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Dispersal of fig wasps (Hymenoptera: Chalcidoidea) across primary and logged rainforest in Sabah (Malaysia)

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Abstract. Selectively logged forests differ from primary forest in species composition and physical structure. Both factors potentially influence the insects that live and disperse within them. Fig wasps (Hymenoptera: Chalcidoidea), which include the pollinators of fig trees (*Ficus* species), are capable of moving between trees several kilometers apart, and previous studies have shown that they predominantly disperse above the canopy of primary forests, taking advantage of the faster wind speeds there. Using arrays of passive sticky traps we examined the flight heights of fig wasps in adjacent areas of primary and logged (secondary) lowland rainforest at Danum Valley, Sabah, Malaysia and also compared the composition of their assemblages. The numbers of wasps trapped were roughly similar, but non-pollinating species were better represented in the primary forest. Amongst the pollinator fig wasps, night-flying pollinators of monoecious fig trees predominated in the primary forest, while diurnal pollinators of monoecious trees were more abundant in the logged forest. Most of the fig wasps were trapped above the canopy in the primary forest, while in logged forest, where a clear cut canopy structure was absent, they were flying closer to the ground. Night- and day-flying species had similar height profiles within the two forest types. The differences between the fig wasp assemblages at adjacent logged and primary forest sites may reflect contrasting local host tree abundance, despite the homogenizing effect of their long-distance dispersal capabilities.

Ecology, altitude, dispersal, *Ficus*, flight, pollination, rainforest, fig wasp, Hymenoptera, Chalcidoidea, Oriental region

INTRODUCTION

Host species-specific fig wasps (Hymenoptera: Chalcidoidea: Agaonidae) are the pollinators of the 700 or more species of fig trees (Moraceae: *Ficus* spp.) (Janzen 1979, Wiebes 1979). Around half the species of fig trees are monoecious, with all trees bearing figs that produce both seeds and pollinating wasps, while the remaining species are functionally dioecious, with trees that produce either seed-producing or wasp-producing figs. Individual fig trees, especially of monoecious species, typically fruit synchronously, with intervals of weeks or months between successive crops. This means that the females of each generation of wasps commonly have to disperse between fig trees if they and their pollinators are to reproduce. In contrast, at the population level fruiting is typically asynchronous and at any one time there are only a small proportion of the trees of any one species that are either releasing pollinators, or waiting to be pollinated. This increases the distances that the pollinators need to travel, as the nearest suitable hosts can be kilometres away from trees that are releasing the wasps. This suggests that fig wasps require exceptional dispersal and host-finding abilities (Compton 2002), and in confirmation of this, recent evidence has shown that desert-living fig wasps can reach trees more than 100 kilometres away from their parent plants (S. Ahmed & S. G. Compton, unpubl.).

Such long distance dispersal between the trees is particularly surprising given the physical characteristics of fig wasps, as the adult pollinators are small, weak-flying insects that do not feed, are prone to dehydration and probably never survive for longer than 48 hours (Compton et al. 1994). There are also non-pollinating species (also belonging to the Chalcidoidea) that must be capable of routine dispersal between fig trees. Their larval biologies are diverse, with some feeding in galled ovules in the same way as the pollinators, while others are parasitoids. These non-pollinating fig wasps have certain advantages relative to the pollinators, in that they may feed as adults, be longer-lived, or may not all be host tree specific (Compton et al. 1994).

For fig wasps to be able to track a resource that is so highly ephemeral and widely dispersed they need to be able to cover large distances quickly and they need to be able to accurately home-in on those hosts which have figs at the correct stage of development. When they are ready to be pollinated, fig trees release species-specific volatiles, which attract their particular pollinators, and no others (van Noort et al. 1989), but because they are so small, fig wasps have low flight speeds, and have no control over their direction of flight once they are in air moving greater than a few metres per second (Ware & Compton 1994a). Based largely on studies in savannah environments (Ware & Compton 1994a, b), Compton (2002) provided a model of how between-tree dispersal may be achieved, given the slow flight speeds and limited longevities of the wasps. This involves an initial passive dispersal phase, involving long-distance down-wind travel within the general air column, followed by a shorter controlled upwind flight, closer to the ground or vegetation, to reach trees that are of the correct species, and have figs at a suitable stage of development.

