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THE BUTTERFLIES OF ANAK KRAKATAU, INDONESIA: FAUNAL DEVELOPMENT IN EARLY SUCCESSION

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ABSTRACT. A survey in 1990 revealed that the butterfly fauna of Anak Krakatau continues to increase: of 41 species now recorded from this recent volcanic island, 18 have arrived since 1986. Habitat relations, faunal development, and the possible future of the island's butterflies are discussed. Continued vegetational succession is likely to result in extinction of a number of species, especially Hesperiidae and Lycaenidae, which depend on grassland or coastal low-growing vegetation formations.

Additional key words: Lepidoptera, conservation, island biogeography, vulcanism.

The pattern of colonization of the Krakatau Islands, Indonesia, by butterflies since the sterilizing eruption of 1883 was described by New et al. (1988) on data available to 1986. The island of Anak Krakatau, which emerged permanently from the sea only in 1930, is an active volcano and was devastated by eruptions in 1952 (when all vegetation was destroyed) and severely damaged by volcanic activity most recently in 1970–71. The island is of particular interest in studies of biotic colonization and community development as it provides one of very few isolated tropical sites in which such processes can be assessed from their earliest stages. Studies there of ecologically informative taxa and the progressive increase in species richness are useful in assessing the relationship between degree of habitat isolation and ability to recover from severe perturbation, a theme relevant to practical conservation. By 1985, 23 species of butterflies had been found on Anak Krakatau. Bush and Whittaker (1991) recorded an additional 13 species in 1989, and 5 more species are noted here from our visit in August/September 1990. Most of these 41 are likely to have arrived from the relatively close older islands of Rakata, Panjang, and Sertung, but other species are clearly from further afield. These are known from Java and Sumatra but not from elsewhere on the Krakataus.

This paper is an account of the butterfly fauna of Anak Krakatau in

1990, when the status and distribution of these insects were appraised in relation to the increasing complexity of this initially simple island environment. Background information on Anak Krakatau is included in Thornton and Rosengren (1988), and a broader picture of invertebrate colonization on the island is provided by Thornton and New (1988) and Thornton et al. (1990).

METHODS

During the period 19 August–3 September 1990, members of our group re-mapped the vegetation of Anak Krakatau to quantify changes in its composition and extent that had occurred during the previous five years. All vegetated areas were surveyed repeatedly for butterflies using three methods. 1. Transect walks (using the method of Pollard 1977) were made over all habitats at intervals during each of 11 days, with a minimum of 5 day-surveys in each. In each habitat, main comparisons are based on transects at 1030 h and 1400 h, but discrete counts were made at seven times on each of several days (Fig. 10), as time permitted. The butterflies were identified, counted and, where possible, sexed to yield data on species incidence, relative abundance in different vegetation types, and activity patterns. 2. Six selected taxa were marked on the hindwing underside using colored felt-tip pens (Pentel®), and released at the point of capture, in the air, within 10 minutes of capture. This technique was employed only in calm weather. Recaptures were used to detect any major individual movement. 3. Casual observations and collecting were undertaken during other work on all parts of the island. Data both from transect counts and recaptured marked butterflies were used to estimate relative abundance of species and their distribution among different vegetation types. The latter data are not strictly quantitative, as most species occurred in only small numbers. The following abundance categories are used for comparison between major habitats: (i) common, at least 10 individuals seen in a representative 100 m transect at some time between 1000 and 1600 h; (ii) moderately common, three to nine individuals seen on at least one transect during the above period; (iii) rare, fewer than three individuals seen on any transect and usually not present on all transects; (iv) singletons.

Status is appraised as follows: (i) resident, species associated with presence of larval foodplants, usually common or moderately common, with both sexes present and (for some) mating pairs observed, or for which any of these have been recorded in the past; (ii) non-resident, species which did not fulfill the above criteria and for which no known larval foodplants are present on Anak Krakatau; (iii) straggler, as non-

resident, but mainly strongly-flying migratory species that were either rare or singletons.

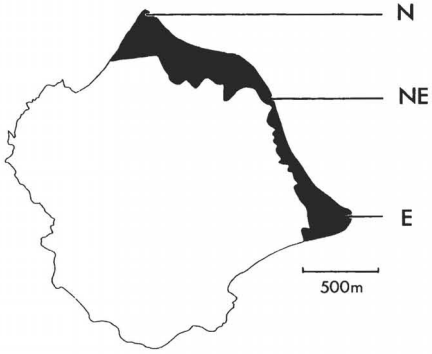
Vouchers of some taxa were taken for confirmation of identity, although singleton females and several easily-recognizable or strongly flying species (noted in the following list) were not captured. Hesperiidae were identified by A. F. Atkins; members of other families were identified from standard literature (such as Corbet & Pendlebury 1978, and many of the papers cited therein) and by comparison with material captured earlier on the Krakataus. A few records were made during a brief visit by IWBT and D. Britton in April 1991; those of significance are noted below. Vouchers of all Krakatau butterflies captured during our surveys are held at La Trobe University or the Zoological Museum, Bogor.

