# Structure of a fig wasp community: Temporal segregation of oviposition and larval diets

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## Abstract

Observations were made on six fig wasp species on *Ficus racemosa* growing in the Xishuangbanna Tropical Botanic Garden, Yunnan Province, China. The oviposition sequence was determined for *Apocryptophagus testacea*, *Apocrypta* sp2, *Apocryptophagus mayri*, *Ceratosolen fusciceps* and *Apocrypta westwood*. An experiment was carried out in which each species of non-pollinating wasp was separately introduced into bagged figs which prevented other species from ovipositing. This showed that the non-pollinators *Apocryptophagus testacea* and *A. mayri* are foragers (gall makers) of the female flowers, and that the other species were parasitoids or inquilines. Additional evidence from naturally unpollinated inflorescences suggested that *A. agraensis* is most likely a parasitoid of the pollinator, *Ceratosolen fusciceps*, and that *Apocrypta westwood* and *Apocrypta* sp. are the parasitoids of *Apocryptophagus mayri* and *A. testacea*, respectively. These results indicate that the fig wasps inhabiting *F. racemosa* figs either utilize different developmental stages of the same resources (female flowers) or utilize different food resources.

Keywords:    Fig, fig wasp, mutualism, coexistence, niche segregation

## 1. Introduction

Figs support both pollinator and non-pollinator wasps and are completely dependent upon the pollinators for the dispersal of pollen. In *F. racemosa*, non-pollinating species provide no service for figs (Yang et al., 2000; Wang et al., 2005a) or the pollinator wasps (Weiblen, 2002; Kerdelhué et al., 2000). Previous studies have considered *Apocrypta* spp. as parasitoids, while *Apocryptophagus* spp. as gall makers (Kerdelhué and Rasplus, 1996; Kerdelhué et al., 2000). The non-pollinators are demonstrated as gall makers of figs or parasitoid pollinators, which are detrimental to fig-fig wasp mutualism, and therefore may affect the process of fig-fig pollinator co-evolution (West et al., 1996; Bronstein, 2001; Harrison and Yamamura, 2003). Diverse assemblages of non-pollinators co-exist within a fig inflorescence and how these communities are structured remains enigmatic (West and Herre, 1994; Kerdelhué et al., 2000; Profitt et al., 2007).

To address these questions, we set out to identify the diet of the fig wasp larvae and thereby elucidate the ecological relationships among species. We also tried to discern whether there is niche segregation among the different fig wasp species, on *Ficus racemosa*, in order to understand how they coexist. This could result from differences in larval diet (Hawkins and Compton, 1992; Cook and Power, 1996), on the fig wasps may utilize the same resources in spatially or temporally distinct ways. The complexity of the fig-wasp communities obscures relationships (West and Herre, 1994; Kerdelhué et al., 2000). Hence, we both make observations of fig wasp oviposition in nature, and used controlled introductions to identify the larval diets of co-existing wasp species. In this way we attempted to identify the impact of each species on the fig-fig pollinator interaction.

## 2. Materials and Methods

*Materials*

The fig wasp community was studied on *F. racemosa* trees at the Xishuangbanna Tropical Botanic Garden,

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Table 1. The number of the galls and wasp offspring (means (SD)) per inflorescence for controlled introductions of each non-pollinator species, separately, to bagged figs.

| Species | Number of treated fruits | Mature fruits collected | Galls | Wasps |
|---|---|---|---|---|
| *Apcryptophagus testacea* | 25 | 14 | 248.8 (64.3) | 220.5 (62.8) |
| *Apcryptophagus mayri* | 20 | 9 | 57.7 (33.6) | 39.9 (24.9) |
| *Apcryptophagus agraensis* | 15 | 0 | 0 | 0 |
| *Apocrypta* sp. | 21 | 0 | 0 | 0 |
| *Apocrypta westwoodi* | 23 | 0 | 0 | 0 |

Table 2. Comparison of bagged inflorescences (only oviposited by pollinators) (n=15) and natural inflorescences collected from the field (n=14) (means (SD)).

| Variable | Treated fruits | Natural fruits | *t* value |
|---|---|---|---|
| Diameter of fruits | 2.91 (0.15) | 2.81 (0.16) | 1.872 ns |
| Foundress | 11.87 (9.43) | 8.64 (3.97) | 1.213 ns |
| Galls | 2444.87 (368.21) | 3503.43 (384.20) | 7.576** |
| Seeds | 1694.47 (452.84) | 1794.64 (404.42) | 0.627** |

