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# FIG WASP DISPERSAL IN URBAN SINGAPORE

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***ABSTRACT***. — In largely urban Singapore, 69% of the 45 recorded native fig species (*Ficus*, Moraceae) are either critically endangered (24 species) or nationally extinct (7 species). Small populations of dioecious fig species are expected to be particularly vulnerable, because of evidence that their species-specific pollinators may be less mobile than those of monoecious figs. We therefore studied the dispersal of pollinating fig wasps (Chalcidoidea: Agaonidae) at an urban site by capturing them with sticky traps set at 25 m, 10 m, and 2 m above the ground. All but one of the pollinator genera expected for Singapore were captured, as well as one genus with no local hosts (*Kradibia*) and one whose only local host is apparently extinct (*Dolichoris*). Pollinators of monoecious host taxa dominated the catch (440 wasps; 90%) and were mostly caught in the 25 m traps. Dioecious pollinators were rare (28 wasps; 6%), despite the abundance and frequent reproduction of their hosts in the vicinity, and were mostly caught in the 2 m traps. These patterns are similar to those reported from previous studies in rural areas and suggests that wasp dispersal in Singapore displays similar trends. This study provides baseline data on fig wasp diversity found in Singapore through dispersal.

***KEY WORDS***. — Agaonidae, dispersal, *Ficus*, mutualism, pollination, urbanisation

## INTRODUCTION

The figs (*Ficus*, Moraceae) are one of the largest genera of tropical woody plants, with approximately 800 species currently known (Berg & Corner, 2005). The genus occurs throughout the tropics, but it is most diverse in terms of species, growth forms, and breeding systems in the tropical Indo-Pacific region (Corlett & Primack, 2011). Figs have a reciprocal, obligate mutualism with pollinating wasps (Agaonidae), which raise their larvae in galled fig ovaries, and also support a community of non-pollinating fig wasps (Janzen, 1979). The flowers are completely enclosed inside a fleshy receptacle, the syconium, which the pollinators enter, while most non-pollinating wasps oviposit from outside. The pollinating wasps have a very short adult lifespan (usually < 2 days) during which they must locate a receptive syconium of their host fig tree. In monoecious fig species each syconium produces both seeds and wasps, while in functionally dioecious figs the plants are either functionally male, producing both pollen-carrying pollinators as well as non-pollinators from their syconia, or functionally female, producing seeds embedded in the ripe syconia, which attract seed dispersal agents.

Plant species involved in an obligate pollination mutualism would be expected to be at increased risk of extinction, since the vulnerabilities of the pollinator are added to those of the plant (Koh et al., 2004). However, the fact that the fig–fig wasp mutualism has persisted for 60 Myr (Ronsted et al., 2005) suggests that this increased risk is more than counterbalanced by the advantages of the efficient pollination mechanism, which allows some fig species to persist at extremely low population densities (Ahmed et al., 2009). The handful of studies that have looked at fig wasp dispersal have shown that pollinating fig wasps of monoecious fig species fly high and are passively dispersed over long distances before being attracted by species-specific volatiles to receptive syconia (Ware & Compton, 1994a, 1994b; Compton et al., 2000; Compton et al., 2005; Harrison & Rasplus 2006; Ahmed et al., 2009). Harrison & Rasplus (2006) documented dispersal at 75 m above the ground and Ahmed et al. (2009) found that wasps can disperse pollen up to 160 km from the source tree. In striking contrast, however, the pollinators of dioecious fig species are rarely caught above the forest canopy and a variety of evidence suggests that they may have more restricted dispersal ranges which may be attributed to the growth forms (mostly small trees, shrubs and climbers) of their hosts (Harrison & Rasplus, 2006; Lin et al., 2008;

Wang & Sun, 2009; Chen et al., 2011; Dev et al., 2011; Moe & Weiblen, 2011). Under natural conditions, the relatively high population densities and frequent reproduction of many dioecious fig species may compensate for—and contribute to—shorter wasp dispersal distances, but increasing habitat fragmentation may have made dioecious fig populations vulnerable to local extinction of their pollinators during extreme drought conditions (Harrison, 2000).