RESULTS AND DISCUSSION

Vegetation

Anak Krakatau (Fig. 1) is largely bare lava and ash, with well-defined vegetation on the eastern coastline extending up to about 200 m inland. The maximum extent of vegetation has increased substantially since 1986, and there have been marked changes in diversity and maturity. The three major areas, designated the Eastern Foreland, Northeast Headland, and Northern Foreland supported fairly discrete vegetational communities in 1986, and still were distinct sufficiently in character in September 1990 to be regarded as different habitats (as different successional stages), though by this time they were no longer separated by distinct vegetation-free areas. Succession is most advanced on the Eastern Foreland, where well-developed *Casuarina equisetifolia* J. R. & G. Forst (Casuarinaceae) woodland is becoming progressively invaded by other secondary forest species. Well defined grassland areas (*Ischaemum muticum* L.) and natural clearings between groups of trees also are present. In contrast, the youngest area, the Northern Foreland, has predominantly grassland (*Ischaemum muticum, Imperata cylindrica* (L.) Beauv., *Saccharum spontaneum* L., Gramineae) communities with younger *Casuarina* to the west. The vegetation of the Northeast Headland is intermediate between these two. There are numerous *Ficus* L. trees (Moraceae) toward the coast on the Northeast Headland and Eastern Foreland, and low vegetation (*Ipomoea pes-caprae* (L.) R. Br. (Convolvulaceae) communities, with *Canavalia maritima* (Aubl.) Urb. and other legumes) extends along much of the coast, but is least developed along about 200 m immediately south of the Northeast Headland.

Clumps of *Saccharum* and occasional small *Casuarina* trees occurring



	Number of butterfly species		
	Total	Resident	Common
N	9	7	6
NE	18	17	9
E	31	26	14

FIG. 1. Anak Krakatau, with summary of numbers of butterfly species found in each of three main vegetated areas in 1990. Extent of vegetation indicated by shading. (E, Eastern Foreland; NE, Northeast Headland; N, Northern Foreland.)

up much of the lower slope of the outer cone are not shown on the map in Figure 1.

Butterflies

Although collecting intensity differed between the three main areas, with most collecting in the more complex habitats of the Eastern Foreland, the surveys collectively included repeated collections over all vegetated areas of Anak Krakatau, so that few species flying at the time of our survey would have been missed, and inferences on distribution and relative abundance are reliable. The following annotated checklist of the species observed gives the year of first record on Anak Krakatau in parentheses and on the archipelago in brackets following the specific name (1982: Yukawa 1984; 1983: Bush 1986; 1984–85: New et al. 1988; 1989; Bush & Whittaker 1991; 1990: this paper).

Papilionidae

Graphium agamemnon (L.) (1984–85) [1982]. Two individuals sighted, both on 22.viii.90 on beachfront vegetation, Eastern Foreland; one resting on *Eupatorium odoratum* L. (Compositae) blossom. Status: straggler.

Graphium sarpedon (L.) (1990). One seen on 20.viii.90 near beach, Eastern Foreland. Not seen previously on the archipelago. Status: straggler.

Pachliopta aristolochiae (F.) (1984–85) [1919–21]. Both forms *adamus* and *antiphus* were seen frequently in treed areas and along woodland edges of the Eastern Foreland and Northeast Headland; seen rarely in the Northern Foreland. Present also iv.91. Status: resident.

Papilio memnon L. (1990) [1983]. One worn specimen seen on 23.viii.90 in the Eastern Foreland. Formerly recorded from Rakata and Sertung only. Status: ? straggler; could

possibly become resident soon, as suitable larval foodplants (Rutaceae) now occur on Anak Krakatau (T. Partomihardjo, pers. comm. 1990).

Troides helena (L.) (1989) [1908]. Moderately common in coastal forest and along woodland edges of the Eastern Foreland (where present also in iv.91); one seen on the Northeast Headland. Previously known from the other three islands. Status: resident, recently established.