The densities of strangler (hemiepiphytic) fig trees in rainforests are often particularly low (Mawdsley et al. 1998), yet these monoecious trees produce large, highly synchronised crops that

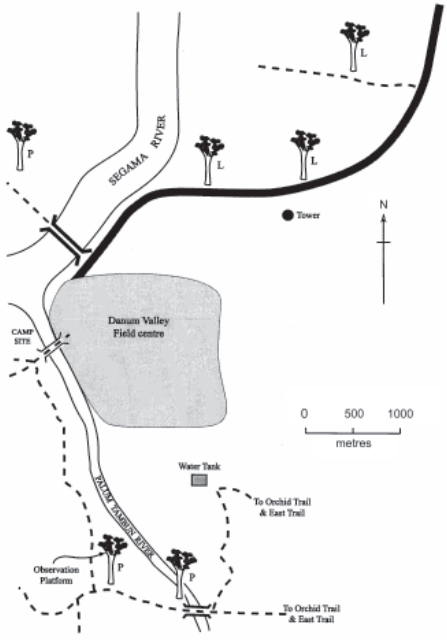

Fig. 1. The locations of trap sites (tree symbols) in primary (P) and secondary (S) forest adjacent to the Danum Valley Field Centre, Sabah.

are able to attract many thousands of pollinating wasps over periods of just a few days (Nason 1996). In rain forest environments, entry into the fast-flowing air above the canopy may provide the means by which long distance dispersal is achieved by fig wasps, followed by descent into the canopy, and below, where wind speeds are lower (Whitmore 1984, Sutton 1989) and controlled flight can be achieved. Descent into the canopy could potentially be in response to the attractants produced by figs in or below the canopy as upward movement of air out of the forest may be quite common (Whitmore 1984, Kira & Yoda 1989).

In a previous study (Compton et al. 2000) we compared the flight heights of fig wasps and other chalcidoids in primary rainforest at Danum Valley in Sabah, Borneo. Most families were represented throughout the range of trap heights, including those above the general canopy, but fig wasps were exceptional in that they were almost entirely trapped above the canopy. These included species associated with host trees that fruit low in the forest, suggesting that they actively fly up above the canopy as part of their dispersal strategy. Using similar techniques elsewhere in Borneo, Harrison (2003) has nonetheless shown that pollinators of dioecious figs are relatively poorly represented in traps placed above the canopy, implying that not all fig wasps disperse there.

As elsewhere in Borneo, South-east Asia and beyond, the rainforests of Borneo are being rapidly logged and cleared. In Sabah, primary forest is effectively restricted to protected areas, with the rest of the country comprising areas of secondary (logged) forest, and, increasingly, plantations. Forest fragmentation and disturbance will clearly have an impact on the ability of fig wasps to disperse between fig trees. Fig trees are often regarded as representing "keystone resources" in tropical forests (Terborgh 1986) because of their all-year-round production of figs, often in large quantities, which can maintain frugivore populations at times when other fruits are not available. If forest fragmentation leads to fewer figs being pollinated, then fewer figs will be available for eating (Mawdsley et al. 1998, Harrison 2003). Furthermore, in Bornean forests at least, different fig trees support different frugivore assemblages, depending on how the figs are presented (Shanahan & Compton 2001). Any disturbance that changes either the abundance or species composition of fig tree assemblages will therefore have consequences for frugivorous animal species.

In this study, passive sticky traps positioned at various heights within primary and secondary rainforest were used to examine the impact of logging on the composition of fig wasp assemblages and the heights at which they fly. The results are discussed in terms of their impact on the pollination of fig trees and the wider consequences for the animals which feed on figs.

METHODS

Trapping was carried out adjacent to the Danum Valley Field Centre (Malaysia: Sabah) in June and July 1999. Rainfall locally averages a little under 3 m a year, and is relatively aseasonal although there are often drier periods around April and September (Marsh & Greer 1992). The field centre is situated at the eastern boundary of the Danum Valley Conservation Area, which comprises 480 km^2 of undisturbed rainforest. It is adjacent to a large area of selectively logged forest which, like the conservation area, forms part of the concession owned by the Sabah Foundation (Yayasan Sabah). The primary forest adjacent to the field centre is lowland evergreen dipterocarp forest with a canopy surface that is rather irregular, with numerous emergents (Newbery et al. 1992). The logged forest would initially have been similar in composition, but selective logging removes the large, commercially valuable timber species and also causes extensive damage to non-target species (Heydon & Bulloh 1997). The logged forest near the field centre consists largely of secondary regrowth, with *Koompassia* (Leguminosae) the only remaining tall trees. The secondary forest immediately to the north of the field centre was logged in 1989.

