PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

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THE BUTTERFLY FAUNA OF THE KRAKATAU ISLANDS AFTER A CENTURY OF COLONIZATION

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CONTENTS

Collections of butterflies from the Krakatau Islands made from 1982–85 are discussed. Twenty species new to the island group and many new records to particular islands imply that the butterfly fauna is far from equilibrium. The colonization trends are discussed in relation to the habitats available, and conservation measures are suggested.

1. Introduction

Butterflies may be considered to be among the better-known groups of insects, as they have attracted the attention of collectors and naturalists over a considerable period. The species are thus mostly named and a large proportion are recognizable on well-documented characters. In addition, the gross distributional ranges of many species are reliably known, even though the geographical boundaries between the many named local forms and subspecies may not be fully understood. Butterflies are thus of very considerable value in biogeographical studies, as the source area of taxa found extending their range can sometimes be inferred with a high degree of accuracy.

The butterfly fauna of the Krakatau Islands has been progressively recorded by Jacobson (1909), Dammerman (1922, 1929, 1948), Yukawa (1984) and Bush (1986*a*, *b*), and these accumulated records constitute a strong framework in which to consider data from the 1984 and 1985 La Trobe University/L.I.P.I. Zoological Expeditions (Thornton & Rosengren 1988). The accounts of Yukawa and Bush contain ecological information on many of the butterfly species present, and Yukawa (1984) also includes substantial discussion on the progress of colonization. Our paper adds further information on Krakatau butterflies, and reflects (in committed man-hours) the most intense period of observation on these insects so far made in the Sunda Strait (figure 1). In 1984, T. R. New and M. B. Bush watched butterflies and captured voucher specimens throughout their stays on all four islands (30 August to 16 September), and several other expedition members netted specimens as time permitted. It is believed that, except for undersampling the higher altitudes of Rakata and the deeper forests of Sertung and Panjang, our sampling was sufficiently comprehensive to incorporate the species flying at the time of our 1984 visit. A more detailed survey of Anak Krakatau and of parts of south Rakata was made by T. R. New in 1985 (13–27 August).

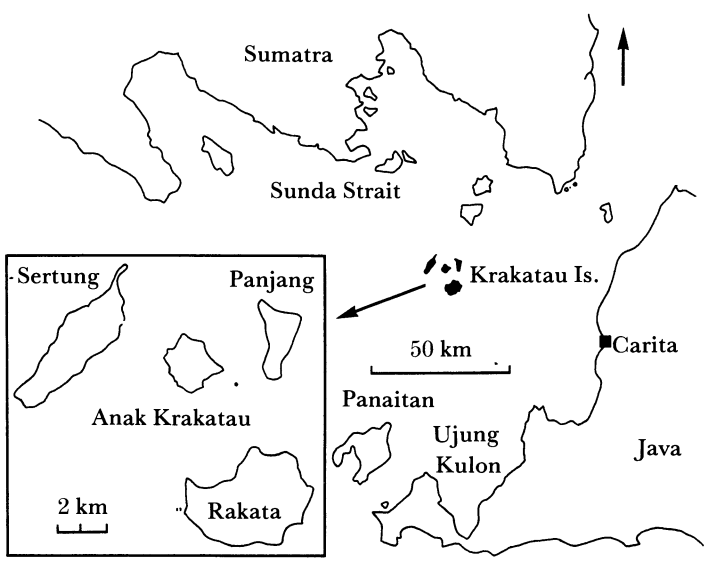

FIGURE 1. Sunda Strait and the Krakatau Islands, 1985.

A series of voucher specimens will be deposited in the Museum Zoologicum Bogoriensis, Bogor. Identifications (except Hesperiidae, determined by A. F. Atkins) were based on comparison with the collections of the British Museum (Natural History) by M.B.B. and from published accounts.

2. THE BUTTERFLIES

The butterflies found in the series of recent collections from 1982 to 1985 are listed in table 1. The following annotated list gives further comments on their possible status and abundance, based predominantly on our observations, and is followed by a short appraisal of the biogeographical aspects of this survey.

(*a*) *Papilionidae*

Graphium agamemnon agamemnon (L.). Seen flying on all four islands, and apparently a recent arrival, being initially sighted on Rakata and Panjang by Yukawa in 1982. Possibly not resident, as no Annonaceae are known from the islands.