Pieridae

Catopsilia pomona (F.) (1984–85) [1933]. Several individuals seen on beachside vegetation of the Northeast Headland and Eastern Foreland; one flying over bare lava in the southwest of the island, 21.viii.90. Status: migrant, ? non-resident.

Eurema blanda (Boisduval) (1983) [1919–21]. Not uncommon on coastal and other low vegetation in all areas; most frequent in the Eastern Foreland. Status: resident.

Eurema hecabe (L.) (1984–85) [1919–21]. Not as common as *E. blanda* and found only in the Eastern Foreland and Northeast Headland. Status: resident.

Nymphalidae

Danaus chrysippus bataviana Moore (1990) [1919–21]. One seen on 26.viii.90 in woodland clearing in Eastern Foreland. Known previously from Rakata and Sertung. Status: ? straggler.

Danaus genutia (Cramer) (1989) [1908]. Form *sumatrana* Moore was fairly common in clearings in the Eastern Foreland and Northeast Headland and a few individuals of form *intensa* Moore also were present. Status: resident.

Euploea modesta Butler (1989) [1908]. Individuals were seen nearly every day in the Eastern Foreland, more rarely on the Northeast Headland. First recorded from a single specimen (Bush & Whittaker 1991), and earlier records of *Euploea* sp. from Rakata and Sertung (New et al. 1988) may be of this species. Status: resident, recent colonist and apparently increasing in numbers. [D. Britton, pers. comm., captured a specimen in Northern Foreland in April 1991].

Ideopsis (Radena) juventa (Cramer) (1983) [1919–21]. Common in the Eastern Foreland and less so in the Northeast Headland, virtually ubiquitous in vegetated areas but most frequent in clearings and along woodland and coastal edges. (Seen also iv.91). Status: resident.

Tirumala septentrionis Butler (1989) [1983]. A single specimen found in a woodland clearing of the Eastern Foreland, 31.viii.90. Status: resident (Bush & Whittaker 1991). Known earlier (1983) from Rakata.

Melanitis leda (L.) (1982) [1933]. Not uncommon in all vegetated parts of the island and roosting under cliff overhangs along the coast southeast of the Eastern Foreland. Status: resident.

Mycalesis janardana Moore (1989) [1919–21]. Few individuals found in shaded clearings and open forest in the Eastern Foreland, more rarely in the Northeast Headland. It was found on all four islands in 1989 and known earlier (1982, of the more recent surveys) from Rakata and Sertung. Status: resident.

Orsotriaena medus (F.) (1983) [1919–21]. One individual seen on 31.viii.90 in the Eastern Foreland. Status: probable resident.

Neptis hylas (L.) (1984–85) [1908]. Not common, but a few individuals seen in both the Eastern Foreland and Northeast Headland. Status: resident.

Precis atlites (L.) (1984–85) [1983]. Not common, but seen daily from 26.viii.90 in open areas in all parts of the vegetated areas. Status: resident.

Precis sp. (?*almana javana*) (1990). Identity not confirmed. A single specimen of a bright orange *Precis* was seen resting on *Saccharum* in E on 1.ix.90 (TRN), but evaded capture. It did not resemble any species earlier recorded from the archipelago, and TRN had little doubt of its identity: the species is widespread in Malaysia and Indonesia. Status: ? straggler.

Lycaenidae

Miletus symethus (Cramer) (1984–85) [1982]. Not common, but seen regularly in forested areas of the Eastern Foreland. Status: resident.

Catochrysops strabo (F.) (1982) [1933]. Common throughout the coastal vegetation and seen occasionally in grassland areas within the Eastern Foreland. Status: resident.

Euchrysops cnejus (F.) (1983) [1919–21]. Rare. Seen only in one clearing in the Eastern Foreland where it was present also in 1985 and 1986. Status: resident.

Jamides aratus (Stoll) (1984–85) [1982]. Infrequent and apparently restricted to coastal vegetation of the Eastern Foreland. Status: resident.

Jamides celeno (Cramer) (1982) [1919–21]. Much more common than *J. aratus* and found along most of the vegetated coastline. Status: resident.

Lampides boeticus (L.) (1982) [1933]. Not common, but widely distributed along the vegetated coastline. Status: uncertain, possible resident but population almost certainly augmented by migration.

Zizina otis lysizone (Snellen) (1982) [1982]. Common on coastal vegetation in Eastern Foreland, more rarely in other clearings and further north. Status: resident.

Zizula hylax (F.) (1984–85) [1982]. Common, but less so than *Z. otis*, and with similar distribution. Status: resident.

