278*	—

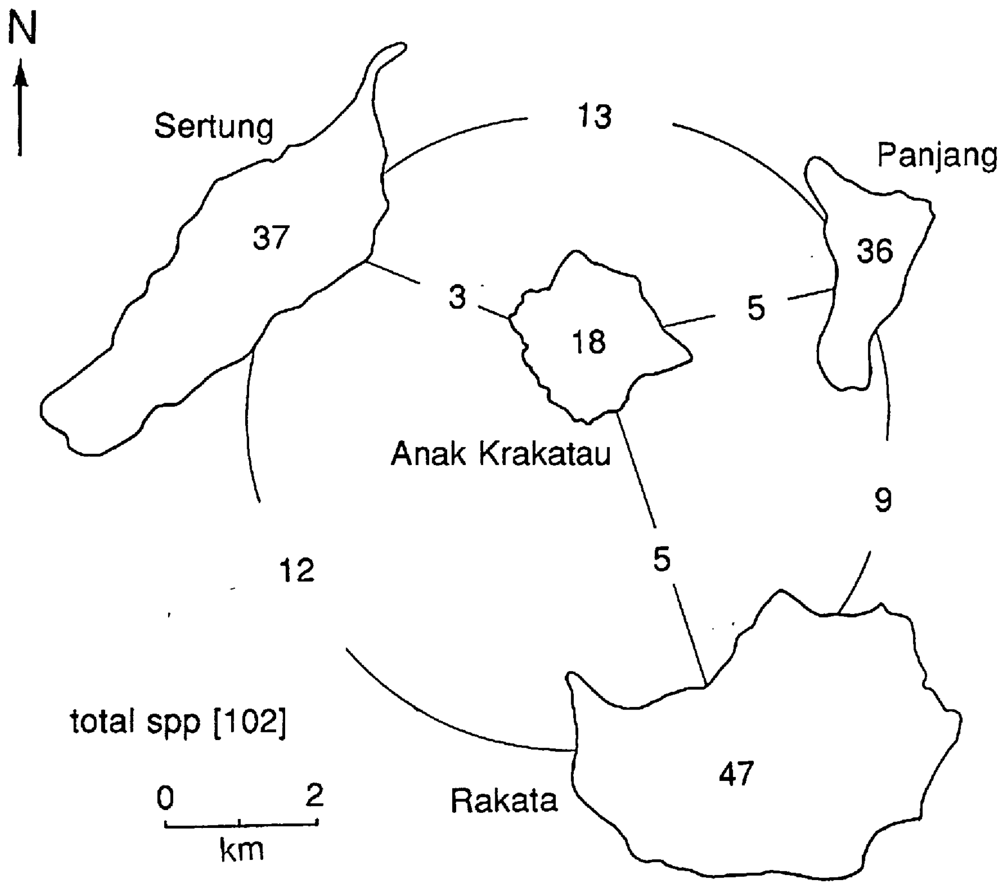

Fig. 2. Number of species of Braconidae on each island of the Krakataus, and in common between island pairs.

Krakatau than for those involving the older islands only, indicating that Anak Krakatau's braconid fauna is somewhat distinct from that of the older islands. Indeed, 10 of its 18 braconid species were not found elsewhere in the archipelago.

The number of species of each parasitoid-mode group found on each island, and the number on Anak Krakatau that is also present on at least one of the older islands, are shown in Table 4. Because coverage of the islands by sweeping and beating was much more even than it was by MALAISE and light trapping, Table 4

Table 4. Number of species of braconids collected on the Krakatau islands (R, Rakata; S, Sertung; P, Panjang; A, Anak Krakatau) between 1984 and 1986 and relative colonizing abilities of five parasitoid modes (abbreviations as for Table 2). CR, colonization ratio of parasitoid mode (for method of calculation see text); RCR, relative colonization ratio as compared to CR of all braconids; A, Anak Krakatau only; AK, Anak Krakatau *and* on other island(s) of the group. Data in brackets relate only to those species collected by sweeping and/or beating.