We monitored flying fig wasps using traps suspended from three trees in the primary forest (numbered P1–P3) and three in the logged forest (S1–S3, Fig. 1). We found no fig trees releasing wasps in the vicinity of the traps, based on thorough searches within approximately 100 metres of each trap site and less thorough searches over larger areas. Most of the lines supporting the traps were shot over branches using a crossbow (Ellwood & Foster

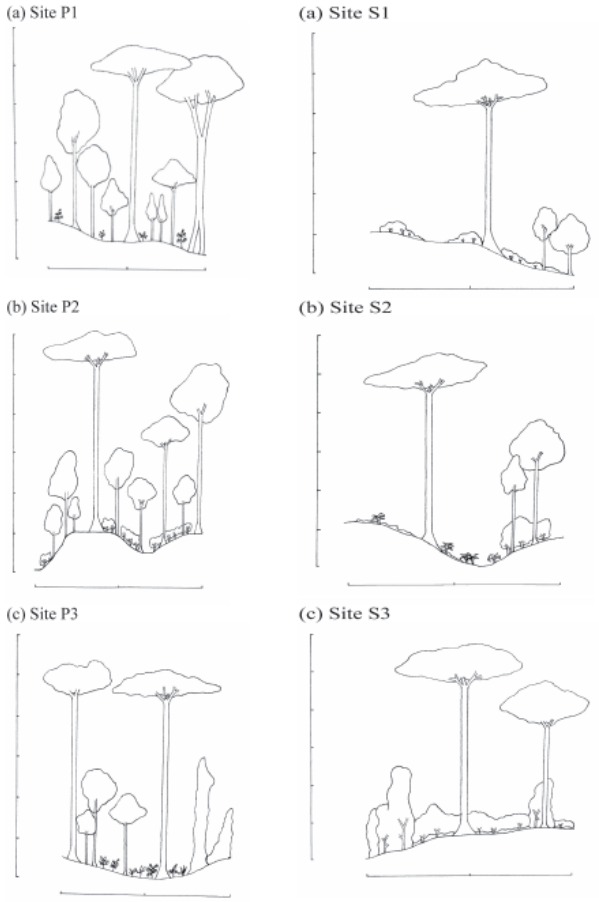

Fig. 2. Vegetation profile diagrams of the six trap locations; (a) – site P1, (b) – site P2, (c) – site P3, (d) – site S1, (e) – site S2, (f) – site S3; note vertical compression: both vertical and horizontal scale intervals equal 10 m.

2001), but P1 was suspended from a canopy observation platform as used previously by Compton et al. (2000). At each trap site, five cylindrical traps (diameter 14 cm, length 90 cm) were suspended vertically at 0, 10, 20, 30 and 40 metres above the ground. Each trap comprised six A4 clear acetate sheets attached to wire mesh frames that were covered with Oecotac® insect trapping adhesive. The adhesive and underlying plastic were shiny, rather than totally transparent. Each trap was topped with a rain guard and the ropes were attached so as to allow the traps to be lowered to ground level when required for examination.

A Bushnell Yardage Pro 400 laser range-finder was used to estimate the heights of the vegetation in the areas surrounding the traps. Primary forest canopy structure was irregular, but the upper two traps were consistently positioned in the overstory, above the general canopy, but below the emergent trees, while the remaining traps were within and below the canopy. Site P1 was situated in riverine forest alongside the Danum Valley nature trail, about 500 m from a tributary of the Segama River. The main canopy was dense, reaching to approximately 30 m, with numerous emergents acending above this to approximately 50m (Fig. 2a). Site P2 was located nearby, inside a bend in the tributary, which at its closest was about 3 m from the base of the tree. Consequently, the site was more open than P1, and the ground sloped more sharply (Fig. 2b). General canopy height was estimated at about 18 m. Site P3 was located on the west bank of the Segama River, about 100 m along West Trail 1.2 (Fig. 1). Vegetation locally was generally dense, with numerous emergents and a general canopy height of around 25 m (Fig. 2c).