Previous studies of fig wasp dispersal have been carried out in primary, secondary or logged secondary forests (Compton et al., 2005; Harrison, 2003; Harrison & Rasplus, 2006) which is in contrast with Singapore, an extreme example of habitat fragmentation, with small areas of forest set in a largely urbanised matrix (Yee et al., 2011). A total of 69% of the 45 recorded native fig species are either critically endangered (24 species) or nationally extinct (seven species), compared with 62% in these two categories for the entire vascular flora (Chong et al., 2009). The ability of pollinating fig wasps to disperse within this landscape, and from the larger areas of forest still present in the surrounding region, may be critical to the survival of both fig wasps and their host fig plants in Singapore. This study therefore assessed the presence, relative abundance, and vertical distribution of dispersing fig wasps at a site in urban Singapore.

## MATERIAL AND METHODS

Two-thirds of the land area of modern Singapore is either non-vegetated (39%; roads, buildings etc.) or covered in managed vegetation (27%; parks, gardens and roadside plantings; Yee et al., 2011). Most surviving fig species are confined to the forested Nature Reserves, but a large shrub, *F. grossularioides*, two tree species, *F. fistulosa* and *F. variegata*, a scandent shrub, *F. heteropleura*, a climber, *F. punctata*, and three hemi-epiphytes, *F. benjamina*, *F. microcarpa* and *F. religiosa*, are common in urban and periurban habitats (Table 1). *Ficus religiosa* is a naturalised alien and the native status of *F. benjamina* is unclear (Chong et al., 2009). An additional climber, *F. pumila*, is a widely planted alien and is pollinated in Singapore (unpublished data).

The study was conducted on Kent Ridge, within the National University of Singapore (NUS), near the southwest coast of Singapore. Kent Ridge is 6.5 km south of the nearest area of primary forest, at Bukit Timah Nature Reserve, and is occupied by young secondary forest, managed vegetation, roads and buildings. In addition to the eight common urban fig species listed above, there are scattered individuals of *F. aurata* and *F. caulocarpa* present in the surrounding area and other species are planted, but not known to be pollinated. Traps were placed at four locations on Kent Ridge: (1) the NUS Geography Weather Station at a height of 25 m above ground level, which is the highest point in the western region of Singapore (90 m above sea level) because of its location on a ridge; (2) the rooftop of a laboratory building (S1A), 10 m above ground level; (3) under the canopy of secondary forest, 2 m above ground; and (4) on an exposed portion of Kent Ridge, 2 m above ground. The height of the traps at 25 m was chosen for high fliers, 10 m for intermediate fliers, and 2 m above ground (under canopy and exposed) for low fliers. The traps consisted of 1.5 L plastic bottles coated with Tanglefoot sticky glue (Harrison, 2003) and supported by 2 m poles. The traps were run for 7 continuous days during which they were checked every 24 hours and fig wasps collected.

Two trapping experiments were used. The first consisted of one sticky trap each at the Geography Weather Station (25 m), S1A (10 m), and under the forest canopy (2 m) run concurrently for seven days and repeated three times, in Mar.2010, May 2010, and Jun.2010. The second experiment consisted of one sticky trap each at three points 200 m apart in an exposed area of Kent Ridge (2 m) concurrently run for seven days, repeated twice in Jan.2011 and Feb.2011. This gave a total of 105 trap days. Data for all 2 m traps were pooled together because the catches from under forest canopy only consisted of eight wasps. Identifications to morpho-species were done by Simon van Noort. Unfortunately, the damage from sticky traps to fig wasps precluded identification to species level for a portion of the entire catch. Wiebes (1994) was used for identification and Cruad et al. (2010) for genera classification. The genus *Kradibia* includes pollinators of both monoecious and dioecious fig species but was included with the pollinators of dioecious hosts since wasps caught were *Kradibia dubium*, pollinator of dioecious *F. heteropleura*.

Spearman's correlation was used to test for association between the abundance of the 24-h fig wasp captures from the 25 m traps (21 trap days) and the corresponding 24-h total rainfall and average wind speed. Data was acquired from the Geography Weather Station, which is situated 1 m away from the trap.

