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Quantitative tests of interaction between pollinating and non-pollinating fig wasps on dioecious *Ficus hispida*

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Abstract. 1. The interaction between *Ficus* species and their pollinating wasps (Agaonidae) represents a striking example of a mutualism. Figs also shelter numerous non-pollinating chalcids that exploit the fig–pollinator mutualism.

2. Previous studies showed a weak negative correlation between numbers of pollinating and non-pollinating adults emerging from the same fruit. Little is known about the patterns and intensities of interactions between fig wasps. In the Xishuangbanna tropical rainforests of China, the dioecious *Ficus hispida* L. is pollinated by *Ceratosolen solmsi marchali* Mayr and is also exploited by the non-pollinators *Philotrypesis pilosa* Mayr, *Philotrypesis* sp., and *Apocrypta bakeri* Joseph. Here, the interaction of pollinator and non-pollinators on *F. hispida* is studied quantitatively.

3. The exact time of oviposition was determined for each species of fig wasp. Based on observational and experimental work it is suggested that (i) the relationship between pollinator and non-pollinators is a positive one, and that the genus *Philotrypesis* appears to have no significant impact on the pollinator population, whereas *Apocrypta* has a significant effect on both *Philotrypesis* and *Ceratosolen*; (ii) gall numbers do not always increase with increasing number of foundresses, but developmental mortality of larvae correlates positively with the number of foundresses; and (iii) there is a positive correlation between non-pollinator numbers and their rates of parasitism, but the three species of non-pollinators differed in their rates of parasitism and show different effects on pollinator production.

4. The rates of parasitism when combined with the coexistent percentage and developmental mortality, underpin the way non-pollinating fig wasps successfully exploit and coexist stably in a fig–pollinator mutualism.

Key words. Agaonidae, *Apocrypta*, *Ceratosolen*, *Ficus*, mutualism, oviposition timing, parasitism, *Philotrypesis*, pollination, reproduction.

Introduction

Ficus and the species-specific pollinator wasps of the family Agaonidae exhibit a remarkable plant–insect obligate mutualism. With few exceptions, seed production by fig trees is dependent on a unique fig-pollinating wasp, and the pollinator's offspring feed only on the ovules (Ramirez, 1970; Wiebes, 1979; Rasplus, 1996). Molecular evidence indicates that this relationship dates back to around 90 million years ago (Jousselin *et al.*, 2003). Figs are also exploited by a large community of chalcidoid wasps that develop within the figs but do not transfer pollen. These wasps include gallers, inquilines, kleptoparasites, parasitoids of the pollinators, and parasitoids of other non-pollinating wasp species. Up to 32 species have been described in association with a single fig species (Bronstein, 1999). Multiple species often develop side by side in a single fig; in New World figs, offspring of non-pollinators can outnumber the pollinator offspring (Bronstein, 1991; Boucek, 1993; Bronstein & Hossaert-McKey, 1996).

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Recently, considerable attention has been paid to the relationship between fig wasps and how they resolve conflicts in monoecious fig species. Pollinators and non-pollinators interact intimately; each species of fig wasp preferentially ovipositing in a different part of the female flower, but non-pollinators show a negative impact on the pollinator population and dynamics (Kerdehué & Rasplus, 1996; Herre & West, 1997; Kerdehué *et al.*, 2000). Previous authors had predicted that the persistence of the pollination mutualism in functionally dioecious figs might also be affected by the stability of the host–parasitoid interaction, as in the case of monoecious figs (Compton & van Noort, 1992; West & Herre, 1994; Nefdt & Compton, 1996; West *et al.*, 1996), but there have been few tests in functionally dioecious figs (Kjellberg *et al.*, 1987; Grafen & Godfray, 1991; Kerdehué & Rasplus, 1996).

Weiblen *et al.* (2001) were the first to study the rates of parasitism in functionally dioecious figs, highlighting the fact that non-pollinators had a direct negative impact on pollinators and an indirect impact on functionally dioecious figs in that gallers compete with pollinators for female flower resources and parasitoids attack pollinator larvae. From a phylogenetic analysis Weiblen (2000) also mentioned that parasitism might have played a role in the origin, maintenance, and geographical spread of dioecious fig pollination. However, what factors could limit the rates of parasitism? Weiblen *et al.* (2001) explained only the factors in the wasp search and ovipositing stages; no factors were addressed in the developmental stage. Therefore, the question of what enables the coexistence of non-pollinators and pollinators in functionally dioecious figs has not been answered clearly.

In considering this problem, species interactions seem most important and these will mostly depend on the ovipositing behaviour (Morris *et al.*, 2003). Moreover, pollinating and non-pollinating fig wasps oviposit at a specific stage of fig maturation. However, regardless of the time when they oviposit in the fig flowers, all fig wasp species will emerge from the galls in the fig cavity at the same time as the pollinator, and all the species use the same exit hole chewed by the male pollinators to escape (Abdurahiman, 1986; Weiblen, 2002). Because the timing of oviposition and the number of foundresses of non-pollinators were not exactly determined, previous studies only highlighted the qualitative relationship between fig wasps, and they were only concerned with the relationship of the pollinator and non-pollinators in a natural community (West & Herre, 1994; West *et al.*, 1996; Kerdehué *et al.*, 2000).

In this study, the oviposition behaviour of each fig wasp was observed for the first time. Quantification of interspecific interactions and niche differentiation between the pollinator and non-pollinators in the natural community were then attempted. After the timing of oviposition was determined, pollinator introduction experiments were carried out to determine the relationship between the number of foundresses and their reproductive success. Here, the relationship between the foundresses was judged by comparing the percentage of galls and larval mortality in their offspring. In order to understand the effect on pollinator production of the number of non-pollinator foundresses ovipositing in a fig, different numbers of female non-pollinators were introduced to the single syconium, to which the appropriate amount of pollinators had been introduced. The final step involved comparing the relationship between fig wasps in a natural community and a controlled community. The aim was to quantify the impact on the pollinator of non-pollinators and the interaction between fig wasps.