Parasitoid mode	Number of species collected						A+AK	RSP+A	CR	RCR
	R	S	P	RSP	A	AK				
IL	6 (4)	2 (2)	2 (2)	10 (8)	2 (1)	0 (0)	2 (1)	12 (9)	0.17 (0.11)	0.95 (0.97)
ICLD	8 (8)	14 (13)	13 (13)	25 (24)	0 (0)	2 (2)	2 (2)	25 (24)	0.08 (0.08)	0.45 (0.73)
KL	15 (9)	8 (8)	10 (10)	26 (21)	8 (5)	6 (2)	14 (7)	34 (25)	0.41 (0.28)	2.34 (2.46)
KD	14 (12)	10 (10)	7 (7)	22 (21)	0 (0)	0 (0)	0 (0)	22 (21)	0.00 (0.00)	—
KCH	4 (4)	3 (3)	4 (4)	9 (9)	0 (0)	0 (0)	0 (0)	9 (9)	0.00 (0.00)	—
Total braconids	47 (37)	37 (36)	36 (36)	92 (83)	10 (6)	8 (4)	18 (10)	102 (88)	0.18 (0.11)	

also includes data using only specimens collected by sweeping and beating. Assuming that the three older islands comprise the source area for Anak Krakatau's braconid fauna, it is possible to quantify relative success of the various parasitoid-mode groups in colonizing Anak Krakatau by calculating the proportion of the fauna of the source that is present on Anak Krakatau. In view of the higher intensity of collecting on Anak Krakatau it is likely that most of the species inhabiting the limited vegetated area of this island are present in the collections, whereas there is no doubt that a substantial number of species might have been missed on the other islands, many areas being unvisited or visited for only a short time. The assumption is made, therefore, that species collected only on Anak Krakatau were present elsewhere on the archipelago but missed during the surveys. Making this assumption, following THORNTON *et al.* (1988 a), a Colonization Ratio (CR) can be calculated for each parasitoid-mode group [CR=(A+AK)/(RSP+A)], where AK is the number of species found on both Anak Krakatau and the source area (at least one of the older islands), A is the number found only on Anak Krakatau, and RSP the total number found on at least one of the older islands. A Relative Colonization Ratio (RCR) can then be calculated by comparing the CR of each parasitoid-mode group with the CR for all braconids (RCR for a given group=CR for that group/CR for all braconids).

Table 4 shows that colonization of Anak Krakatau by parasitoid-mode group IL (idiobiont ectoparasitoids of Lepidoptera) has been average, that of ICLD (idiobiont ectoparasitoids of Coleoptera, Lepidoptera or, rarely, Diptera) has been less than average for the braconids, and colonization by group KL (koinobiont endoparasitoids of Lepidoptera) has been over twice the average. Groups KD (koinobiont endoparasitoids of the cyclorrhaphous Diptera) and KCH (koinobiont endoparasitoids of Coleoptera or Hemiptera) have not colonised the island. Restricting the data base to collections made only by sweeping and beating (see Methods,

Table 5. Number of species of three groups of Krakatau braconids present on and absent from Anak Krakatau, compared with numbers expected if presence on this island was determined by chance. Abbreviations as for Table 4, explanation in text.

Parasitoid mode	Absent from Anak Krakatau (RSP−AK)		Present on Anak Krakatau (A+AK)		Total
	Observed	Expected	Observed	Expected	
Idiobiont ectoparasitoids (IL+ICLD)	33.0	30.5	4.0	6.5	37
Koinobiont endoparasitoids of Lepidoptera (KL)	20.0	28.0	14.0	6.0	34
Koinobiont endoparasitoids of other insects (KD+KCH)	31.0	25.5	0.0	5.5	31
Total	84.0	84.0	18.0	18.0	102

X^2=20.812 (2 d.f.), P<.001.

above) does not change this general trend (data in brackets in Table 4).

If the parastitoid categories are lumped into three major groups, idiobiont ectoparasitoids (IL & ICLD), koinobiont endoparasitoids of Lepidoptera (KL), and koinobiont endoparasitoids of non-lepidopteran hosts (KD & KCH), numbers become high enough to validate statistical treatment. Numbers of species present on or absent from Anak Krakatau may be compared with numbers expected if presence on Anak Krakatau is determined only by chance (Table 5). A X^2-test shows that the difference between observed and expected numbers of species is significant (P<.001), confirming the unusually high representation on Anak Krakatau of koinobiont endoparasitoids of Lepidoptera (KL).