Pachliopta aristolochiae (F.). Not recorded from Panjang. Dammerman (1929) first recorded the Javanese subspecies *adamas* (Zinken) and the predominantly Sumatran *antiphus* (F.) from Rakata in April 1920, and Toxopeus (1950) saw adults resembling these and the west Javan *ascanius* (L.) on Sertung in 1949, *adamas* and *ascanius*-like insects inter-mating. We found *adamas* and *antiphus* on Anak Krakatau.

Papilio memnon L. Observed on Rakata and Sertung in 1983 and again on Rakata in 1984; not seen in 1985. Not confirmed breeding on the islands, and no Rutaceae have been recorded (Bush 1986*a*). Probably migratory, but there is a possibility that *Citrus* might have been planted on Rakata by its former resident, a Mr Händl.

Troides helena helena (L.). Most commonly seen on Rakata, but also taken in forests or feeding from flowers on Panjang and Sertung. Some of the specimens are intermediate between *T. h. helena* and *T. cuneifera*, but we believe that only one taxon is represented on the islands, and this was figured by Tagawa (1984) as *T. h. helena*. First recorded on Rakata in 1908, and noted there by all workers since then, this species is undoubtedly resident, with larvae presumably feeding on *Aristolochia tagala* (Bush 1986*a*).

(*b*) *Pieridae*

Anapheis java java Sparrman. This is a strongly migratory species, and a specimen collected on Rakata in October 1919 was regarded as 'probably a straggler' by Dammerman (1948). Yukawa's (1984) record from Panjang is the only other from the Krakataus. No Capparidaceae occur on the islands.

Catopsilia pomona pomona (F.). Another well-known migratory species, seen by both Yukawa (1984) and ourselves in 1984; we have no doubt over its identity, and specimens were seen flying over the sea between the islands and Java (see also New *et al.* 1985). Initially recorded from Rakata in 1932, and abundant throughout Indonesia.

Eurema alitha sankapura (Fruh.). This species, formerly referred to as *E. hecabe sankapura*, occurs in Java and various islands to the east. *E. a. sankapura* was listed as new to the islands by Yukawa (1984), but Dammerman (1948) noted *E. h. sankapura* from Sertung (in 1921 and 1933) and Rakata (in 1932). Historically, *E. a. sankapura* and *E. h. hecabe* (= *E. h. sankapura*) may have been confused.

Eurema blanda blanda (Boisduval). Now known to be widespread and reasonably common on all four islands.

Eurema hecabe hecabe (L.). See comment under *alitha*. Found by us on all islands, and first recorded on the Krakataus in 1921. A spectrum of possible food plants for larvae of *Eurema* occurs on the islands and, although *Eurema* species are recorded migrants, both the latter species (at least) are undoubtedly resident.

(*c*) *Nymphalidae*

Danainae

Some taxonomic confusion has occurred over the identity of species of *Danaus* on the Krakataus.

TABLE 1. BUTTERFLIES RECORDED ON ISLANDS OF THE KRAKATAUS FROM 1982 TO 1985

(A: 1982 (Yukawa 1984); B: 1983 (Bush 1986*a*); C: 1984–85.)