**P<0.01. NS, P<0.05.

Yunnan Province, China (21°41'N, 101°25'E) from November 2003 to December 2004. *Ficus racemosa* (section *Sycomorus*) is a monoecious fig distributed from India to Australia (Corner, 1965). It forms a large tree that can reach 30 m in height and grows in moist valleys or along rivers (Yang et al., 2000). This species bears very large numbers of fruits that are produced on branches and trunks rather than on the ends of twigs (cauliflorous). A survey of 218 fruits, in the Xishuangbanna Tropical Botanic Garden Botanic garden, revealed that mature fruits of *F. racemosa* range in size from 2.92 cm to 5.4 cm. At this site, the pollinator of *F. racemosa* is *Ceratosolen fusciceps* (Agaonidae). In addition, there are five species of non-pollinators, namely, *Apocryptophagus testacea*, *A. mayri*, *A. agraensis* (Caliimomidae), and *Apocrypta westwood* and *Apocrypta* sp. (undescribed) (Pteromalidae) (Weiblen, 2002; Wang et al., 2005a,b). The non-pollinator wasps insert their ovipositors through the wall of the inflorescence.

*Methods*

We conducted direct observations of oviposition behaviour. We selected 22 fruits on 2 trees for observation and made observations three times per day (09:00–10:00, 14:00–15:00, and 17:00–18:00). Observations started from the first day that the non-pollinator wasps began to oviposit and continued for 30 days at which time no more wasps were observed ovipositing.

To identify the diet of non-pollinating fig wasps of *F. racemosa,* we made controlled introductions. We enclosed receptive fruits with organdy bags, and then separately introduced the non-pollinator wasps in the same sequence we observed in the field. Twenty-five branches were treated, and each bag contained 4–6 inflorescences. Wasps were

introduced every two days, so that approximately 30 wasps of each species were introduced per bag. We collected aborted inflorescences and examined them for gall development. After the inflorescences matured, we collected them, allowed the adult wasps to exit naturally, and preserved the wasps in 75% alcohol. We counted all of the galls and adult wasps from each fruit. Galls containing dead wasps were opened to identify the wasps.

To determine the impact of non-pollinators on the fig-fig pollinator interaction, we bagged 15 inflorescences before the oviposition of any non-pollinating wasps. At the receptive stage we opened the bags to allow the pollinators enter naturally. We then re-bagged them again until the figs matured. The mature inflorescences were collected and the contents were counted. We simultaneously collected 14 untreated inflorescences from the same trees.

*Data analysis*

We used the Student's t test to test hypotheses relating oviposition of non-pollinators to viable seed and pollinator offspring production, or other quantitative characteristics of the fruits of *F. racemosa*. Correlation analysis (Pearson) was used to analysis the quantitative relationship between different fig wasps contained in the mature fruits of *F. racemosa*.

### 3. Results

*Oviposition sequence of non-pollinating wasps*

Non-pollinating wasps of *F. racemosa* oviposited in the sequence: *Apocryptophagus testacea*, *Apocrypta* sp, *Apocryptophagus mayri*, pollinator wasp (*C. fusciceps*),
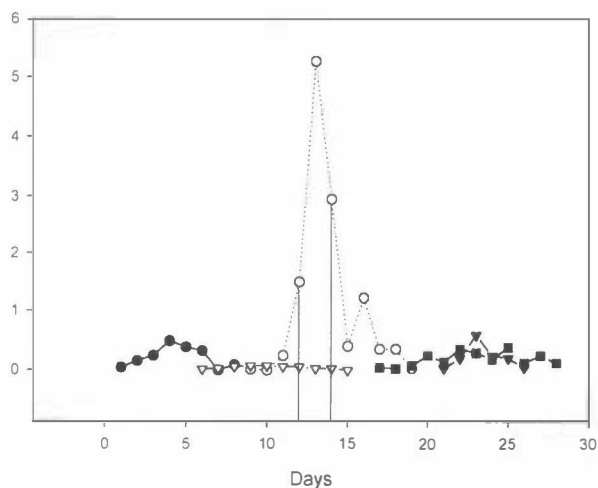
Figure 1. The oviposition frequency and temporal sequence of fig wasps on *Ficus racemosa* at Xishuangbanna Tropical Botanic Garden. China. over a period of 30 days.
( ─ ● ─ *Apocryptophagus testacea* ─ ·· ▽ · ─ ··· *Apocrypta* sp2 ·····○····· *Apocryptophagus mayri* ‖ *C. fusciceps* ─ ─ ■ ─ ─ *Apocrypta westwoodi* ─ ─ ▼ ─ ─ *Apocryptophagus agraensis*).
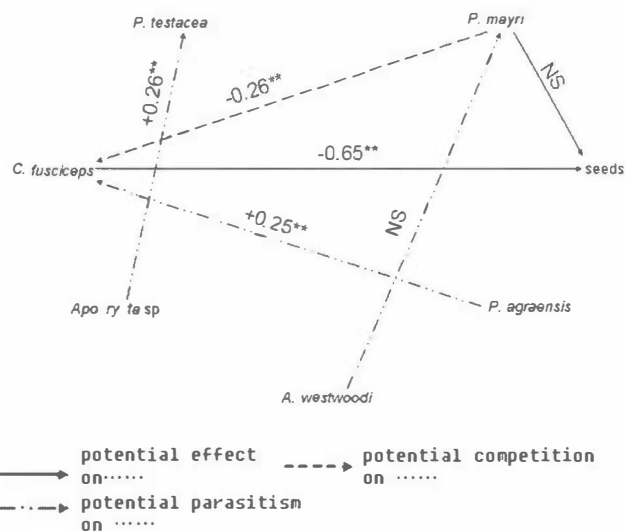


