

The Flight Heights of Chalcid Wasps (Hymenoptera, Chalcidoidea) in a Lowland Bornean Rain Forest: Fig Wasps are the High Fliers¹

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ABSTRACT

Tropical rain forests are characterized by their rich plant diversity and highly diverse insect faunas containing mainly rare species. Phytophagous and parasitoid insects utilizing such fragmented resources often must travel considerable distances to find suitable hosts. For small, weak-flying insects, entry into the fast-flowing air above the canopy can provide one way by which long-distance dispersal is achieved. Using sticky traps placed at different heights in a lowland rain forest of Borneo, we compared the diurnal and nocturnal flight heights of chalcids, a group of mainly very small parasitoids and phytophages, to determine if the air above the canopy was used for dispersal. Most families were represented throughout the range of trap heights, including those above the general canopy. A higher proportion of individuals were trapped above the canopy at night than during the day. Fig wasps were exceptional in that they were trapped almost entirely above the canopy. They included species associated with host trees that do not fruit in the canopy, suggesting that these short-lived, slow-flying insects actively fly up above the canopy and then use the wind to passively carry them the long distances needed to reach their highly localized and ephemeral hosts. Once the fig wasps detect the species-specific volatiles released by their host figs, they then may fly down into the canopy, where the lower wind speeds would allow them to fly actively upwind to their hosts.

Key words: Agaonidae; dispersal; Ficus; fig wasp; flight height; Mymaridae; parasitoid; rain forest; Sabah; vertical stratification.

ADULT FEMALE FIG WASPS (Hymenoptera, Chalcidoidea, Agaonidae) are the sole pollinators of fig trees (*Ficus* spp., Moraceae). Each species of fig tree, of which there are > 700, usually is pollinated by a single species of fig wasp that is not associated with any other fig tree species (Janzen 1979, Wiebes 1979). Fig wasps are able to successfully track a resource that is highly ephemeral and dispersed, especially in rain forests, where many fig trees produce large, highly synchronized crops attracting thousands of pollinating wasps over periods of only a few days (Nason 1996). Fruiting phenologies vary among fig tree species, but at the population level, fruiting is typically asynchronous, and continues throughout the year. Consequently, at any one time, only a small proportion of the trees belonging to any one species either are releasing pollinators

or requiring their services. The difficulties faced by the wasps are made more urgent by their short adult life spans (probably 48 hours at most) and the typically low densities of rain forest fig trees, particularly strangler figs (Mawdsley *et al.* 1998); it is clear that rain forest fig wasp pollinators often need to both cover large distances quickly and accurately to home-in on those hosts having figs at the correct stage of development. The same problems are faced by the numerous fig wasps that do not pollinate figs (currently also placed in Agaonidae), which are either seed predators or parasitoids, although the majority of these species probably have longer adult life spans.

When they are ready to be pollinated, fig trees release species-specific volatiles that attract their particular pollinators, and no others (Ware *et al.* 1993, Ware & Compton 1994a). Because they are so small, fig wasps have low flight speeds, and therefore have no control over their direction of

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flight once they are in air moving greater than a few meters per second (Ware & Compton 1994b). Given the often great distances between fig trees, there may be a trade-off between needing faster-moving air to aid random long-distance dispersal and slower wind speeds in which the wasps can control their direction of flight toward suitable host trees. Studies in South Africa and India (Ware & Compton 1994b,c; P. Kathuria & S. G. Compton, pers. obs.) have suggested that in savanna environments, fig wasps disperse upwards and downwind after emergence and are carried by the wind until they detect odors of fig trees with fruits at the correct stage of development. They then descend out of the air column, and by moving in and above the ground flora (where wind speeds are lower; Whitmore 1984, Sutton 1989), they make their way upwind to the source.