species	Rakata	Sertung	Panjang	Anak Krakatau
Papilionidae				
*Graphium agamemnon**	A — C	— — C	A — C	— — C
Pachliopta aristolochiae	A B C	A B C	— — —	— — C
*Papilio memnon**	— B C	— B —	— — —	— — —
Troides helena	A B C	A B C	A — C	— — —
Pieridae				
Anapheis java	— — —	— — —	A — —	— — —
Catopsilia pomona	A — C	A — —	— — C	— — C
Eurema alitha	A — —	— — —	— — —	— — —
E. blanda	A B C	A B C	A — C	— B C
E. hecabe	— — C	A — C	— — C	— — C
Nymphalidae				
Danainae				
Danaus chrysippus	— B —	A B —	— — —	— — —
D. genutia	— — —	A — —	— — —	— — —
D. melanippus	— — C	— — C	— — —	— — C
Euploea sp.*	A — —	A B —	— — —	— — —
Ideopsis (Radena) juventa	A B C	A B C	A B C	— B C
*Tirumala septentrionis**	— B —	— — —	— — —	— — —
Satyrinae				
*Elymnias hypermnestra**	— — C	— — C	— — —	— — —
Melanitis leda	A B C	A B C	A B C	A B C
Mycalesis horsfieldii	— — C	A — C	— — C	— — —
M. janardana	A — C	A — C	— — —	— — —
Orsotriaena medus	— B C	— B —	— — —	— B —
Ypthima horsfieldii	A — C	— — —	— — —	— — —
Nymphalinae				
Chersonesia rahria	— B C	— — C	A — —	— — —
Hypolimnas anomala	A — C	A — —	A — —	A — —
H. bolina	A — C	A — —	— — C	— — —
Neptis hylas	A B C	A B C	— — C	— — C
*Precis atlites**	— B C	— B C	— — C	— — C
Lycaenidae				
Miletinae				
*Allotinus felderi**	— — C	A — —	— — —	— — —
*Miletus boisduvalii**	— — C	— — —	— — —	— — —
*M. symethus**	A — C	— — —	— — C	— — C
*Spalgis epius**	— — C	— — —	— — —	— — —
Polyommatinae				
*Anthene emolus**	— — C	— — —	— — —	— — —
Catochrysops panormus	— — —	— — C	— — —	— — —
C. strabo	A B C	A B C	— B C	A B C
Catopyrops ancyra	— — C	— — —	— — —	— — —
Euchrysops cnejus	— — C	A B C	— — —	— B C
*Jamides aratus**	A B C	— — C	— — —	— — C
J. bochus	— — —	A — —	— — —	— — —
J. celeno	A B C	A B C	A B C	A B C
*J. pura**	— B —	— — —	— — —	— — —
Lampides boeticus	— — C	— — C	A — C	A — C
*Megisba malaya**	A — —	— — —	— — —	— — —
*Petrelaea dana**	A — —	— — —	— — —	— — —
*Prosotas dubiosa**	— — —	— — —	A — —	— — —
*P. lutea**	— — —	A — —	— — —	— — —
Zizina otis	— — C	A — C	— — C	A — C
*Zizula hylax**	— — C	A — —	— — —	— — C

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TABLE 1. (*Cont.*)

(A: 1982 (Yukawa 1984); B: 1983 (Bush 1986*a*); C: 1984–85.)

species	Rakata	Sertung	Panjang	Anak Krakatau
Theclinae				
Arhopala pseudocentaurus	— — C	A — C	A — —	— — —
Hypolycaena erylus	A B C	A — —	A — —	— B C
Loxura atymnus	— B C	— — —	— — —	— — —
Hesperiidae				
Borbo cinnara	— — C	A — C	— — C	A — —
*Notocrypta curvifascia**	— — C	— — —	— — —	— — —
?Tagiades japetus	— — C	— — —	— — —	— — —
*?Pelopidas agna**	— — —	A — —	— — —	— — —
Potanthus confucius	A B C	A — C	A — C	A B C

(* First record for Krakataus.)

Danaus chrysippus bataviana Moore was found on Sertung and Rakata by Bush in 1984, and sighted on Sertung by Yukawa (1984). Until then, it had not been seen since an initial record on Sertung in 1921. Possibly now resident, as several possible larval food plants occur.

Danaus genutia (Cramer). The Javanese subspecies *intensa* Moore was recorded on Rakata by Jacobson (1909) and thereafter on Panjang and Sertung by Dammerman (1948). On Rakata and Sertung it occured with the Sumatran race *D. g. sumatrana* Moore in 1933. We did not see this species in 1984–5, and all similar individuals taken then represent the following species. Referred to as *D. plexippus* by Dammerman.

Danaus melanippus melanippus (Cramer). Another early arrival to the islands (Jacobson 1909) and noted for the three larger islands by Dammerman (1948). Not recorded by Yukawa, but taken on three islands and seen commonly in 1984 and 1985. It is possible that *D. genutia* and *D. melanippus* have occasionally been confused.

Euploea sp. Initially observed on Rakata and Sertung by Yukawa, and seen again by Bush (1986*a*, *b*), this tantalizing genus has not yet been captured, and its specific identity is unknown. An individual glimpsed on Rakata in 1985 looked very like *E. mulciber* (Cramer) (T. R. New), one of several species common elsewhere in Indonesia. As *Ficus* and various Asclepiadaceae occur on the islands, there seems no reason why at least one resident species of *Euploea* should not occur.