Figure 2. Results of correlation analyses among populations of six fig wasp species, and the relationships between the fig wasp species and viable seeds in the inflorescences of *F. racemosa* at Xishuangbanna Tropical Botanic Garden, China. The data of adult wasps is collected over one year (N=133) and the data of viable seeds and wasp offspring (galls) of pollinators is collected in November (N=26). NS: P>0.05, *P<0.05. **P<0.01.

*Apocrypta westwoodi* and *Apocryptophagus agraensis* (Fig. 1). The oviposition peaks did not overlap and the duration of oviposition differed greatly among species. These data indicate that niche segregation, in oviposition behavior, exists among the fig wasps on *F. racemosa* growing in the Xishuangbanna Tropical Botanic Garden, Yunnan Province, China.

### Diet of fig wasp larvae

The controlled introductions indicated that *Apocryptophagus testacea* and *A. mayri* were able to oviposit in inflorescences not occupied by other wasp species, including the pollinator. However, all inflorescences with just *A. agraensis* or *Apocrypta* spp. aborted, and we did not observe any galls in the aborted inflorescences (Table 1).

### Impact of non-pollinating wasps on the fig-fig pollinator interaction

A comparison between the 15 bagged and 14 open inflorescences revealed that the non-pollinators had no detectable impact on the fruit diameter, foundress number, pollinator production, or seed production. However, as expected, there was a significant increase of the number of galls (Table 2).

### 4. Discussion

The oviposition sequence (Fig. 1) we observed shows

that *Apocryptophagus testacea* and *A. mayri* can independently oviposit into the female flowers, indicating that both species are gall makers. These two non-pollinator wasps may be resource competitors of the pollinators, and hence should not be directly detrimental to the pollinator wasp population, unless oviposition sites are limiting. However, the non-pollinators *Apocrypta* sp.2, *A. westwoodi* and *Apocryptophagus agraensis* cannot oviposit in inflorescences unless they are already occupied by either the pollinator or the aforementioned *Apocryptophagus* spp. Non-pollinator species may be either inquilines (and depend on the other gallers to initiate gall formation), or parasitoides.

In naturally unpollinated fruits, four non-pollinator species were observed: *Apocryptophagus testacea*, *A. mayri*, *Apocrypta* sp. and *A. westwoodi*. *Apocrypta* sp.2 and *A. westwoodi* may be inquilines or parasitoids of *Apocryptophagus testacea* and *A. mayri* (Yang et al., 2005). Moreover, there was a positive correlation between the populations of *Apocrypta* sp. and *Apocryptophagus testacea* (Fig. 2). This suggests that higher populations of *A. testacea* can lead to increased oviposition opportunities for *Apocrypta* sp. The populations of *A. westwoodi* and *Apocryptophagus mayri* were not significantly correlated.

In naturally unpollinated inflorescences, *Apocryptophagus agraensis* was never found and no galls were produced in the figs when only *A. agraensis* was introduced (Table 2). This suggests that *A. agraensis* is an inquiline or parasitoid of the pollinator. The galls occupied

by *A. agraensis* are also derived from short-styled flowers, similar to those occupied by the pollinators (Yang et al., 2005).

*Ceratosolen fusciceps*, *Apocryptophagus testacea* and *A. mayri* utilize the same resource: un-fertilized female flowers. However there is a clear temporal segregation of oviposition, indicating that these wasps utilize different developmental stages of the unfertilized ovules. In the present study, the pollinator wasp population was the dominant fig wasp in the community on *F. racemsoa* throughout the year (Yang et al., 2005), although the community composition varies greatly in different seasons (Wang et al., 2005b).

Except in the case of *Apocryptophagus agraensis*, the non-pollinating wasps do not directly destroy viable seed or pollinator offspring. Most of the non-pollinating wasps are essentially resource competitors with the viable seeds and pollinator offspring. In figs the female flowers are rarely saturated by pollinators (Bronstein and Hossaert-McKey, 1996; Herre and West, 1997), and this applies to *F. racemosa* at the Xishuangbanna Tropical Botanic Garden (Wang et al., 2005b). Therefore, the impact of non-pollinator wasps on the fig-fig wasp interaction maybe less intense than was originally thought. The segregation of larval diets may promote the coexistence of non-pollinating wasp species.

Our results indicate that the fig wasp species on *F. racemosa* occupy distinct niches, through either temporal segregation of oviposition, and thus utilization different developmental stages of the resource, or through the segregation of larval diet.

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