Arhopala pseudocentaurus (Doubleday) (1989) [1919–21]. Several individuals seen patrolling forest edges of the Eastern Foreland. Status: presumed resident and recent colonist from other islands.

Hypolycaena erylus (Godart) (1983) [1919–21]. Not common, but seen most days in forest clearings of the Eastern Foreland. Status: resident.

Hesperiidae

Potanthus confucius (C. & R. Felder) (1982) [1919–21]. (See comments on identity of this taxon in New et al. 1988). Abundant in grasslands in the Eastern Foreland; few seen in open areas of the Northeast Headland; occasional individuals in the Northern Foreland. Status: resident.

Polytremis lubricans (Herrich-Schaeffer) (1989) [1908]. Confirmed from Anak Krakatau by Bush and Whittaker (1991), with earlier record erroneous (New et al. 1988). Rare in open grassland and woodland clearings of the Eastern Foreland. Found on Rakata in 1908 and 1919–21, but not seen on the archipelago since then except on Anak Krakatau. Status: presumed resident.

Pelopidas conjunctus (Herrich-Schaeffer) (1990) [1919–21]. Rare in open grassland in the Eastern Foreland. Found on Rakata and Sertung prior to 1921 and on Rakata in 1933. Not seen on the archipelago since then, although Yukawa (1984) recorded a *Pelopidas* as ?*agna* (Moore) from Sertung. Status: presumed resident.

Previously Recorded Species Not Found in 1990

Danaus melanippus (Cramer) (1984–85) [1908]. Seen commonly in 1984–86, but not found in 1989 (Bush & Whittaker 1991) nor in 1990. Specimens from our earlier collections have been compared carefully with recently captured *D. genutia*, and differ clearly in identity. It is possible that *D. genutia* has now replaced *D. melanippus* on Anak Krakatau.

Hypolimnas anomala (Wallace) (1982) [1919–21]. Possibly a sporadic migrant rather than resident on Anak Krakatau.

Precis orithya L. (1989). Seen by Bush in 1989 and then new to the archipelago (Bush & Whittaker 1991).

Anthene emolus (Godart) (1989) [1984]. Previously known only from Rakata, and recorded from Sertung and Anak Krakatau in 1989 (Bush & Whittaker 1991).

Jamides bochus (Stoll) (1989) [1982]. Previously recorded from Sertung (Yukawa 1984) and recorded from Rakata and Anak Krakatau in 1989 (Bush & Whittaker 1991).

Borbo cinnara (Wallace) (1982) [1982]. Not found in 1989 or in 1990.

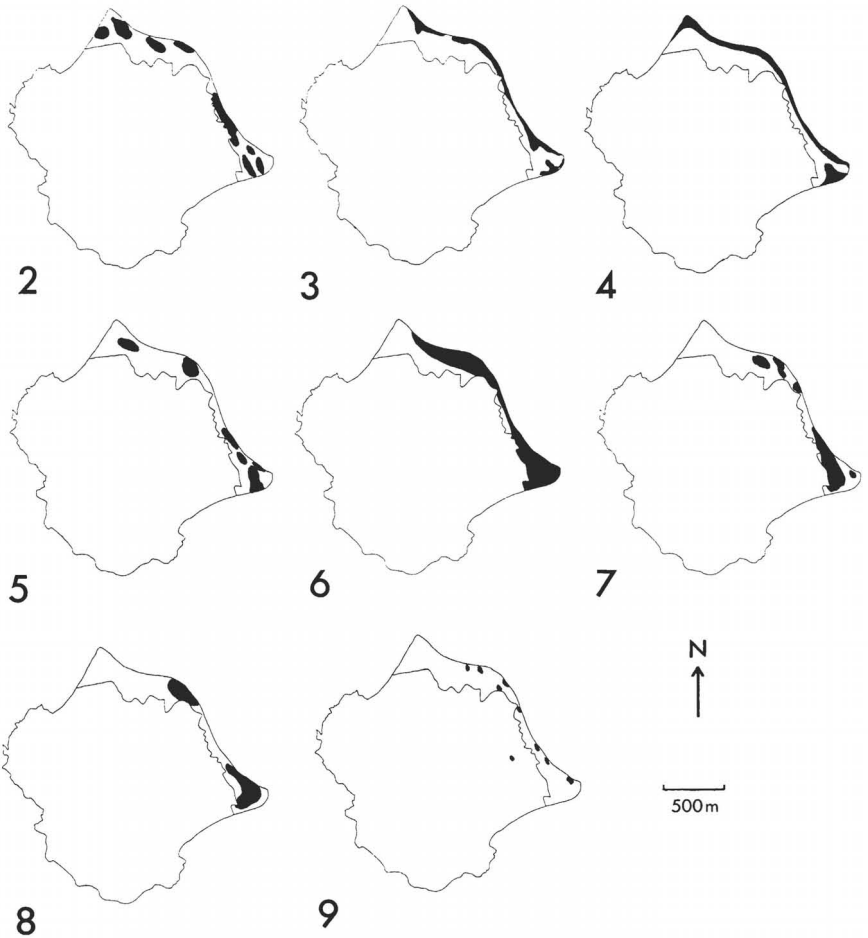
Hasora taminatus Huebner (1989). Recorded as new to the archipelago from Anak Krakatau in 1989 (Bush & Whittaker 1991).