Similar movement patterns are unlikely to apply in a rain forest environment. Here, figs are produced at a great range of heights, from below the ground to emergents rising above the general canopy at 50 meters or more. Wind speeds are typically lower than in savanna situations, while at the lower levels of the forest, the air is often effectively still. Understory flight by fig wasps therefore could be more easily controlled and directed, but the distances they could travel would be limited by their low flight speed (recorded as < 37 cm/sec; Compton 1993) and short life span. This maximum flight speed translates to > 1 km/h, if flight could be maintained continuously, and potentially would allow them to travel several kilometers during their one or two days of adult life. The fig wasps, however, clearly cannot orient to suitable hosts over such long distances and the chances of coming within the attractant radius of a tree with figs at the correct stage will be correlated strongly with the distances that can be traveled (upwind directed movements toward figs of 100 m have been recorded, but the true extent of the attractant radii is unknown; P. Kathuria & S. G. Compton, pers. obs.). The same problems arise for other small, weak-flying insects in rain forests, such as other chalcid hymenopterans. Many of these species, however, are likely to be associated with resources that are not as spatially concentrated as figs, and so they are unlikely to be as dependent on long-distance flights to reach potential hosts.

Given the difficulties faced by rain forest fig wasps, how do they manage to get from tree to tree? Dispersing fig wasps may stay more or less at the heights where they are released by the trees, essentially searching the forest in only two dimen-

sions. Such movements, at least when the figs are produced within and below the canopy, will be largely limited in distance by the flight speeds of the wasps, which nonetheless can control the direction of their flights. Alternatively, fig wasps may take advantage of the faster-moving air that is available above the canopy to facilitate long-distance movement, initially flying upwards but then descending after a certain time period or once they have detected attractive volatiles. For attractants from figs produced in or below the canopy to reach the general air column above the forest, it is necessary for some upward movement of air to occur; however, this may be quite common (Whitmore 1984, Kira & Yoda 1989). Movement above the canopy by fig wasps would allow greater areas of the forest to be covered, but poses problems for such delicate insects, especially during the day when temperatures can be much higher, and humidities lower, than beneath the canopy. Flight above the canopy therefore may be an option only for night-flying fig wasps and other chalcids of a similar size.

There are few studies of the heights at which fig wasps and other chalcids fly. In open situations among savanna-type vegetation, approximately even densities of flying fig wasps were found within the air column from the ground to four meters (Ware & Compton 1994a). Using light traps in rain forest of Zaire and Sabah, Sutton and others (Sutton & Hudson 1980; S. L. Sutton, pers. comm.) found that night-flying fig wasps were more abundant within the canopy than at ground level, a conclusion also reached by Kato *et al.* (1995). In contrast, Ng (1978), based on malaise trap catches in western Malaysia, concluded that hymenopterans, of which chalcids were the most abundant group, mainly flew close to the ground and during the day.

Although night-flying fig wasps and small numbers of other chalcids are readily attracted to ultraviolet lights positioned from ground level to above the general canopy in rain forests (Kato *et al.* 1995; S. G. Compton & M. D. F. Ellwood, pers. obs.), the large potential radius of attraction produced by the lights makes this trapping method unsuitable for determining the heights at which wasps are moving before they are attracted. Furthermore, most chalcids, including some fig wasps, are day-flying, and so cannot be collected in this way. In this study, clear plastic sticky traps positioned at various heights in the canopy were used to examine the following hypotheses relating to the dispersal of fig wasps and other chalcids in rain

forests: (1) fig wasps are more likely than other chalcids to travel above the canopy, because the resources they need to locate are so localized that long-distance dispersal is required; (2) night-flying fig wasps and other chalcids are more likely to fly above the canopy than day-flying species because of the extreme physical conditions they would encounter above the canopy during the day; and (3) fig wasps disperse between trees by flying above the canopy, irrespective of the heights of their host figs.

STUDY SITE AND METHODS

Trapping was carried out in Borneo at the Danum Valley Field Centre in the Malaysian state of Sabah in June and July 1998. The traps were suspended from a 40-m observation platform erected in lowland riverine dipterocarp forest adjacent to the field center. In this area, the canopy surface is irregular, with numerous emergents (Newbery *et al.* 1992). Five cylindrical traps (diameter 14 cm, length 90 cm), each comprising six-A4 clear acetate sheets attached to a wire mesh frame, were covered with Oecotac® insect trapping adhesive. The adhesive and underlying plastic were shiny, rather than entirely transparent, which may have influenced the behavior of some flying insects. They were suspended at 9-m intervals vertically above each other from ground level to 37 meters above the ground. The main canopy at this location reached *ca* 30 m, with individual trees ascending above this to *ca* 50 m. Consequently, traps 4 and 5 were in the overstory (above the general canopy, but below the highest emergents), while 3 and 2 were within and slightly below the main canopy layer, respectively. Ground-level trap 1 was standing in a small clearing. Each trap was equipped with a rain guard immediately above it. The traps could be lowered for examination at ground level when required using a pulley system.