Traps located in the logged forest were suspended from the only remaining emergents (*Koompassia* trees). No general canopy had reformed at the sites, and all but the ground-level traps were above the vegetation in the areas immediately surrounding the trap sites. The nearest of the three secondary (logged) forest sites to the primary forest (S1) was located about 2 km from site P3, down slope from the field centre access road. The trees in the area were widely dispersed with only a few individuals greater than a few metres in height, and most of the vegetation only reaching about 2 m (Fig. 3a). Site S2 was around 1km east of S1, and also down slope from the road (Fig. 3b). Only low-growing vegetation was present around the base of the tree, but some adjacent trees reached 11 m. Site S3 was located alongside an elephant track about 200 m from S2. Regrowth around the base of the tree was dense, with numerous creepers (Fig. 3c). Some adjacent trees reached approximately 12 m in height.

We started the trapping in the primary forest in early June and all the traps were removed after having been suspended for 19 days The effectiveness of the adhesive was checked periodically and renewed if necessary. Individual acetate sheets were inserted inside clear plastic bags for transport and subsequent examination using a binocular microscope. Fig wasps that required more detailed study were removed from the acetate sheets, treated in n-heptanal to remove the adhesive (Henshaw 1993), relaxed in water and then glued on to card points. Taxonomic placement followed Bouček (1988).

Wind speeds are generally slight beneath the rainforest canopy, but increase progressively with height above the canopy (Sutton 1989). The numbers of fig wasps trapped on the acetates at different heights are therefore not true indicators of densities per unit volume of air, but represent the numbers of wasps passing through the areas 'sampled' by the traps. Because of the more rapid air movement above the general canopy, more air will come into contact with the traps there. The flight heights of the fig wasps collected on the traps could not be related directly to the heights of the figs they pollinate, because the host relationships of most of the species are unknown and many remain undescribed. Indirect comparisons are nonetheless possible for the pollinator fig wasps, 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 (but not exclusively) produce their figs at lower levels. The diel flight activity of the pollinators can also be determined, based on their colouration and the size of the eyes. The general appearance (facies) of nocturnal (and crepuscular) species have a paler colouration and larger eyes (Compton et al. 2000) compared with the darker brown and smaller eyes of day-flying species.

RESULTS

Faunal comparisons

Approximately two thousand fig wasps were collected on the sticky traps during the 19 day sampling period (Tab. 1), with the numbers of individual wasps trapped at each site ranging from 168 (site P1) to 765 (site P2). Overall there were roughly similar numbers of fig wasps collected in the primary and secondary forest, but the compositions of the fig wasp faunas were different,

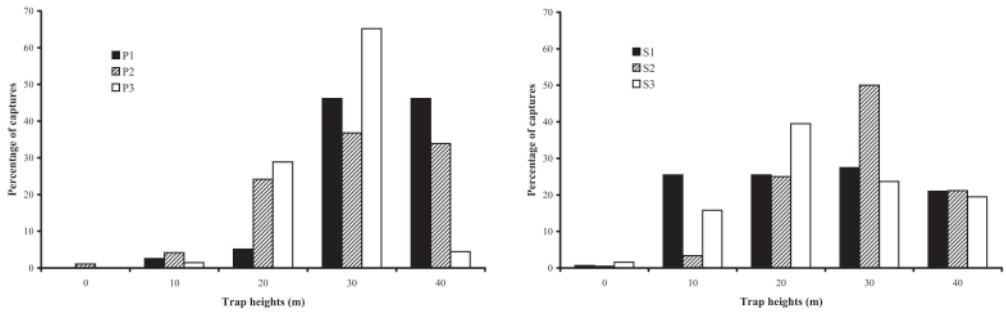

Fig. 3. (a) – the proportion of pollinator fig wasps trapped at different heights above the ground at three sites located in primary forest (P1–P3); (b) – the proportion of pollinator fig wasps trapped at different heights above the ground at three sites located in secondary forest (S1–S3).