## RESULTS

A total of 468 pollinating fig wasps representing at least 17 species, 21 non-pollinating fig wasps in four genera, and eight unidentified fig wasps were caught over the entire study (Tables 1, 2). The pollinators of monoecious figs dominated the catch (440 wasps; 90%), with three genera, *Platyscapa* (55%), *Eupristina* (33%), and *Dolichoris* (10%), making up 98% of the monoecious pollinators caught. *Platyscapa* comprised of four species, *Platyscapa quadraticeps* (the pollinator of *F. religiosa*), which was the most abundant wasp species overall, *Platyscapa corneri* (pollinator of *F. superba*), and two others. *Eupristina* comprised of *Eupristina verticillata* (the pollinator of *F. microcarpa*), *Eupristina koningsbergeri* (pollinator of *F. benjamina*), and *Eupristina leightoni* (pollinator of *F. kerkovenii*). Because of the damage from sticky traps to fig wasps, especially their antenna and wings, it was difficult to differentiate species in *Dolichoris*. Numbers of pollinators for dioecious fig species were much lower (28; 6%), despite a much higher density of dioecious host plants in the study area. *Valisia malayana* (the pollinator of *F. grossularioides*) was the most caught with just nine individuals, followed by *Kradibia dubium* (pollinator of *F. heteropleura*) and *Ceratosolen* (for which *F. fistulosa* is by

Table 1. Pollinator genera caught and the corresponding host figs in Singapore with checklist status according to Chong et al. (2009). Information on pollinator–host figs taken from Wiebes (1996) and Cruad et al. (2010). *indicate species seen on Kent Ridge.

| Genera | Wasp species | Wasps | Host species | Sexuality | Singapore status |
|---|---|---|---|---|---|
| *Platyscapa* | 4 | 243 | *F. religiosa** | Monoecious | Naturalised alien |
| | | | *F. superba* | Monoecious | Endangered |
| | | | *F. caulocarpa** | Monoecious | Common |
| | | | *F. virens* | Monoecious | Critically Endangered |
| *Eupristina* | 3 | 147 | *F. microcarpa** | Monoecious | Common |
| | | | *F. kerkhovenii* | Monoecious | Critically Endangered |
| | | | *F. benjamina** | Monoecious | Common, possibly non-native |
| | | | *F. benghalensis* | Monoecious | Casual alien |
| *Waterstoniella* | 1 | 1 | *F. xylophylla* | Monoecious | Critically Endangered |
| | | | *F. consociata* | Monoecious | Critically Endangered |
| | | | *F. binnendijkii* | Monoecious | Critically Endangered |
| | | | *F. crassiramea* | Monoecious | Critically Endangered |
| | | | *F. retusa* | Monoecious | Critically Endangered |
| | | | *F. sundaica* | Monoecious | Critically Endangered |
| *Pleistodontes* | 1 | 3 | *F. elastica* | Monoecious | Casual alien |
| *Dolichoris* | >1 | 43 | *F. vasculosa* | Monoecious | Endangered |
| *Deilagaon* | 1 | 3 | *F. annulata* | Monoecious | Extinct |
| *Kradibia* | 2 | 12 | *F. heteropleura** | Dioecious | Common |
| | | | *F. obscura* | Monoecious | Critically Endangered |
| *Valisia* | 1 | 9 | *F. grossularioides** | Dioecious | Common |
| | | | *F. aurata** | Dioecious | Vulnerable |
| | | | *F. chartacea* | Dioecious | Vulnerable |
| | | | *F. glandulifera* | Dioecious | Critically Endangered |
| *Blastophaga* | 0 | 0 | *F. deltoidea* | Dioecious | Critically Endangered |
| *Ceratosolen* | 1 | 6 | *F. hispida* | Dioecious | Rare, possibly non-native |
| | | | *F. variegata** | Dioecious | Common |
| | | | *F. fistulosa** | Dioecious | Common |
| *Wiebesia* | 1 | 1 | *F. punctata* | Dioecious | Common |
| | | | *F. pumila** | Dioecious | Casual alien |
| | | | *F. villosa* | Dioecious | Critically Endangered |
| | | | *F. trichocarpa* | Dioecious | Critically Endangered |
| | | | *F. apiocarpa* | Dioecious | Endangered |
| | | | *F. sagittata* | Dioecious | Critically Endangered |
| | | | *F. laevis* | Dioecious | Critically Endangered |

far the commonest potential host). Only 21 non-pollinating fig wasps were caught, mostly in the genus *Philotrypesis*. This genus is represented on Kent Ridge by non-pollinating fig wasps of *F. grossularioides* and *F. fistulosa* and *F. aurata*, and may also be associated with other species that have not been studied.