During period 1 of the study, the traps were examined twice daily at approximately dusk and dawn to differentiate between night- and day-flying species. Insects were removed by eye from the traps starting at 0615 and 1625 h, rather than true dusk and dawn, because light was needed to view the trapped insects. Dawn was at *ca* 0600 and dusk at 1815 h. The "nighttime" period therefore included any catches of crepuscular species. When being examined, the traps were suspended at approximately head height and all the small insects present were removed with a fine metal wire prior to subsequent microscopic examination. Fig wasps and other specimens requiring further study were treated in

n-heptanal to remove the adhesive (Henshaw 1993), then stored in 70 percent ethanol. The traps were examined twice daily between 26 June and 5 July, giving nine daytime and nine nighttime trapping periods. Continuous trapping was extended for an additional ten days (period 2). At the end of this period, the acetate sheets were removed and covered by thin transparent plastic sheets for transportation back to the laboratory and subsequent identification. Placement into families of Chalcidoidea followed Boucek (1988), with all fig wasps relegated to Agaonidae and pollinating species placed in the subfamily Agaoninae.

RESULTS

Representatives of eleven families of Chalcidoidea were present on the traps, with the better-represented families generally found throughout the range of trap heights (Table 1). The traps situated in the overstory above the general canopy (traps 4 and 5) and at ground level (trap 1) captured more chalcids than those in the canopy (Table 1). Numbers trapped are not straightforward indicators of densities, however, because the more rapid air movement above the general canopy would have resulted in more air being "sampled" by the traps there.

When fig wasps were distinguished from other chalcids, very different height profiles were evident. About as many non-fig wasps were trapped at ground level as on the highest of the traps, despite the lower volumes of air sampled at ground level (Fig. 1A). Pollinator fig wasps, in contrast, were restricted almost entirely to the traps above the general canopy (Fig. 1B). The small number of non-pollinator fig wasps that were trapped showed a similar pattern (Table 1). Differences in the profile of abundance with height also were present within different families of non-fig wasps (Table 1); encyrtids (the best represented family), for example, were much more active above the canopy than mymarids, which were present mainly at ground level (Figs. 1c, d).

Relatively fewer mymarids, aphelinids, and trichogrammatids were recorded during period 1, when the chalcids were removed directly from the traps at the beginning and end of each day, compared to period 2, when the traps were left in place and then removed to the laboratory (Tables 2 and 3). These three families contained the smallest chalcids (often < 1 mm in length), and some clearly were being missed during the twice-daily scanning of the traps.

TABLE 1. Captures of chalcids on sticky traps positioned from ground level (trap 1) to 37 m (trap 5). Periods 1 and 2 were combined. "Other fig wasps" were non-pollinators belonging to the subfamilies Epichrisomallinae, Sycoryctinae, and Sycophaginae. "Others" were damaged chalcids that could not be placed to family.

	Traps					Total	Trap position (\bar{x})	Trap positions (range)
	1	2	3	4	5			
Fig pollinators	0	1	0	17	56	74	4.7	2-5
Other fig wasps	0	0	0	6	25	31	4.8	4-5
Aphelinidae	13	9	9	12	5	48	2.7	1-5
Chalcididae	1	0	1	1	4	7	4.0	1-5
Elasmidae	0	1	0	0	0	1	2.0	2
Encyrtidae	28	30	32	49	93	232	3.6	1-5
Eulophidae	52	11	4	23	43	133	2.9	1-5
Eupelmidae	5	9	11	24	49	98	4.1	1-5
Myrmariidae	97	41	32	16	13	199	2.0	1-5
Pteromalidae	0	11	0	8	7	26	3.4	2-5
Torymidae	0	0	0	0	1	1	5.0	5
Trichogrammatidae	8	5	4	4	14	35	3.3	1-5
Others	20	12	3	1	5	41	2.0	1-5
Total chalcids	224	130	96	161	315	926	3.2	1-5