Ideopsis (*Radena*) *juventa juventa* (Cramer). Now common on all islands, although not found on Anak Krakatau by Yukawa (1984).

Tirumala septentrionis septentrionis Butler. So far known only from Rakata in 1983 (Bush 1986*a*), and not seen in 1984–5.

Likely food plants for all the above Danainae are not uncommon on the islands.

Satyrinae

Elymnias hypermnestra (L.). Sighted by M. B. Bush in 1984 and by T. R. New in 1985, but specimens have not been captured; also seen by M. B. Bush in 1983, but identity not then recognized.

Melanitis leda (L.). Common on all four islands, in lowland and coastal forest areas, and may have broadened its distribution there relatively recently as recorded only on Rakata by Dammerman (1948). Initially found on the other islands in 1982 (Yukawa 1984).

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Mycalesis horsfieldii horsfieldii (Moore). In common with several other sylvan Satyrinae, this species is rather furtive, and could easily be overlooked. It is here recorded for the first time from Panjang, and its apparent absence from Anak Krakatau probably reflects dependence on forest vegetation.

Mycalesis janardana janardana Moore. Like *M. horsfieldii*, this species is rather elusive, but it apparently has been established on both Rakata and Sertung for a considerable period, and seems not yet to have spread to the other islands.

Orsotriaena medus (F.). Probably now on all four islands, although not recently recorded from Panjang.

Ypthima horsfieldii Moore. Recorded by Dammerman (1948) from both Rakata and Sertung, but found only on Rakata in recent collections, mainly in localized clearings at higher altitudes.

All the above (except *Elymnias*, which feeds on palms) are Gramineae feeders as larvae, and a broad range of likely food plants occurs on the islands.

Nymphalinae

Chersonesia rahria (Moore). Initially found on Rakata in 1920 by Dammerman (1922), and now known also from forests of Panjang and Sertung.

Hypolimnas anomala (Wallace). This strongly flying species is now probably resident, at least on Rakata, and Yukawa (1984) noted it from all the islands. Various likely larval food plants (Urticaceae) are found on Rakata. The few individuals of this and the next species seen by us were all worn and were probably migrants.

Hypolimnas bolina bolina (L.). Also likely to be resident, but see comment on *H. anomala*. Found on Rakata in all collections made since about 1919, and on Sertung in 1932 and 1933.

Neptis hylas (L.). Now known from all four islands, apparently the only species of *Neptis* on the Krakataus, and one of the first butterflies recorded from Rakata. A wide range of likely larval food plants are present there.

Precis atlites atlites (L.). Apparently a recent arrival on the Krakataus, this species has rapidly become common and appears to be well established. No larval food plants have yet been recognized on the islands. Yukawa (1984) noted *P. atlites* as common in Carita (west Java), which we confirm, but he did not see it on the Krakataus.

(*d*) *Lycaenidae*

The Lycaenidae present unusual problems of recognition and species identification, as noted below, as the Oriental members of several large genera are in need of critical revision.

Miletinae

Allotinus felderi Semper. The only species of *Allotinus* found on the Krakataus, initially noted from Sertung by Yukawa (1984) and found flying on southern Rakata in 1985.

Miletus boisduvali Moore: This small species occurred on Rakata in 1985 and, in common with other Lycaenidae, may have been overlooked because of its 'preference' for forest environments.

M. symethus (Cramer). This striking species appears to be a recent arrival to the islands and, except on Sertung, was found in small numbers in coastal forest.

Spalgis epius (Westwood). Found on Rakata in 1984, not seen in 1985. Apparently very local, and seen only around *Caesalpinia bonduc* at Zwarte Hoek.

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Polyommatinae

Anthene emolus (Godart). Recorded on Rakata in 1984, not seen in 1985.

Catochrysops panormus (Felder). Initially found on Rakata in 1933, and found by us on Sertung. Very similar to *C. strabo*; the two have possibly been confused on the islands in the past.

Catochrysops strabo (F.). One of the most abundant lycaenids, well established on all four islands.

Catopyrops ancyra (Felder). Noted on Rakata in 1919, and apparently not seen there again until 1984.

Euchrysops cnejus cnejus (F.). Apparently an early arrival to both Rakata and Sertung, its range has now extended to Anak Krakatau.

Jamides aratus (Stoll). Apparently the subspecies *adana*, which is darker than the nominal subspecies found on Java and Sumatra.