Parnara cf. *guttatus* Bremner (1989). Also recorded as new to the archipelago from Anak Krakatau in 1989 (Bush & Whittaker 1991).

Telicota augias L. (1989) [1919–21]. The first record of the species on the archipelago since its occurrence on Rakata in 1919–21 (Bush & Whittaker 1991).

DISCUSSION

Forty-one species of butterfly have been recorded from Anak Krakatau (an increase of 18 since 1986), and up to about 30 of these are likely to be resident, some with populations augmented by regular migration. Only *C. pomona* has been observed migrating in the area by us, but the following species also are known migrants: *G. agamemnon, G. sarpedon, P. aristolochiae, E. hecabe, D. chrysippus, D. genutia, E. modesta, T. septentrionis, M. leda, P. atlites, L. boeticus.* Records of many of these are included in Williams (1930). Most species are clearly associated with the Eastern Foreland, fewer with the Northeast Headland, and fewest with the Northern Foreland (Fig. 1). All species of uncertain status in 1990 occurred in the Eastern Foreland, and no species were confined to the Northern Foreland. The general distributional picture is one of progressive attenuation both in species richness and overall abundance from the Eastern Foreland northward, corresponding to the less diverse vegetation structure and composition of other areas (Thornton & Rosengren 1988). About half the species recorded from each area were common there, but relative abundance in the areas differed (below). Distribution patterns of selected resident species are shown in Figs. 2–9. *Potanthus confucius* (Fig. 2) occurs in all grassland habitats on the island and was numerically the most abundant species during our survey. It was conspicuously more abundant in the Eastern Foreland (up to 14/100 m of grassland transect; mean of 26 transects between 0715 and 1730 h, 9/100 m) than in the Northeast (mean of 5.8/100 m in 14 transects) and in the Northeast than in the Northern Foreland (<2/100 m, 12 transects). It exemplifies well an impending slow expansion from a well-established population, largely dependent on *Ischaemum* (the larval food plant), in the Eastern Foreland and is a morning-active species (Fig. 10). As examples of the several widely distributed Lycaenidae associated with *Ipomea pes-caprae* formations, *Z. otis* (Fig. 3) and *C. strabo* (Fig. 4) both have coastal distributions; that of *C. strabo* is somewhat more extensive. Several residents appear to have wide but disjunct distributions on the island: *P. atlites* (Fig. 5) was found in all three main vegetated areas, but was not observed between these. In contrast, *R. juventa* (Fig. 6) was absent from the Northern Foreland but widely distributed elsewhere. *Euploea modesta* (Fig. 7) occurs in the more densely wooded areas and was not



FIGS. 2–9. Distribution (in black) of selected butterfly species on Anak Krakatau, 1990: **2**, *Potanthus confucius*; **3**, *Zizina otis*; **4**, *Catochrysops strabo*; **5**, *Precis atlites*; **6**, *Radena juventa*; **7**, *Euploea modesta*; **8**, *Troides helena*; **9**, *Catopsilia pomona*. Margin of vegetated area shown.

found in the Northern Foreland (but was present there by 1991), and the distribution of *T. helena* was generally similar (Fig. 8). In contrast to these residents, the incidence of the migrant *C. pomona* (Fig. 9) was very patchy, and a number of other migrants were seen only in the Eastern Foreland. All resident species (Table 1) occurred in the Eastern Foreland.

Many resident species are restricted in their distribution on Anak Krakatau; Table 1 ranks the more common species by relative abundance. The abundances of several species appear to have changed

TABLE 1. Relative abundance (1 = most abundant) of butterfly species in the three main habitat areas of Anak Krakatau, Aug.–Sept. 1990. Status of each species in each area shown as common (C), moderately common (MC), rare (R), as defined in text.