Most pollinators of monoecious figs (73%) were caught in the 25 m traps, including 97% of *Platyscapa* and 91% of *Dolichoris*, but only 31% of *Eupristina*, most (65%) of which were caught at 2 m (Table 2). Most pollinators of dioecious figs (68%), in contrast, were caught at 2 m (Fig. 1), although two genera (*Ceratosolen*, *Kradibia*) were represented in the 25 m traps. The 2 m subcanopy traps captured two *Platyscapa* and six *Eupristina*. Few wasps of any type were caught at 10 m although this was probably because of the obstruction by buildings on most sides.

There was no significant correlation between 25 m catches and average wind speed ($r_s = 0.35$, $p = 0.16$) or total rainfall ($r_s = 0.20$, $p = 0.41$).

## DISCUSSION

In general, the results concur with previous studies in rural areas, suggesting that the fig wasp fauna in Singapore displays similar trends in dispersal (Compton et al., 2000; Compton et al., 2005; Harrison & Rasplus, 2006). As in other studies, the pollinators of monoecious fig species were caught in much higher numbers and at greater heights above the ground than those of dioecious species. Moreover, while *Platyscapa quadraticeps*, which was the commonest species caught, may have come from a large and frequently reproducing *F. religiosa* host tree less than 100 m from the 25 m trap site, the catch of monoecious pollinators also included 34 individuals of at least two species of *Dolichoris*, whose only host in Singapore is the endangered *F. vasculosa*, and three of *Deilagaon*, whose only known host in Singapore, *F. annulata*, is believed to be nationally extinct (Davison et al., 2008). *Dolichoris* was also captured at Lambir, where potential hosts are similarly very rare (Harrison & Rasplus, 2006). While the possibility of pollinators switching or sharing host figs

Table 2. Capture heights of fig wasp genera over the entire study.

| | 25 m | 10 m | 2 m |
|---|---|---|---|
| **Dioecious** | | | |
| Valisia | 0 | 0 | 9 |
| Ceratosolen | 1 | 0 | 5 |
| Kradibia | 8 | 0 | 4 |
| Wiebesia | 0 | 0 | 1 |
| Total | 9 | 0 | 19 |
| **Monoecious** | | | |
| Platyscapa | 236 | 3 | 4 |
| Waterstoniella | 1 | 0 | 0 |
| Eupristina | 46 | 6 | 95 |
| Dolichoris | 39 | 0 | 4 |
| Deilagaon | 0 | 1 | 2 |
| Pleistodontes | 1 | 0 | 2 |
| Total | 323 | 10 | 107 |
| **Non-pollinators** | | | |
| Philotrypesis | 10 | 0 | 2 |
| Sycoscapter | 1 | 0 | 5 |
| Apocryptophagus | 1 | 0 | 0 |
| Epichrysomallinae | 1 | 0 | 0 |
| Total | 13 | 0 | 8 |

(Cook & Rasplus, 2003) cannot be entirely ruled out, the disparity in dispersal heights is generally consistent with the idea that monoecious pollinators fly high and are dispersed far, with the likelihood that Singapore's wasp populations are merely part of continuous regional populations. The most striking difference from previous studies is the capture of most *Eupristina* wasps at an open site 2 m above the ground. This exception, however, may be explained by the positioning of the traps on the top of the c. 50 m high Kent Ridge, which may have deflected high-flying wasps to near ground level.