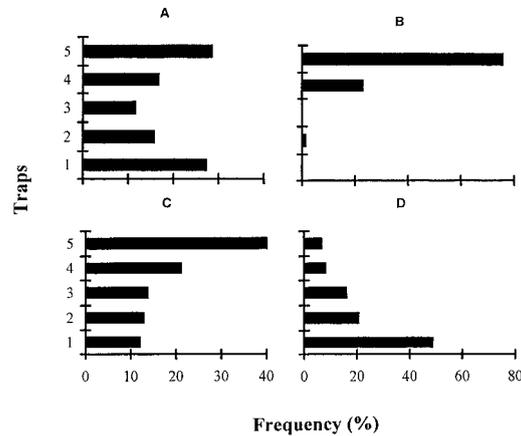


FIGURE 1. Captures on sticky traps positioned from ground level (trap 1) to 37 m (Trap 5) in rain forest at Danum Valley Field Centre, Sabah. (A) Chalcids other than fig wasps (Agaonidae); (B) Pollinator fig wasps (Agaonidae, Agaoninae); (C) Encyrtidae; and (D) Myrmariidae.

During period 1, when day and nighttime samples were collected separately, the total number of chalcids trapped during the day was almost twice as many as at night, despite the shorter daytime trapping interval (Tables 2 and 3). Therefore, general activity was probably greater during daylight hours, although greater wind speeds during the day could have biased the results, at least for traps above the canopy, and the traps would be more visible during the day. Fig wasps again provided an exception to this activity pattern, with more individuals being trapped during the night. The heights at which chalcids in general were flying showed some diel variation, with 63 percent of the chalcids on overstory traps 4 and 5 during the day, compared to 82 percent at night. The proportion of the total chalcid captures on the overstory traps (4 and 5 combined) at night was significantly higher than during the day (Tables 2 and 3; Fig. 2; $\chi^2_{[1]} = 46.9, P < 0.001$). This pattern was still evident when the predominantly nighttime and high-flying fig wasps were excluded ($\chi^2_{[1]} = 27.2, P < 0.001$). Almost all the fig wasps (both pollinators and non-pollinators) were collected above the canopy on traps 4 and 5. Furthermore, the highest trap captured 89 percent of the pollinators at night compared to 29 percent during the day (day:night captures on trap 5 compared to traps 1-4 combined; $\chi^2_{[1]} = 27.6, P < 0.001$), suggesting that they tended to fly even higher at night.

The flight heights of the fig wasps collected on

TABLE 2. *Nighttime captures of chalcids on sticky traps positioned from ground level (trap 1) to 37 m (trap 5). Period 1 only: no Elasmidae, Torymidae, or Trichogrammatidae were recorded during this period. "Other fig wasps" were non-pollinators belonging to the subfamilies Epichrysohallinae, Sycoryctinae, and Sycophaginae.*

	Traps					Total	Trap position (\bar{x})	Trap positions (range)
	1	2	3	4	5			
Fig pollinators	0	0	0	2	17	19	4.9	4–5
Other fig wasps	0	0	0	0	2	2	5.0	5
Aphelinidae	0	0	0	5	0	5	4.0	4
Chalcididae	0	0	0	1	0	1	4.0	4
Encyrtidae	4	2	3	12	22	43	4.0	1–5
Eulophidae	0	0	0	4	7	11	4.6	4–5
Eupelmidae	0	2	1	1	4	8	3.9	2–5
Mymaridae	0	0	0	1	0	1	4.0	4
Pteromalidae	0	7	0	7	1	15	3.8	2–5
Total chalcids	4	11	4	33	53	105	4.1	1–5