Tab. 1. Captures of pollinating and non-pollinating fig wasps on sticky traps at sites in primary and logged forest at Danum Valley Field Centre, Sabah

site	pollinators	non-pollinators	% non-pollinators	total
primary forest				
P1	117	51	30.4	168
P2	555	210	27.5	765
P3	135	76	36.0	211
total	807	337	29.5	1144
secondary (logged) forest				
S1	448	45	9.1	493
S2	208	28	11.9	236
S3	190	42	18.1	232
total	846	115	12.0	961

despite the relative proximity of the trap sites. Non-pollinators were better represented in primary forest, where they represented about 30% of the total fig wasps, compared with only 12% in the logged forest (Tab. 1).

Five subfamilies of non-pollinating fig wasps were recorded, with epichrysomallines particularly well represented, especially at the primary forest sites where they formed around 75% of the total (Tab. 2). Of the five subfamilies of non-pollinators, only the Sycoryctinae is known to include species that are known to be parasitoids that attack the larvae of pollinating fig wasps. These were far outnumbered by representatives of the other subfamilies, all of which, so far as is known, are gallers of fig seeds and ovules (for example Compton & van Noort 1992).

Tab. 2. The numbers and taxonomic representation of non-pollinating fig wasps captured on sticky traps in primary and logged forest

site	Epichrysomallinae	Otitesellinae	Sycoryctinae	Sycoecinae	Apocryptophaginae
primary forest					
P1	20	2	26	3	0
P2	167	26	6	10	1
P3	67	8	1	0	0
total (%)	254 (75.4)	36 (10.7)	33 (9.8)	13 (3.9)	1 (0.3)
secondary (logged) forest					
S1	13	19	11	2	0
S2	16	3	4	4	1
S3	17	13	9	2	1
total (%)	46 (40.0)	35 (30.4)	24 (20.9)	8 (7.0)	2 (1.7)

A majority of the pollinator fig wasps were associated with monoecious host trees in both the primary forest (73.1%) and the secondary forest (69.3%, Tab. 3). The predominant flight periods differed between the two habitats however, with nocturnal fig wasps the more common group in the primary forest, but in a minority in the logged forest (Tables 3 and 4). Pollinator fig wasps with nocturnal flight activity and monoecious host trees were by far the most common combination among the wasps trapped in the primary forest. In contrast, diurnal pollinators of monoecious trees were the most numerous group among the wasps trapped in the logged forest, with combinations other than nocturnal pollinators of dioecious species also well represented. In both forest

Tab. 3. Flight periods (nocturnal or diurnal) and host tree breeding systems (monoecious or dioecious) of pollinating fig wasps based on their morphological characteristics. The host breeding systems of 17 damaged individuals could not be determined ("uncertain")

	nocturnal		diurnal		nocturnal	diurnal
	monoecious	dioecious	monoecious	dioecious	uncertain	uncertain
primary forest						
P1	45	9	27	35	1	0
P2	320	80	92	61	2	0
P3	65	6	37	25	1	1
total	430	95	156	121	4	1
secondary (logged) forest						
S1	97	14	228	102	2	5
S2	61	13	74	60	0	0
S3	50	7	68	60	1	4
total	208	34	370	222	3	9

types the proportion of wasps with diurnal flight activity was far more common among species associated with dioecious host species than those associated with monoecious hosts (Tab. 4).

Flight heights

The numbers of pollinator fig wasps trapped at different heights varied significantly among the three trap sites located in the primary forest and also among the three sites located in the logged forest ($X^2_{[6]} = 82.7$, $P<0.001$ and $X^2_{[6]} = 73.4$, $P<0.001$ respectively; captures at 0 and 10 metres were combined because of low cell counts). Few pollinator fig wasps were trapped at ground level and at 10 m in the primary forest, and most were captured above the canopy, at 30 m and above (Fig. 3a). Fewer, or about the same number of individuals, were captured at 30 m compared with 40 m, despite the faster air flow to which the 40 m traps will have been exposed, suggesting that aerial densities are likely to have been higher at 30 m, just above the canopy, than at 40 m. No pollinators were captured at ground level in the logged forest, where there was a much denser ground flora than in the primary forest, but the proportions captured at 10 m were generally higher than those recorded in the primary forest (Fig. 3b). Captures on the traps were most frequent at 20 or 30 m at two of the logged forest trap sites, while at the third site (S1) the numbers trapped were roughly similar across the height range from10 to 40 m.