Jamides bochus (Stoll). Noted from Sertung by Yukawa (1984) and not found during our surveys.

Jamides celeno (Cramer). The most abundant species of *Jamides* present, and well established on all four islands. Seen ovipositing on *Canavalia maritima* on Sertung by Bush.

Jamides pura Moore. Noted on Rakata by Bush (1986) and not yet found again. Larvae of *Jamides* spp. feed on various Leguminosae and Meliaceae.

Lampides boeticus (L.). A well-known migratory species found intermittently on Rakata and Sertung since 1933 (Dammerman 1948) and now known from all islands.

Megisba malaya malaya (Horsfield). Recorded from Rakata by Yukawa, but not seen by us.

Petrelaea dana dana (de Nicéville), *Prosotas dubiosa* (Semper), and *Prosotas lutea* (Martin) were all found on single islands by Yukawa, and were not seen by us.

Zizina otis lysizone (Snellen). Together with the next species, found associated with legumes in sheltered coastal areas, and found on all four islands in 1985. Possibly spreading rapidly into suitable habitats. Recorded on Anak Krakatau's beach in 1949 on *Canavalia* flowers (Toxopeus 1950).

Zizula hylax (F.). Also now apparently more widespread than formerly, and seemingly more common in 1985 than in 1984.

Theclinae

Arhopala pseudocentaurus pseudocentaurus (Doubleday). Apparently resident on Rakata, Sertung and Panjang. Seen ovipositing on *Terminalia catappa* on Rakata.

Hypolycaena erylus erylus (Godart). Not common, although apparently resident on all islands. A female was observed frequenting *Merinda citrifolia*, but actual oviposition was not observed.

Loxura atymnus (Stoll). Found in small numbers on Rakata, where it was first noted in 1933, and seen only in deeply forested areas. The likely food plant, *Smilax zeylanica*, is limited to such areas.

(*e*) *Hesperiidae*

Borbo cinnara (Wallace). Now recorded from all four islands, and probably resident. Initially found by Yukawa in 1982.

Notocrypta curvifascia (C. & R. Felder). A single specimen was seen on Rakata in 1985. An

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individual of *Notocrypta* found on Rakata in 1919 was doubtfully determined (Dammerman 1948) as *restricta*, and the genus has not otherwise been recorded previously on the islands.

Pelopidas agna (Moore). Tentatively recorded from Sertung by Yukawa (1984); not found by us.

Polytremis lubricans (Herrich-Schaeffer). Recorded from Rakata in 1908 and 1920, but not seen there since. Noted from Anak Krakatau by Bush (1986*a*), but this record is based on a misidentification of a single poor specimen of *Borbo* sp.

Potanthus confucius (C. & R. Felder). The most abundant and widespread skipper on the islands, and clearly well established on all four. On Anak Krakatau, apparently restricted to stands of *Ischaemum muticum* (Gramineae). The identity of this species is somewhat doubtful, and examination of type material of several species is necessary to clarify it. Our male specimens have genitalia that do not exactly conform to any published figures, and appear very close to *P. omaha* (Edwards) (possibly ssp. *copia* Evans). Only one species of *Potanthus* appears to be present.

? *Tagiades japetus enganicus* Fruhstorfer. A very damaged individual from Rakata in 1984 may represent this taxon. An undetermined individual of *Tagiades* from Sertung in 1933 (Dammerman 1948), the only previous record of the genus from the Krakataus, is counted as *japetus*.

3. Discussion

Twenty species of butterfly new to the Krakatau Islands are included in recent collections (table 1), together with a substantial number of new records for individual islands in the group (table 2), in particular the important younger island, Anak Krakatau.

Table 2. Summary of new butterfly records for the Krakatau Islands 1982–84

	1982[a]	1983[b]	1984–85	total
to island group[c]	11	4	5	20
to Rakata[d]	2	1	5 (1)[e]	8
to Sertung[d]	4	2	4	10
to Panjang[d]	10	1	8	19
to Anak Krakatau[d]	7	6	10	22

[a] Yukawa (1984).
[b] Bush (1986*a*).
[c] Numbers initially recorded on each island, with some species being found on more than one island at the same time, are: 16 Rakata, 9 Sertung, 1 Panjang, 2 Anak Krakatau.
[d] Omitting species new to island group; 1983 figure is an increase from 1982, and 1984–85 figure is an increase from 1982 and 1983.
[e] Figure in parentheses is *Notocrypta* sp., omitted from group total because of uncertainty of identification of early record of genus from Rakata.