the traps could not be related directly to the heights of the figs they pollinate, because the host relationships for many of the species are unknown. Indirect comparisons are nonetheless possible, using the breeding systems of their host plants. These are readily distinguishable, because those wasps that pollinate monoecious *Ficus* species have considerably longer ovipositors than those associated with dioecious hosts. Strangler fig trees, with their figs placed high in the canopy, are monoecious, whereas dioecious species mainly produce their figs at lower levels. Species associated with monoecious hosts dominated the catches, both in numbers of individuals and species (Fig. 3); 78.6 percent of the pollinators of the monoecious *Ficus* were present on the highest trap, compared to 64.3 percent of those pollinating dioecious hosts (Table 4). This difference was not significant ($\chi^2_{[1]} = 1.9$, $P > 0.05$), suggesting that fig wasps pollinating figs situated at lower elevations may fly as high above the

canopy as those fig wasps that pollinate strangler figs.

Pollinating fig wasps were represented by at least 21 morphologically distinct taxa on the sticky traps (based on 68 individuals in suitable condition for assignment to taxonomic units). This represents *ca* 15 percent of all species likely to be found in Borneo as a whole, assuming the general 1:1 host: pollinator relationship (Corner 1963, Wiebes 1979). Given that a vertical column of air only 14 cm in diameter was sampled passively along a fraction of its length, for a period that was no longer than the duration that fig trees would remain attractive to pollinators, this high species richness illustrates the tremendous dispersal ability and host finding potential of the wasps. A small number of pollinator fig wasp species nonetheless dominated the total catch, with many of the other species represented by just one or two individuals (Fig. 3). The more abundant taxa may have arisen from a

TABLE 3. *Daytime captures of chalcids on sticky traps positioned from ground level (trap 1) to 37 m (trap 5). Period 1 only: "Other fig wasps" were non-pollinators belonging to the subfamilies Epichrysohallinae, Sycoryctinae, and Sycophaginae.*

	Traps					Total	Trap height (\bar{x})	Trap heights (range)
	1	2	3	4	5			
Fig pollinators	0	1	0	4	2	7	4.0	2–5
Other fig wasps	0	0	0	0	0	0	—	—
Aphelinidae	0	0	1	0	1	2	4.0	3–5
Chalcididae	1	0	1	0	4	6	4.0	1–5
Encyrtidae	10	11	13	14	22	70	3.4	1–5
Eulophidae	2	0	1	8	5	16	3.9	1–5
Eupelmidae	2	5	5	16	29	57	4.1	1–5
Mymaridae	1	2	0	1	0	4	2.2	1–4
Pteromalidae	2	12	1	4	10	29	3.3	1–5
Total chalcids	18	31	22	47	73	191	3.7	1–5

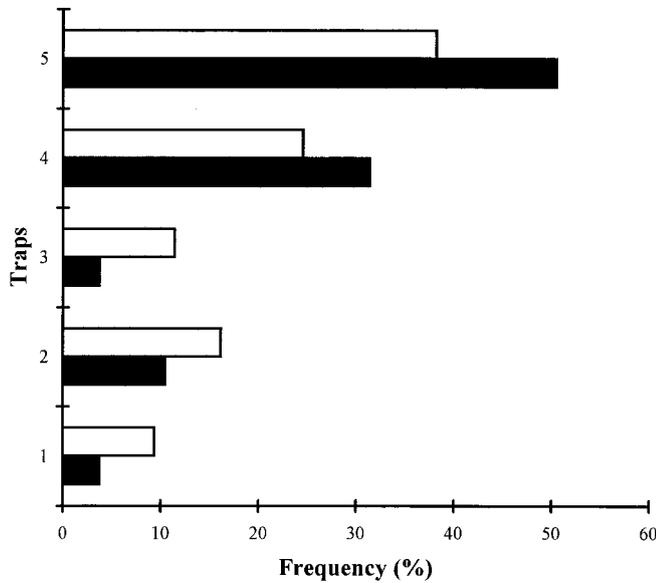


FIGURE 2. The chalcids (all families, including Agaonidae) captured during daytime (open bars) and nighttime (solid bars) on sticky traps positioned from ground level (trap 1) to 37 m (trap 5) in rain forest at Danum Valley Field Centre, Sabah.

small number of fig trees that were releasing fig wasps in the general area, with the remainder coming from more distant sources; however, no trees releasing wasps were found in a thorough search within an *ca* 100-meter radius of the traps, or by a less thorough survey beyond this.