Tab. 4. Nocturnal and diurnal pollinators associated with monoecious or dioecious host trees. The host trees of "uncertain" specimens could not be established

host trees	nocturnal	diurnal	% nocturnal
primary forest			
monoecious	430	156	73.4
dioecious	95	121	44.0
uncertain	4	1	80.0
total	529	278	65.6
secondary (logged) forest			
monoecious	208	370	36.0
dioecious	34	222	13.3
uncertain	3	9	25.0
total	245	601	29.0

Tab. 5. Capture heights of day- and night-flying pollinating fig wasps

location	night				day						
	0&10 m	20 m	30 m	40 m	0&10 m	20 m	30 m	40 m	X^2	D. F.	P
P1	1	0	24	30	2	6	30	24	7.27	3	0.06
P2	18	114	141	129	11	20	63	59	14.78	3	0.002
P3	1	19	48	4	1	20	40	2	0.82	3	0.84
S1	51	29	21	12	66	85	102	82	33.37	3	<0.001
S2	2	20	41	11	6	32	63	33	3.40	3	0.33
S3	13	18	13	14	20	57	32	23	3.72	3	0.29

Flight above the canopy during the day exposes fig wasps to more extreme temperatures than they would experience within the forest. It might therefore be expected that night-flying species would be more likely to be trapped above the canopy than day-flying species. Because of the heterogeneity between sites within forest types, comparisons of the flight heights of different sub-groups of pollinators were carried out on a tree by tree basis. Frequencies of day- and night-flying pollinator fig wasps were significantly different with respect to height at several of the sites (Tab. 5), but there was no consistent trend for one or other group to be better represented on the higher traps. Overall, the day-flying and night-flying fig wasps had very similar trap height profiles in both forest types (Figs 4a, b). Similarly, pollinators associated with dioecious host plants, many of which produce figs that are located beneath the canopy, were not consistently better-represented at the lower trap heights than the pollinators of monoecious fig trees, most of which are stranglers that fruit in the canopy (Tab. 6, Figs 5a, b).

Tab. 6. Capture heights of fig wasp pollinators with monoecious and dioecious host trees

location	monoecious hosts				dioecious hosts						
	0&10 m	20 m	30 m	40 m	0&10 m	20 m	30 m	40 m	X^2	D. F.	P
P1	1	0	37	34	2	6	16	20	12.24	3	0.01
P2	18	107	148	139	11	27	54	49	4.57	3	0.21
P3	1	27	69	5	1	11	18	1	1.95	3	0.58
S1	89	77	95	64	28	33	26	29	3.7	3	0.29
S2	2	32	71	30	6	20	33	14	6.57	3	0.09
S3	18	50	25	25	14	25	17	11	1.88	3	0.60

Individual taxa

At least 40 distinguishable species of fig wasp pollinators were present on the traps, and assuming that each species of *Ficus* has one species of pollinator associated with it, then this represents around 30% of the total number of species that are expected to be present in the whole of Borneo. The poor condition of the specimens after extraction from the glue, in combination with the very small differences between many fig wasp species (many of which are undescribed), made it impossible to routinely assign the fig wasps to species level. Three of the more abundant and distinctive taxa were nonetheless distinguished (Tab. 7). As with the fauna as a whole, there was considerable variation in the numbers of each taxon recorded between individual trees, but their relative abundance was similar in the primary and secondary forest. Despite differences in their host trees and flight times (Species One was a night-flying species associated with a monoecious host tree, Species Two was also nocturnal, but with a dioecious host, whole Species Three was diurnal, with a monoecious host), the flight height profiles of the three species were largely similar in both the primary and secondary forest. The most frequent trapping height for Species Two was nonetheless unusually close to the ground (10 m) in the secondary forest, but not the primary forest (Figs 6a, b).