Discussion

DAMMERMAN (1984) listed nine braconid species as having been collected on the Krakataus between 1908 and 1933. Apart from *Iphiaulax* sp. (Braconinae) which is group ICLD (idiobionts of Coleoptera, Lepidoptera or Diptera), and *Eubadizon luteum* SZÉPLIGETI (probably Helconinae, KCH, koinobionts of Coleoptera or Heteroptera), all the other species, *Chelonus striatigena* CAMERON, *Chelonus* sp. and *Phanerotoma* sp. of the Cheloninae, *Cremnops* sp., *Disophrys erythrocephala* CAMERON and *Microdus* sp. of the Agathidinae, and *Orgilus* sp. of the Orgilidae, are presumably KL (koinobionts of Lepidoptera). Remarkably, the proportion of KL species in this sample of the archipelago's earlier fauna (7 of 9, 78%) is identical to the proportion of KL species in Anak Krakatau's fauna of 1984–1986 (14 of 18) and differs markedly from the proportion of KL in the 1984–1986 braconid fauna of the three older islands (26 of 92, 28%). The exact match of the proportions on Anak Krakatau is of course coincidence but certainly suggests that koinobionts of Lepidoptera were the preponderant group of braconids both on the Krakataus six to eight decades ago and on Anak Krakatau (but not on the older islands) in the period 1984–1986, suggesting that they are better colonizers of early successional habitats than are braconids of other parasitoid modes.

THORNTON *et al.* (1992) have recently provided supporting evidence for earlier suggestions by DAMMERMAN (1948), TAGAWA *et al.* (1985), THORNTON and NEW (1988) and THORNTON *et al.* (1988 b, 1990) that, in general terms, the biotic development of Anak Krakatau has offered an analogy of the early colonization and succession on the lowlands of the older islands in the first decades after 1883. They provided evidence that changes in the dispersal mode spectra of colonizing 'waves' of vascular plants, as well as the order of arrival of species of spermatophytes, pteridophytes and resident land birds were significantly similar in the two cases. In addition, there is some evidence that in reptiles, frugivorous birds, bats, fig species and spiders, successful colonists of Anak Krakatau, probably from the older islands, also tend to have been early colonists of the archipelago from the mainland (THORNTON *et al.*, 1992). Braconids evidently provide yet another such parallel.

An interesting feature of the braconid data is that the three parasitoid-mode categories that are successful colonizers all include Lepidoptera as hosts, and the two parasitoid-mode categories that have not yet reached Anak Krakatau are koinobionts that do not have Lepidoptera as hosts (Table 4). The most striking feature of Table 4 is the dominance of the KL mode on Anak Krakatau, although it is the most species-rich mode on the older islands by only a very small margin. This indication of the remarkable relative success of the KL mode in colonizing Anak Krakatau demands an examination of what may be the colonization advantages for braconids with this particular combination of features — koinobionts with Lepidoptera as hosts.

The evident lack of KD parasitoids (*i.e.* Opiinae and Alysiinae) on Anak Krakatau, although 22 species were collected on the older islands, is probably due to paucity of suitable hosts (Diptera) on the young island. The principal hosts of this group of braconids are dipterous leafminers and flies with larvae that are associated with fungi or fruit. In the period 1984–1986 Anak Krakatau's vegetated area was almost wholly grassland and *Casuarina* woodland; the transition to mixed forest was in only the very early stage and the island's habitat was probably unsuitable for these dipteran host species. For example, YUKAWA (1984 a) collected 6 speices of tephritid fruit flies on the archipelago in 1982 but only one of them occurred on Anak Krakatau. On the La Trobe University/Bogor Zoology Museum expedition of 1990, by which time diversification of Anak Krakatau's woodland had proceeded further and some of its fig species were fruiting, nine tephritid species were collected on the archipelago, four of them occurring on Anak Krakatau (E. R. SCHMIDT *et al.*, personal communication).

It will be interesting to see if catches by MALAISE trap and by sweeping during the 1990, 1991 and 1992 zoological expeditions, collections which are now being analysed, contain any KD braconids. It might be expected that as Anak Krakatau's woodland diversifies and incorporates more fruiting, broad-leaved trees, its habitat will become more suitable for the dipterous hosts of this group of braconids, and we predict they will then quickly colonize the island.

The impediment to colonization of KD braconids suggested above, lack of suitable hosts, is unlikely to apply to KL braconids. For a number of reasons, their host insects (Lepidoptera) are likely to be much better represented on Anak Krakatau than are the dipterous hots of KD braconids. Although little is known, quantitatively, of the moth fauna of the archipelago, YUKAWA (1986) found only 10 species in 1982. The light-trap collections of the La Trobe-L.I.P.I. expeditions in 1984–1986, although comprising many more than 10 species, were also poor compared to the diversity of moth species found on Java, and much less diverse than the Krakataus' fauna of 113 species reported by DAMMERMAN (1948). On Anak Krakatau two arctiids were present, a *Ficus*-feeder and a legume-feeder. A legume-feeding noctuid occurred in association with the pioneer beach creeper *Canavalia maritima* of the *Ipomoea pes-caprae* association (a widespread association of creepers on accreting beaches in tropical SE Asia and the Pacific), and a large fruitmoth, *Othreis fullonia*, was caught each year. MALAISE traps set on the barren ash uplands of the island collected small pyralids and other moths (THORNTON & NEW, 1988). Collections made by NEW and THORNTON have not been worked up but the impression after preliminary appraisal was that moth diversity was not high.