DISCUSSION

These results were obtained from a single location, over a relatively brief period of time. Furthermore, the traps did not extend above the emergent trees in the forest. The generality of the results therefore must be treated with caution. At Danum Valley at least it is clear that insect activity above the general canopy is not insignificant. Because of the much more rapid movement of air in the overstory (and

above), compared to that within and below the canopy, the air column above the general canopy offers insects, particularly smaller, slower-flying species, the potential to disperse over much greater distances than they could otherwise achieve. Our hypotheses that fig wasps are more likely to travel above the canopy than other chalcids and that this would be irrespective of where their host figs were positioned were supported insofar as they were the only group that was almost entirely restricted to traps placed in the overstory. The opportunities for dispersal above the canopy, however, were utilized not only by fig wasps, as most other families of chalcids were also numerous on the traps above the canopy and were found also at lower levels in the forest. The mymarids (a family of minute egg parasitoids) appeared to be an interesting exception in that they were restricted largely to the lower levels in the forest.

Physical conditions above the canopy can be much harsher than below, with higher temperatures and lower humidities. These conditions are likely to pose particular physiological problems for the small insects like chalcids, which might be expected to benefit most from using the “highway” above the forest. We hypothesized that flying at night above the canopy, rather than during the day, was one way in which fig wasps and other chalcids might circumvent this problem. Relatively more

TABLE 4. *The trap heights of fig wasps from ground level (trap 1) to 37 m (trap 5) in relation to the pollination system of their host trees (monoecious or dioecious). Four additional individuals were too badly damaged for host determination.*

	Traps 1-3	Trap 4	Trap 5
Monoecious pollinators	0	12	44
Dioecious pollinators	1	4	9

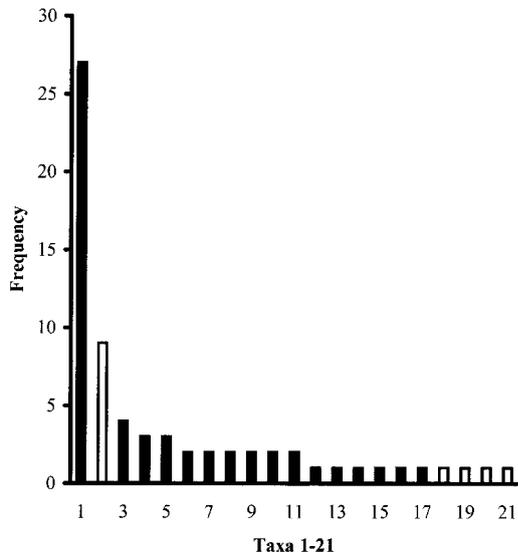


FIGURE 3. The frequency of capture for individuals belonging to the 21 pollinating fig wasp taxa on sticky traps in rain forest at Danum Valley Field Centre, Sabah. Open bars: species with dioecious *Ficus* hosts; solid bars: species with monoecious hosts.

chalcids were trapped above the canopy at night than during daylight, but overall chalcid activity was nonetheless greater during daylight hours. Several pollinator fig wasps with typical diurnal facies (dark body, small eyes) were recorded on the traps that were collected just after dawn. Some were still alive, indicating that they had been trapped very recently and had been flying at or around dawn.

Crepuscular activity therefore may be a feature of some of the species.

Discussions on vertical stratification of insects in rain forests tend to treat the canopy as the uppermost layer of the forest, ignoring the air above. Yet it clearly cannot be ignored when the dispersal of animals is being considered because the overstorey appears to be the preferred region for dispersal of fig wasps, some other chalcids, and perhaps other small insects. Fig trees have a broad importance in many tropical forests because their figs provide resources for many species of vertebrates (Terborgh 1986). Forest disturbance, including logging operations, not only reduces the densities and spatial distribution of many species of fig trees, but also changes the nature of the physical environment through which fig wasps have to disperse. Knowing how fig wasps get from one tree to another is important if we are to predict how the pollination of figs, and consequently the availability of figs for frugivores to eat, is being changed by rain forest exploitation.