Sequence	Region		
	North	Northeast	East
1	*P. confucius* (R)	*C. strabo* (C)	*P. confucius* (C)
2	*Z. otis* (R)	*P. confucius* (MC)	*Z. otis* (C)
3	*E. blanda* (R)	*E. blanda* (MC)	*Z. hylas* (C)
4	*Z. hylas* (R)	*Z. hylas* (MC)	*C. strabo* (C)
5	*C. strabo* (R)	*Z. otis* (MC)	*E. blanda* (C)
6	*P. atlites* (R)	*P. aristolochiae* (MC)	*R. juventa* (C)

considerably since 1986, although the substantial natural fluctuations that can occur in insect populations imply the need for caution in this suggestion. The decline of *D. melanippus* is anomalous, but declines of several Lycaenidae (e.g., *Jamides, C. strabo*) may reflect some reduction of the extent of *Ipomoea pes-caprae* formations, especially around the southern part of the Eastern Foreland. Other taxa have remained remarkably constant. For example, it seems that the small colony of *E. cnejus* may have persisted without expansion of size or range since 1986. Some conspicuous recent colonizers, such as *T. helena* and *E. modesta*, have become very well-established within a short time.

As Bush et al. (1990) noted, butterfly assemblages on the Krakataus are strongly 'habitat-determined,' and the relatively early stage of succession on Anak Krakatau enables reliable correlation between resident butterflies and their preferred or obligate habitats. Anak Krakatau also is important in providing butterfly habitats not otherwise readily available on the archipelago. Several extinctions on the older islands in the 1920's, particularly of Hesperiidae, were attributed to forest closure eliminating grassland habitats (New et al. 1988). It is notable that three of those species, *T. augias, P. conjunctus*, and *P. lubricans*, that were not seen in the Anak Krakatau grasslands in 1984–86, and possibly others, have appeared recently in similar areas on Anak Krakatau after apparent absence from the archipelago of some 60 years. Their future on the island merits detailed appraisal to clarify the role of the island in the 'ecological rescue' (Thornton et al. 1990:152) of such early succession taxa whose habitats are declining elsewhere on the archipelago. The danaine *D. genutia sumatrana*, which inhabits *Casuarina* clearings, also now may be limited to Anak Krakatau. Another species, *C. panormus*, now persists only on the Sertung spit, which also supports *Casuarina* grassland; this species, too, should be studied in the future to determine whether or not it persists there.

The recent arrival on the archipelago (to Anak Krakatau) of two

TABLE 2. Incidence and relative abundance of resident Anak Krakatau butterflies in major vegetation types, Aug.–Sept. 1990. Vegetation types (1–6) are (1) *Ipomoea pes-caprae* associations, (2) *Ischaemum* grassland, (3) *Imperata, Saccharum* grassland, (4) *Casuarina,* (5) other woodland, (6) woodland clearings; — = absent, c = common, MC = moderately common, R = rare (see text); number in table list = more abundant species in each habitat from 1 (most abundant), down.

Species	Vegetation type					
	1	2	3	4	5	6
P. aristolochiae	—	R	R	5R	1MC	4MC
T. helena	—	—	—	R	4MC	MC
E. blanda	4MC	2MC	4MC	R	—	R
E. hecabe	MC	3R	MC	R	—	—
D. genutia	R	R	R	2MC	R	2MC
E. modesta	—	—	R	6R	2MC	R
R. juventa	6MC	R	R	1MC	3MC	1MC
T. septentrionis	—	—	—	—	—	R
M. leda	R	R	R	R	5MC	R
M. janardana	—	—	—	—	R	R
O. medus	—	R	—	—	—	—
N. hylas	R	—	—	R	R	R
P. atlites	R	R	R	R	R	MC
M. symethus	—	R	—	R	R	R
C. strabo	2C	4R	R	R	—	—
E. cnejus	—	—	—	—	—	R
J. aratus	R	R	—	—	—	—
J. celeno	5MC	R	2MC	R	—	—
L. boeticus	R	R	R	R	—	R
Z. otis	1C	R	3MC	3MC	—	R
Z. hylas	3C	R	—	—	—	R
A. pseudocentaurus	—	—	—	—	—	R
H. erylus	—	—	—	—	—	R
P. confucius	MC	1C	1MC	R	—	3MC
P. lubricans	—	R	R	—	—	R
P. conjunctus	—	R	R	—	—	—
Total resident species	14	18	15	16	10	20

hesperiids, *H. taminatus* and *P. guttatus*, and the nymphalid *P. orithya*, and (to the Sertung spit) of the lycaenids *Allotinus unicolor, Nacaduba beroe*, and *Prosotas lutea* illustrates the biogeographical roles that these two areas, both of which carry early vegetational stages, may play in permitting colonization of the archipelago by open country butterflies that would otherwise find no suitable habitat on the islands.