The butterflies, in contrast to moths, have received considerable attention (YUKAWA, 1984 b; BUSH, 1986; NEW *et al.*, 1988; NEW & THORNTON, 1992). In the period 1984–1986, 23 species were recorded on Anak Krakatau, of a total Krakatau fauna at that time of 54 species. Butterflies are an exception to the colonization sequence analogy mentioned above; the correspondence between sequence of colonization of the archipelago after 1883 and that of Anak Krakatsu is not as close as it is with other segments of the Krakatau biota. Nevertheless, THORNTON *et al.* (1992) pointed out that the archipelago arrival wave-sets of butterflies that are best represented on Anak Krakatau are those that colonized the archipelago between 1883 and 1921, the period up to the beginning of forest formation.

Few of the archipelago's butterflies, even now, are true forest species; the butterfly fauna of the Krakataus is strongly disharmonic, heavily biased towards species of coastal or near-coastal habitats which feed on plants characteristic of these habitats. It is likely that most forest butterflies are not sufficiently vagile to reach the archipelago except very rarely, by chance. Their colonization, if it does occur, is likely to be much later than species of secondary vegetation and transitional seral stages, butterflies which are usually characterized by good powers of dispersal and wide distributions. Limitation of larval food plants is probably an additional reason for the paucity of forest butterflies. BUSH and WHITTAKER (1991) have pointed out that the coastal flora of the archipelago, in contrast to that of the islands' interiors, has changed very little since 1897, and Anak Krakatau's flora, of course, comprises almost entirely coastal or near-coastal species. This very biased, youthful, but limited flora of Anak Krakatau probably provides less impediment to colonization of the island by Krakatau butterflies than it does for colonization by other insect groups such as the dipteran hosts of KD parasitoids, simply because there are so few k-selected forest butterflies on the archipelago to be excluded. The success of koinobiont braconid parasitoids of Lepidoptera in colonizing Anak Karakatau is thus partly explained by the relatively good representation of their hosts on the island.

Koinobiotic braconids of the subfamilies Microgastrinae, Cheloninae and Agathidinae are thought to be r-selected species with high fecundity (e.g. IWATA, 1959). In addition, many koinobiotic parasitoids can readily parasitise hosts that live in well-exposed situations, and these include species such as looper caterpillars and armyworms. Such hosts are usually not available to idiobiont ectoparasites, which are thus likely to be less successful colonists of early successional habitats.

Although KL koinobionts do not kill their host immediately, they emerge from the mature host larvae. Thus they cannot arrive with the adult moth or butterfly but may be carried by dispersing host larvae. In contrast, idiobionts kill or paralyse the host when they oviposit and so would always require a separate immigration from that of their host. Koinobionts would thus again have an advantage over idiobionts as colonizers.

We have outlined several possible reasons for the relatively high success of koinobiotic parasitoids of Lepidoptera in colonizing both Anak Krakatau in recent decades and the older islands in the early decades following 1883. We close with one further suggestion. Koinobionts, in general, are oligophagous, in general, host insects for a particular species of braconid being usually confined to a number of related species or genera. Once host diversity has increased in a developing biota, koinobionts are therefore likely to suffer to a greater degree than the more polyphagous idiobionts from the resulting fragmentation of host resources, as suggested by ASKEW and SHAW (1986) for climax tropical forests. On the Krakataus, the emergence of Anak Krakatau and its subsequent provision of earlier successional stages than those obtaining on the older islands may have provided a less host-diverse ecological refuge (THORNTON *et al.*, 1988 b, 1992; THORNTON, 1991) for such species as host diversity on the older islands increased.

We have MALAISE trap and sweepnet collections of insects from the Krakataus from expeditions in 1990, 1991 and 1992, a period when Anak Krakatau's vegetation appeared to be on the threshold of rapid diversification in some parts of the island, and we intend to study the braconid fauna represented in these and future collections, paying particular attention to the relative colonizing abilities of koinobiont and idiobiont braconids as the archipelago's ecosystem, and that of Anak Krakatau, develop and diversify.

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