DISCUSSION

Logged forests are an increasingly important refuge for wildlife in states such as Sabah, where primary forest cover has been greatly reduced. The relatively careful logging that has taken place around Danum Valley Field Centre has resulted in a forest that, while lacking the grandeur of the primary forest, is nonetheless a significant resource for many species, including rarities such as Asian elephants. Similarly, the suitability for invertebrates of the logged forest appears to vary

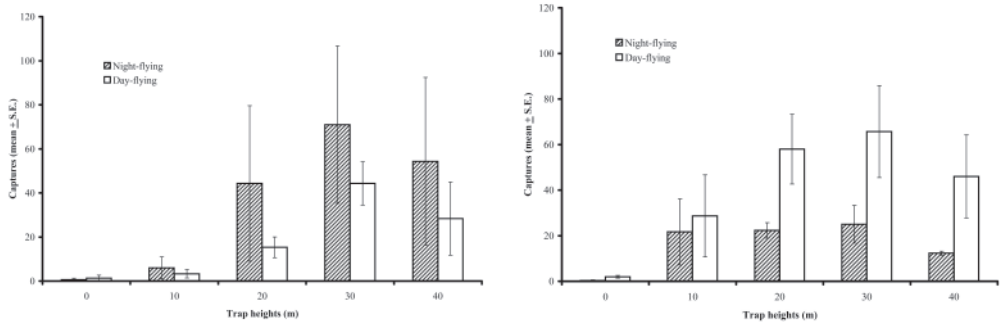

Fig. 4. (a) – the numbers of night- and day-flying pollinator fig wasps trapped at different heights above the ground in primary forest (three sites combined); (b) – the numbers of night- and day-flying pollinator fig wasps trapped at different heights above the ground in secondary forest (three sites combined).

according to the taxon (Davis & Sutton 1998, Willott et al. 2000) with some species faring better in logged forest than others. Logging directly influences rainforest fig wasps by changing the abundance of their host plants (large strangler figs tend to be destroyed during logging operations, while species associated with disturbance, such as some geocarps, appear to be favoured). The question addressed in this paper was whether logging also influences fig wasps indirectly, by changing the physical structure of the forest through which they must travel to find suitable host trees.

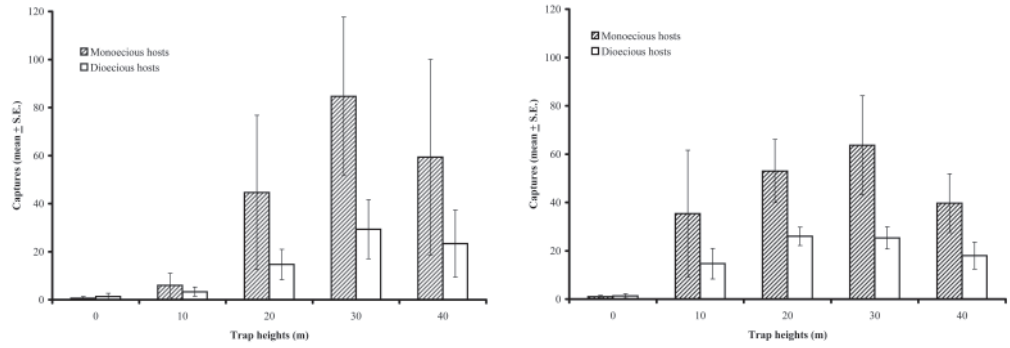

Fig. 5. (a) – the numbers of pollinator fig wasps associated with monoecious or dioecious host trees trapped at different heights above the ground in primary forest (three sites combined); (b) – the numbers of pollinator fig wasps associated with monoecious or dioecious host trees trapped at different heights above the ground in secondary forest (three sites combined).

Daily capture rates of the fig wasps were considerably higher than those during a previous study at Danum Valley (Compton et al. 2000), possibly because the earlier studies were carried out shortly after a major drought period in northern Borneo that had a considerable impact on fig tree fruiting (Harrison 2000). There were gross differences in the fig wasp faunas trapped in the logged and primary forest, most notably the much higher proportion of non-pollinators collected at the primary forest sites. Amongst the pollinator fig wasps, night-flying pollinators of monoecious fig trees predominated in the primary forest, while diurnal pollinators of monoecious trees were more abundant in the logged forest. Whether these differences reflect the relative abundance of their host trees in the two forest types is unknown, but differences in trap composition over such small spatial scales are perhaps surprising, given the great distances traveled by the wasps, which might be expected to have a homogenizing effect on the faunas encountered at nearby locations. Such differences in the composition of fig wasp faunas between primary and secondary forests, if not a purely local or transient phenomenon, will have implications for the reproductive success of the fig trees as pollinator arrival rates at trees are likely to be affected, as will seed losses to non-pollinators.