In contrast with pollinators of monoecious figs, but in agreement with previous studies, the catch of pollinators of dioecious figs was low and concentrated near ground level, and was dominated by taxa that probably originated from host plants on the ridge itself, with the most common wasp (*Valisia malayana*) associated with the most common fig (*F. grossularioides*). These observations are generally consistent with the idea that dioecious pollinators fly low and are dispersed shorter distances. The low numbers caught could also be due to the presence of common hosts (*F. grossularioides* and *F. fistulosa*) displaying receptive phase, which may encourage directed flight guided by volatile organic compounds instead of passive dispersal. However, in contrast to previous studies, a larger proportion of the dioecious pollinators (but no *Valisia malayana*) were caught at 25 m above the ground. The contribution of pollinators through the horticultural fig trade cannot be ruled out and may account for the captures of *Dolichoris*, *Deilagaon*, and high-flying *Ceratosolen* (the pollinator of *F. racemosa*).

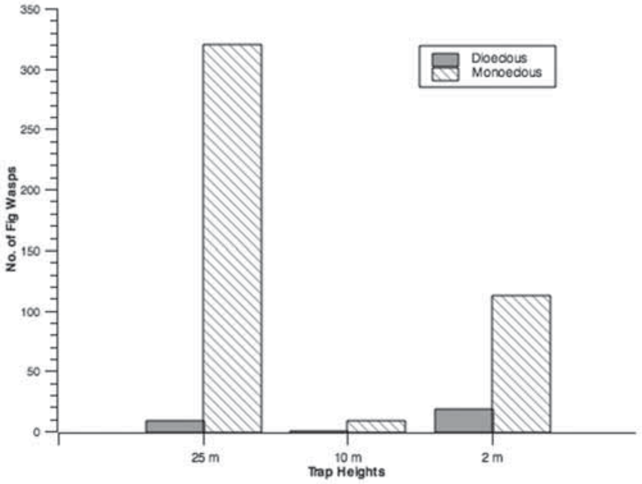

Fig. 1. Distribution of dioecious and monoecious pollinators between 25 m, 10 m, and 2 m trap heights.

Given the inconsistency between the abundance and frequent reproduction of the dioecious hosts plants for *Valisia*, *Ceratosolen* and *Kradibia* within 200 m of the trapping sites and the low catches, the dispersal pathway of dioecious pollinators is still unclear. The very low captures of non-pollinating wasps are also notable. Future studies should trap at a greater range of heights, but directed, powered flights, near ground level, between nearby hosts could account for the observed patterns, with the small proportion of high fliers accounting for the long-distance gene flow suggested by some molecular studies (Yu et al., 2010). Sticky traps located within the canopies of plants of *F. fistulosa* and *F. grossularioides* captured larger numbers of pollinators and smaller, but consistent numbers, of the associated non-pollinating fig wasps (unpublished data), which is consistent with directed dispersal. The phenology of some dioecious fig species (including *F. aurata* and *F. grossularioides*, Singapore; unpublished data) sometimes allows 'recycling' of pollinating wasps between successive, overlapping, male crops, which would further reduce the need to disperse far (Jia et al., 2008).

***Conservation of* Ficus *in Singapore*.** — The diversity in the fig wasp fauna and trends in dispersal displayed in this study are promising for the conservation of *Ficus* in Singapore. Long distance dispersal of pollinators increases the potential for local host figs, whose pollinators have gone extinct, to recover pollination services over time (Harrison, 2000; Harrison & Yamamura, 2003; but see Jia et al., 2008). This, coupled with actively increasing host densities of critically endangered figs by planting, can play a role in stabilising local pollinator populations (Anstett et al., 1997; Kameyama et al., 1999). The impacts of the potentially short dispersal distances of the pollinators of the dioecious figs could be mitigated by planting endangered host figs along green corridors in Singapore thus bridging the gaps between host populations (Mawdsley et al., 1998). These actions could in turn make the fig–fig wasp mutualism more resilient against collapses as a result of fluctuations in pollinator densities.

In tropical Asian cities, urban figs, both cultivated and spontaneous, can attain similar densities to figs in tropical forests and play a similar role in supporting urban wildlife (Corlett, 2006). The ability of large, monoecious, hemi-epiphytes to produce huge crops (>10,000) of ripe syconia in the Central Business District is testament to the continuing effectiveness of fig-wasp dispersal in a novel environment.

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