None of the species at present on Anak Krakatau can be considered a true 'forest butterfly.' Most are taxa associated with secondary or transitional seral stages, and are characterized by relatively good dispersal powers and broad geographical distributions. The most abundant species in each major habitat are listed in Table 2, and most of these are highly characteristic of the habitat noted. Butterfly species richness in grassland is rather similar to that on low coastal vegetation and also to open woodland and associated small clearings. However, closed wood-

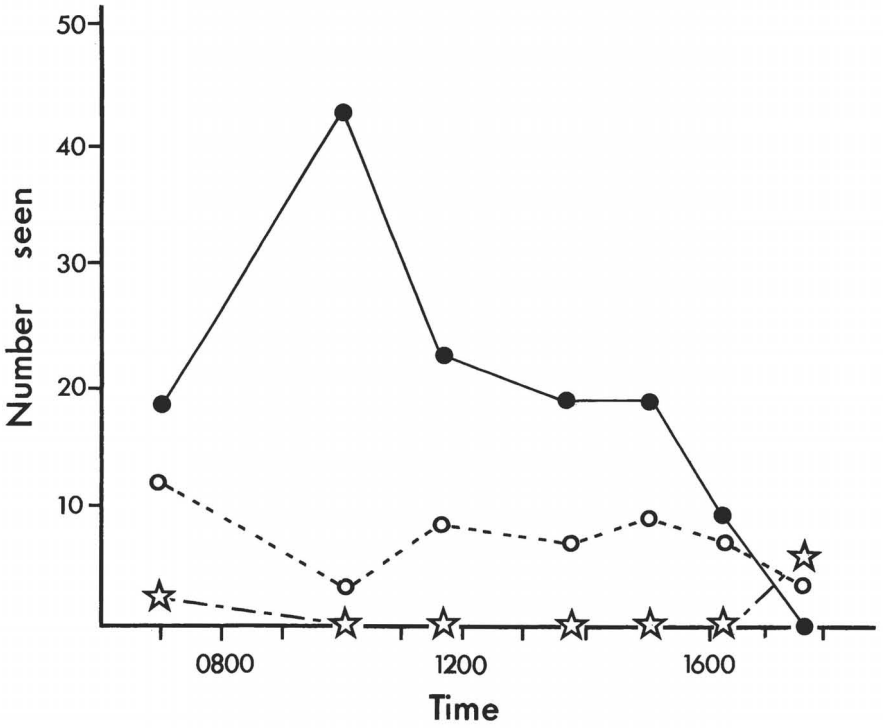


FIG. 10. Daily activity patterns of selected butterfly species on Anak Krakatau, based on transect walks. Solid circles: *Potanthus confucius*; open circles, *Radena juventa*; stars, *Melanitis leda*.

land-secondary forest has relatively few species associated with or restricted to it. Much of this limitation reflects availability of larval foodplants. As examples, New et al. (1988) emphasized the key nature of legume-dominated low coastal vegetation in promoting the establishment of many species on the Krakataus; Gramineae-dependent Hesperiidae depend on stands of grasses with little over-story; and *Aristolochia* L. (Aristolochiaceae) vines are restricted largely to secondary forest areas in the Eastern Foreland, coinciding with the major distribution of consumers such as *T. helena* and *P. aristolochiae*. In woodlands, these two species and *E. modesta* were restricted almost completely to denser areas, but most others occurred more commonly along edges and in smaller clearings where sunlight could penetrate. The most common such species, *R. juventa*, flew throughout the day without any major activity peaks (Fig. 10), and *D. genutia* also was common. The Satyrinae are 'furtive' and occurred in long grass in shaded clearings. Several Lycaenidae (e.g., *A. pseudocentaurus, H. erylus, E. cnejus*) were found only along woodland edges.

There was little evidence of interchange or movement of butterflies between habitat patches. Recaptures were obtained for all of the species marked and released at their points of capture: *I. juventa*—40 marked (18 recovered); *D. genutia*—24 (5); *E. blanda*—30 (4); *P. aristolochiae*—15 (9); *P. confucius*—32 (11); and *C. strabo*—8 (2). *Radena juventa* and *E. blanda* were marked with different colors in the Eastern Foreland and Northeast Headland, and none was recaptured in the other area. Most recaptures were within 20–40 m of the release points, with maximum distances (*R. juventa*—2, *D. genutia*—1) of about 200 m. In general, recaptures were too sporadic for reliable interpretation of population sizes but the estimates of relative abundance noted earlier incorporate inference from this study in addition to transect counts.