The results obtained here agree with previous studies showing that many primary rainforest pollinator fig wasps journey above the canopy before arriving at host trees (Compton et al. 2000, Harrison 2003). Small numbers of some species associated with dioecious host trees were nonetheless only trapped at or near ground level, as shown by Harrison (2003) elsewhere in Borneo, suggesting that they employ a different dispersal strategy. Daytime physical conditions above the canopy are harsher than below, with higher temperatures and lower humidities. Perhaps related to this, diurnal flight facies were predominant among the pollinators of dioecious species, in contrast to the mainly nocturnal facies shown by the pollinators of monoecious fig trees. Night- and day-flying pollinator species as a whole nonetheless had similar height profiles within the two forest types, and there were no clear-cut differences between the flight profiles of the three individual species that were monitored, despite their differing hosts or flight times.

The secondary forest lacked a clear cut canopy structure, and in response to this the fig wasps were found to be traveling much closer to the ground. At one of the secondary forest sites roughly equal numbers of pollinator wasps were present on traps within the range of 10–40 metres, while roughly equal numbers were trapped between 20–40 metres at the other two sites. Given that wind speed increases with altitude, this suggests that in the secondary forest aerial densities of the wasps were probably highest just 10–20 metres above the ground.

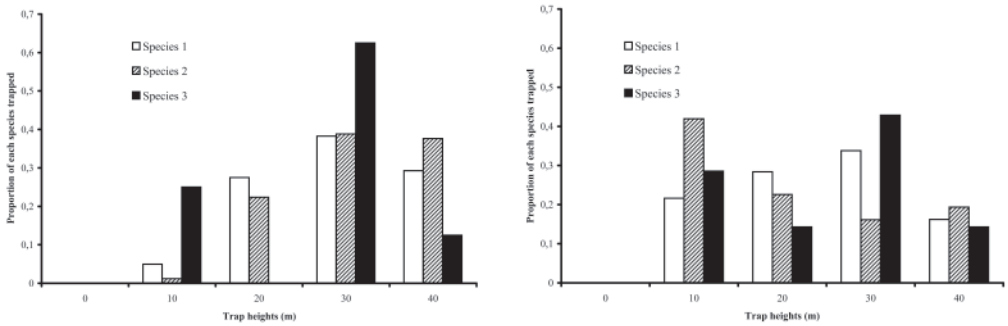

Fig. 6. (a) – the heights at which three pollinator fig wasp species were trapped in primary forest (three sites combined); (b) – the heights at which the same three pollinator fig wasps were trapped in secondary forest (three sites combined).

Tab. 7. Capture locations of three individual taxa of pollinator fig wasps

location	taxa of pollinator fig wasps		
	species 1 (nocturnal, with monoecious host tree)	species 2 (nocturnal, with dioecious host tree)	species 3 (diurnal, with monoecious host tree)
P1	18	6	1
P2	182	74	2
P3	22	5	7
P total	222	85	10
S1	32	14	5
S2	24	11	0
S3	18	6	2
S total	74	31	7

Fig wasps are typical of other small insects that utilize fast moving air for dispersal (Compton 2002) and their modified flight height profiles in logged forest may well be replicated by small insects in general, with implications beyond fig trees and their host trees. Dispersing fig wasps are often highly abundant in tropical forests, contributing, for example, 84% of all the canopy insects collected at light in Sarawak by Kato et al. (1995) and one third of all the food items collected by the edible-nest swiftlet (*Aerodramus fuciphagus*) in peninsular Malaysia (Langham 1980). Behavioural responses amongst predators on "aerial plankton" are therefore to be expected.

A c k n o w l e d g e m e n t s

Back in 1980 or early 1981, a doctoral student interested in chalcids was planning his first trip to the tropics and sought advice at what was then the British Museum (Natural History Museum London). Fortunately for him, Zdeněk Bouček suggested that there was much to be done with fig wasps, particularly the non-pollinators. Almost 25 years later, the senior author would like to express his gratitude to Zdeněk, and to concur with his assessment.

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