(*a*) *Colonization trends*

Several other species absent from some earlier collections were also 'resdiscovered'. The immediate implication is that the fauna is far from equilibrium and is still accumulating rapidly. As Yukawa (1984) commented, it is difficult to evaluate the relative completeness of the various surveys, and 'seasonality effects' are also difficult to assess, as a species may be regarded as absent if adults are not seen. Many of the species present, especially in Lycaenidae, are rare and localized on the islands and are easily overlooked. In 1985, for example, T. R. New

made a special attempt to find the lycaenids earlier recorded by Yukawa and Bush but which were not seen in 1984: five of these species were not seen. The time of the 1985 visit was marginally later than that of Bush in 1983, and between the two periods covered by the Japanese workers in 1982, and it is possible that the short flight period of the species concerned may be reflected in differences between the collections itemized in table 1. However, many species did occur in all three collections and, together, they may be taken as adequately reflecting the butterfly fauna present in 1982–5: Rakata 47, Sertung 38, Panjang 24, Anak Krakatau 23, 54 species in all.

Even accepting these figures as definitive, problems of interpreting butterfly communities are formidable (see discussion by Gilbert (1984)) and, more generally, single-occasion surveys may not reveal the true nature of the communities present (Wiens 1981). Several species appear at present to be restricted to particular islands: 13 to Rakata, 5 to Sertung, and 2 to Panjang. Anak Krakatau has none.

Nymphalidae and Lycaenidae include the greatest numbers of species on the island group and also on each individual island. An important implication from the species numbers on individual islands is that Panjang has been undersampled: the environment there is at least as complex as Sertung, and the total of Lycaenidae (8) appears to be unrealistically low (but see p. 456). The butterfly faunas of Rakata and Sertung have much in common, with 33 shared species, 6 of which are not yet known from the other islands. Numbers of shared species from the other combinations of island pairs range from 17 (Panjang/Anak Krakatau) to 23 (Rakata/Anak Krakatau). Of the 20 species new to the islands in 1982–5, 14 were initially recorded on Rakata, 8 on Sertung, 0 on Anak Krakatau and 2 on Panjang. The low incidence of Panjang records is anomalous.

Development of the fauna of Anak Krakatau is of particular interest for comparison with the early stages of butterfly colonization on Rakata noted by Jacobson (1909). Twenty-three species occur on Anak Krakatau, of which six were first recorded on the island group in 1982–5. Several species (*D. melanippus*, *N. hylas*, *P. lubricans*) were among the earliest Rakata records. The remainder were known from Rakata by 1934, and most have been recorded in surveys of the islands since then.

The earliest survey of Rakata (Jacobson 1909) yielded only five species (*T. helena*, *D. genutia*, *D. melanippus*, *N. hylas*, *P. lubricans*), of which only the last named seems to have disappeared from the island. *Ypthima philomela* (L.) has not been seen since 1920 but could still be present, as it is a 'retiring' species. *Phalanta phalantha* (Drury) was sighted only, but there is no reason to doubt its identification. The other two nymphalids (*Cirrochroa tyche* C. & R. Felder, *Moduza procris minoe* Fruhstorfer) are likely to be vagrants and never to have been resident. *Deudorix jarbes* Fruhstorfer has been taken only once, as has the skipper *Telicota augis* (L.). Three other skippers (*Pelopidas conjunctus* (Herrich-Schäeffer), *P. mathias* (F.), *Polytremis lubricans* (Herrich-Schäeffer)) appear to have been clearly established and to have been resident over a considerable period. All feed on Gramineae or Palmae, and are widespread in Indonesia; Yukawa (1984) suggested that their apparent extinction from the islands could be related to the large-scale replacement of these plants by forest trees as succession proceeded. Yukawa considered *C. panormus* to be a 'genuine extinction' due to vegetation succession. Its recent discovery on the Sertung spit may represent a re-invasion but, more likely, may indicate its persistence in a localized early successional habitat. Relatively few species seem to have become

extinct from the islands, and the extinction rate has been considerably lower from 1928–34 to the present than in the decade before 1928 (table 4). The closure of the forest on much of Rakata in the late 1920s (Whittaker 1982) may have been associated with the high extinction rate of Lycaenidae around that time.