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LITERATURE CITED

- BOUCEK, Z. 1988. Australasian Chalcidoidea (Hymenoptera). CAB International, Wallingford, England. 832 pp.
- COMPTON, S. G. 1993. One way to be a fig. *Afr. Entomol.* 1: 151-158.
- CORNER, E. J. H. 1963. *Ficus* on Mt. Kinabalu. *Proc. Linn. Soc. Lond.* 175: 37-39.
- HENSHAW, D. J. DE C. 1993. Specimen recovery from sticky traps. *Entomol. Mon. Mag.* 129: 236.
- JANZEN, D. H. 1979. How to be a fig. *Annu. Rev. Ecol. Syst.* 10: 13-51.
- KATO, M., T. INOUE, A. A. HAMID, T. NAGAMITSU, M. B. NERDEK, A. R. NONA, T. ITINO, S. YAMANE, AND T. YUMOTO. 1995. Seasonality and vertical structure of light-attracted insect communities in a dipterocarp forest in Sarawak. *Res. Popul. Ecol.* 37: 59-79.
- KIRA, T., AND K. YODA. 1989. Vertical stratification in microclimate. *In* H. Leith and M. J. A. Werger (Eds.). *Ecosystems of the world 14b. Tropical rain forest ecosystems*, pp. 55-72. Elsevier, Amsterdam, The Netherlands.
- MAWDSLEY, N., S. G. COMPTON, AND R. J. WHITTAKER. 1998. Population persistence, pollination mutualisms, and figs in fragmented tropical landscapes. *Conserv. Biol.* 12: 1416-1420.
- NASON, J. D. 1996. Paternity analysis of the breeding structure of strangler fig populations: evidence for substantial long-distance wasp dispersal. *J. Biogeogr.* 23: 501-512.
- NEWBERY, D., E. J. F. CAMPBELL, Y. F. LEE, C. E. RIDSDALE, AND M. J. STILL. 1992. Primary lowland dipterocarp forest at Danum Valley, Sabah, Malaysia: structure, relative abundance and family composition. *Philosophic. Trans. R. Soc. Lond. B* 335: 341-356.

- NG, R. 1978. The vertical distribution of aerial insects in Pasoh Forest Reserve. *Malay. Nat. J.* 30: 299–305.
- SUTTON, S. L. 1989. The spatial distribution of flying insects. In H. Leith and M. J. A. Werger (Eds.). *Ecosystems of the world 14b. Tropical rain forest ecosystems*, pp. 427–436. Elsevier, Amsterdam, The Netherlands.
- , AND P. J. HUDSON. 1980. The vertical distribution of flying insects in the lowland rain forest of Zaire. *Zool. J. Linn. Soc.* 68: 111–123.
- TERBORGH, J. 1986. Keystone plant resources in the tropical forest. In M. E. Soulé (Ed.). *Conservation biology: the science of scarcity and diversity*, pp. 330–344. Sinauer Associates, Sunderland, Massachusetts.
- WARE, A. B., AND S. G. COMPTON. 1994a. Fig wasp responses to host plant volatiles. *J. Chem. Ecol.* 20: 785–802.
- , AND ———. 1994b. Dispersal of adult female fig wasps I: arrivals and departures. *Entomol. Exp. Appl.* 73: 221–230.
- , AND ———. 1994c. Dispersal of adult female fig wasps II: movements between trees. *Entomol. Exp. Appl.* 73: 231–238.
- , P. T. KAYE, S. G. COMPTON, AND S. VAN NOORT. 1993. Fig volatiles: their role in attracting pollinators and maintaining pollinator specificity. *Plant Syst. Evol.* 186: 147–156.
- WHITMORE, T. C. 1984. *Tropical rain forests of the Far East*. Clarendon Press, Oxford, England. 282 pp.
- WIEBES, J. T. 1979. Co-evolution of figs and their insect pollinators. *Annu. Rev. Ecol. Syst.* 10: 1–12.
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