Leps and Spitzer (1990) compared the butterflies of forest climax, transitional, and ruderal communities in northern Vietnam by transect counts and indicated that high density and faunal heterogeneity were associated with the less advanced vegetation, whereas forest butterflies exhibited lower diversity but higher constancy. Fifty-five of the total of 82 species they recorded (Lycaenidae and Hesperiidae were excluded) had relatively broad geographical ranges, and some of these were characteristic of ruderal habitats (17 of 55 species) or forest clearings (6 of 55). If all records for each Vietnam habitat are combined, the totals for each habitat become 45 of 82 species (ruderal) and 62 of 82 (forest clearings), with a combined total of 75 species; only 7 of 82 species were confined to closed forest and all of these have restricted geographical ranges. Thus, there was a trend for broad range species to be excluded from more specialized or later succession plant associations. 'Ruderal systems' are the result of shifting agriculture, and they represent secondary simplification from the cultivation of fields derived from clearing forests and their subsequent abandonment and transformation to grasslands with low shrubs. Few such studies of habitat or successional segregation of butterflies have been made in southeast Asia, but Leps and Spitzer (1990) emphasize that many of the characteristic ruderal species are extremely good colonizers of early successional habitats, and their Vietnam list includes some of the Anak Krakatau taxa: *P. aristolochiae, P. memnon, G. sarpedon, C. pomona, E. hecabe* and *N. hylas*. In Vietnam, *T. helena* was most characteristic of forest clearings, coinciding (in part) with its habitat on Anak Krakatau.

To date, there are few true forest butterflies on any of the Krakatau islands and none on Anak Krakatau. As suitable habitat develops, some may be expected to appear—although there is a strong possibility that most such specialist species may not be sufficiently vagile to reach the islands except by rare chance. The mosaic of habitats at present available on Anak Krakatau increasingly fosters the establishment of many of

the earlier succession species that may arrive, and their persistence will depend on the continuance of the full array of such habitats, including *Ipomoea pes-caprae* communities and relatively pure grassland stands. The 'arrival wave' of butterfly species to the archipelago that is best represented on Anak Krakatau is the set that colonized the archipelago between 1908 and 1921, from 25 to 38 years after 1883, the period of forest formation. The biological age of Anak Krakatau, assuming a self-sterilizing volcanic eruption in 1952, was 38 years at the time of the last survey, and mixed forest was beginning to develop. Thornton et al. (1990) review numerous examples of the extinction of animals on the archipelago coinciding with the main period of canopy closure and elimination of more open habitats, and New et al. (1988) point out that the extinction rate for butterflies was highest during that period (1919–34). Monitoring the sequence of vegetational succession on Anak Krakatau over the next two decades could shed considerable light on the need to manage such open areas elsewhere to conserve the early successional habitats necessary for many invertebrate animals. This theme scarcely has been documented in tropical areas, especially those sufficiently distant from putative sources to render colonization by late successional 'specialist' taxa relatively difficult.

As Thomas (1991:270) commented 'Butterflies are becoming sufficiently well-studied for them to be used . . . for general conservation planning in some parts of the tropics, as a representative insect group.' His study in Costa Rica also emphasized that species frequenting modified habitats tend to be those with broad distributions, and that conservation of primary forest is necessary to conserve narrow endemic 'specialist' butterflies. Comparison with the pattern of butterfly colonization inferred on the older Krakatau islands suggests strongly that some widespread species on Anak Krakatau could be conserved locally only by maintenance of early seral stages of vegetation. For example, *D. genutia* and *P. conjunctus* appear to survive on the archipelago only because they inhabit the early successional habitats provided by Anak Krakatau. Others, such as *H. taminatus* and *P.* c.f. *guttatus*, may have been able to colonize the island group only because early successional habitats have been available. Altogether, some eleven butterfly species may owe their presence on the archipelago, either as recent colonists or as declining resident species, to the habitats provided by Anak Krakatau and the Sertung spit (Thornton et al. 1992). We suggest that such species will eventually disappear from Anak Krakatau as its communities move towards later successional phases. Such a move is by no means inevitable, however. Future volcanic activity could set back the succession, thus again postponing the extinction of such butterflies from the island. Rejuvenation of Anak Krakatau through sporadic vol-

canic activity may prove to be an important factor in assuring that such butterflies persist on the island.

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