TABLE 3. SUMMARY OF DATA FOR CALCULATING TURNOVER OF BUTTERFLIES ON EACH OF THE KRAKATAU ISLANDS

(Figures refer to numbers of species recorded.)

	1908	1919–22	1928–34	1982–5
Rakata				
actual species	5	28	27	47
gains	5	23	8	26
losses	—	—	9	6
cumulative species	5	28	36	59
Sertung				
actual species	0	14	20	38
gains	0	14	10	21
losses	—	—	4	3
cumulative species	0	14	24	43
Panjang				
actual species	1	0	5	24
gains	1	0	5	23
losses	—	1	0	4
cumulative species	1	1	5	29
Anak Krakatau				
actual species	—	—	0	23
gains	—	—	0	23
losses	—	—	0	0
cumulative species	—	—	0	23

Other than undercollecting, it is difficult to explain the paucity of species on Panjang, especially in relation to Sertung (table 3). The Panjang fauna appears to have been very low for a considerable period, but has more than quadrupled since 1934, compared with an approximate doubling on Sertung and a somewhat lower increase on Rakata. However, surveys in the 1920s and 1930s concentrated on Rakata and Sertung, and the figures for Panjang in those decades are clearly unrealistic. The diversity of butterflies on Anak Krakatau is in marked contrast to that on Rakata in 1908, and numerically parallels the 1919–22 Rakata sample. Colonization of Anak Krakatau must be considered as spanning only the period since 1952, when almost all vegetation there was destroyed by volcanic activity. However, source areas of butterflies for Anak Krakatau are much closer than they were to Rakata in the early years of its community development, and it is not surprising that a substantial number of species (23) is already present.

The overall colonization pattern for butterflies on the Krakataus (tables 4 and 5) shows that the number of species has increased markedly since 1928–34 after an apparent levelling of numbers during the preceding decade. A number of species are treated as recolonizations: they were included in the losses of 1928–34, and have been found in recent collections. The cumulative number of species continues to rise dramatically, although there is some suggestion that the immigration rate (together with the turnover rate) may be slowing. It seems that immigration rate, colonization rate – and thus turnover rate – peaked in the decade before

Table 4. Colonization of the Krakatau Islands by butterflies

	1908	1919–22	1928–34	1982–5
actual number of species	6	33	30	54
gains	6	28	8	27
losses	—	1	11	3
cumulative number of species	6	34	42	64
immigration rate (spp. per year)	0.24	2.24	0.76	0.51
immigration rate (%)[a]	8.00	11.49	2.42	1.22
extinction rate (spp. per year)	—	0.08	1.05	0.06
extinction rate (%)[a]	—	0.41	3.33	0.14
colonization rate	0.24	2.16	−0.29	0.46
colonization rate (%)[a]	8.00	11.08	−0.91	1.09
turnover rate	0.24	1.16	0.90	0.29
turnover rate (%)[b]	100.00	5.95	2.87	0.68

[a] Percentage of average number of species in period between surveys.
[b] Immigration and extinction rates as percentage of total number of species in successive surveys.

Table 5. The representation of butterfly families on the Krakatau Islands

(Figures are numbers of species recorded.)

	1908	1919–22	1928–34	1982–85
Papilionidae				
actual species	1	2	2	4
gains	1	1	0	2
losses	—	0	0	0
cumulative species	1	2	2	4
Pieridae				
actual species	0	4	4	5
gains	—	4	1	1
losses	—	0	1	0
cumulative species	0	3	4	5
Nymphalidae				
actual species	4	14	12	17
gains	4	11	2	6
losses	—	1	4	1
cumulative species	4	15	17	21
Lycaenidae				
actual species	0	7	8	23
gains	—	7	4	15
losses	—	—	3	0
cumulative species	0	7	11	24
Hesperiidae				
actual species	1	6	4	5
gains	1	5	1	?3[a]
losses	—	0	3	2
cumulative species	1	6	7	?10[a]

Query denotes uncertainty of identification of early records of *Notocrypta* and *Tagiades*.

canopy closure, and extinction rate was highest while closure was occurring. Colonization rate was at that time negative, reflecting the extinction of taxa dependent on, especially, Gramineae and Palmae. With the secondary development of open areas and grasslands, especially around the coasts on better developed soil profiles than those of the initial primary succession, resources are now again available to foster the re-establishment of a range of species.

The greatest recent gain has undoubtedly occurred in the ecologically complex family

Lycaenidae; those in other families have been relatively small. Yukawa (1984) regarded most of the new Lycaenidae as *K*-selected species, a view with which we concur. As the Krakatau forests have not yet reached a mature stage, further Lycaenidae may be expected to become established in the future as the vegetation becomes yet more complex and diverse. Many of the Lycaenidae are likely to have intricate relationships with ants in addition to dependence on particular food plants, and the increased ant diversity (from 43 species in 1933 to 68 by 1982 (Yamane 1983)) may also facilitate establishment by associated lycaenids.

The potential future fauna of the islands is reflected in the current butterfly listings for nearby areas such as Carita and Panaitan (Yukawa 1984) and Ujung Kulon. Panaitan yielded 29 species in a brief survey in 1982 (Yukawa 1984), and our collections on Pulau Peucang and the Ujung Kulon Peninsula contain about 93 species, several of the Panaitan species not being found by us (New *et al.* 1987). More fragmentary data from our Sumatran collections (see also Corbet & Pendlebury 1978) again emphasize the very substantial diversity of butterflies in areas bordering the Sunda Strait. Both sides appear to have contributed to the Krakatau fauna: the foregoing list of species includes a number of Javanese subspecies, but 10 subspecies noted by Yukawa (1984) on the islands occur in both Java and Sumatra, so that the precise origin of their Krakatau populations cannot be determined. It is not at present possible to allocate all our taxa precisely to subspecies.

(*b*) *Conservation*

Many of the island butterflies are limited to particular habitats, and this poses some serious general questions for conservation on the Krakataus. Much colonization is linked substantially to the *Ipomoea pes-caprae* associations which occur only on low-energy beach environments. Butterfly distribution suggests that specific vegetation communities may be more important than island area, altitude, coastline length and extent of general forest development in influencing butterfly diversity (Bush 1986*b*). As yet, inland forest development seems to play only a small role in determining butterfly species diversity, as *Loxura atymnus*, and perhaps one or two other lycaenids, are the only species of habitual deep forest butterfly recorded.

Genolagani (1985) listed gently sloping beaches as high in his priorities for promoting tourism on the Krakataus. This measure should be viewed with concern, as it would surely lead to destruction of the *pes-caprae* formations now suspected to be so vital for butterfly colonization. Many species (perhaps as many as 15–18) of Lycaenidae and *Eurema* appear to be wholly dependent on this formation, which is rich in Leguminosae, and we believe this to be the 'key' vegetation type for butterflies on the islands. It has been one of the more constant floral communities on the islands and has essentially stabilized the presence of Leguminosae (which are scarce in other communities there) since the early phases of plant colonization. *Pes-caprae* formations are best developed on the few parts of the Krakatau coastlines on which landings can easily be made. At least part of the apparent lack of butterfly species on Panjang could be attributed to lack of well-developed *pes-caprae*, as only about half the species associated with this formation on other islands were found there. Many of the *pes-caprae* butterfly populations do not occur far from it: the southern end of Sertung, which is cliff-girt and where *pes-caprae* formations are absent or rare, yielded only 7 species in 10 days in 1983 (Bush), and the diversity of butterflies on Sertung is undoubtedly inflated by the well-defined *pes-caprae* formations on the northern spit. Likewise, Anak Krakatau butterfly diversity clearly has been influenced substantially by the extensive *pes-caprae* formations there. Anak Krakatau has been repeatedly

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disturbed by the effects of ongoing volcanic activity and the source pool of butterflies on the other islands is close and diverse. The parallel with colonization during the early years of Rakata is by no means a close one, because source areas for Rakata at that time were some 10–20 times as distant.

The development of Anak Krakatau may have influenced butterfly diversity on other islands. Both Panjang and Sertung suffered defoliation and considerable ash fall as recently as 1952 (van Borssum Waalkes 1960). Volcanic ash on leaves is likely to result in the death of caterpillars feeding on them: Gennardus (1983) found death of several species to occur within two days, and several common species of butterfly declined sharply in abundance about two weeks after a volcanic eruption on Java. Although such events may be infrequent, they cannot be discounted in considering the period of development of the present diversity.

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