Materials and methods

Study site

The study was carried out in the Xishuangbanna Tropical Botanical Garden (101°15′E, 21°55′N), located in south-west China and the northern margin of tropical South-east Asia. The five trees used in the experiments were distributed in secondary forests and by the side of an ornamental lawn.

Study species

Ficus hispida L. is in section Sycocarpus. *Ficus hispida* is a small- to medium-sized free-standing tree, the inflorescences of which are pollinated by *Ceratosolen solmsi marchali* Mayr (Yang *et al.*, 2002). In the Xishuangbanna tropical area experiments, non-pollinator species in *F. hispida* were collected and identified (by J. Y. Rasplus). Three species of non-pollinating fig wasps, *Philotrypesis pilosa* Mayr, *Philotrypesis* sp., and *Apocrypta bakeri* Joseph, oviposit from outside the syconium into ovaries containing pollinator eggs on a male tree. However, there are only two non-pollinator species, *A. bakeri* and *P. pilosa*, which inhabit the tree in India (Abdurahiman & Joseph, 1976, 1978, 1979; Abdurahiman, 1986). *Ficus hispida* has trees that produce syconia all year-round. Wasp reproduction and seed production also occur all year-round, although there are seasonal peaks in production (Patel, 1996). The tree bears figs on leafless branchlets hanging down from the trunk and bigger branches. A mature fig is a subglobose syconium that measures 32.217 ± 6.541 (SD) mm in diameter and contains 2558 ± 627 (SD) flowers.

Observing oviposition behaviour of each fig wasp

From January to May 2003, 30 receptive syconia were sampled and checked for fig wasps ovipositing every day during the female-floral and inter-floral phase. The day the pollinator entered was considered as the beginning of the experiment. The syconia that had been entered by pollinators were marked. Each species of non-pollinator and its time of visiting the marked syconia was then recorded until the last non-pollinator finished oviposition. The whole observation was carried out for 25 days and repeated three times. The diameter and thickness of each fig wall was measured when each non-pollinator laid her eggs. Finally, the oviposition times of the three non-pollinators species were obtained.

Quantification of the relationships of pollinator and non-pollinators in the natural community

To determine the species interactions occurring within the syconium, quantitative data on the number of fig wasps had to be obtained, so 358 near-mature syconia from four male trees of *F. hispida* were collected in 2003. Syconia were collected before any exit holes were observed but while the figs were soft. They were then sliced open and placed in emergence bags until winged wasps exited. The insects were removed from the bag, wingless males were carefully collected, and all wasps were killed in 70% ethanol. Afterwards, they were sorted out by species and sex, identified, and counted.

To determine the actual quantitative relationships between species, a path analysis was used to study the interactions between fig wasps on *F. hispida*, because this method had been used successfully to quantify interspecific interactions in African fig wasps (Kerdehué *et al.*, 2000). Here, the path coefficient was obtained using SPSS statistical software. Moreover, the percentage of wasps coexisting with other species was also used to show the relationships between fig wasps. This amount ranges from zero to one, with a number closer to one meaning a closer relationship. The following formula was used to calculate the coexistence percentage:

$$\text{Coexistence percentage} = a/(a+b+c) \qquad (1)$$

where a is the numbers of two species coexisting in a syconium from the total sampled syconia, b is syconium numbers having species 1 but not species 2 among the total sampled syconia, and c is syconium numbers having species 2 but not species 1 among the total sampled syconia.

Reproductive success and number of foundresses

The success in terms of total pollinator numbers in figs has often been determined by foundress density (Patel & Hossaert-Mckey, 2000). Here, both the percentage of galls and larval mortality were used to judge optimum foundress density and reproductive success in a syconium. The following formulae were used for calculation:

$$\text{Percentage of galls} = [(f+m+g)/(f+m+g+\mathrm{uf})] \times 100 \qquad (2)$$

$$\text{Larval mortality} = g/(f+m+g) \times 100 \qquad (3)$$

where g is the number of aborted galls, f is the number of female pollinators, m is the number of male pollinators, and uf is unparasitised female flowers.

To obtain estimates of optimum foundress density and reproductive success in a syconium, experiments introducing pollinators were carried out. The methods for introducing pollinators have been described by Hossaert-Mckey and Bronstein (2001).

Once a suitable male tree was located, some branches bearing pre-female-phase syconia were selected for the experiment. After removing syconia in other phenological stages, the branch was then enclosed in a fine-meshed nylon bag (200 × 200 mm) to prevent entry by pollinators that arrived naturally at the tree. Each bag was sealed tightly around the branch. Once syconia reached receptivity (diameter: 18.50 ± 1.61 mm, $n = 30$), foundresses hovering around the male tree were collected; the bags were then removed and one, three, and five foundresses, respectively, were introduced into a single syconium. Afterwards, these syconia with various numbers of foundresses were bagged until near maturity. By the end of this process, 39, 80, and 34 mature syconia having one, three, and five foundresses, respectively, were collected. The figs were then sliced open and placed in emergence bags until winged wasps exited. The insects were removed from the bag, wingless males were carefully collected, and all wasps were killed in 70% ethanol. The number of males and females was then recorded, and the numbers of aborted galls and unparasitised female flowers were also counted.

The impact of various non-pollinator numbers on pollinator production

Three individual pollinators were introduced to a single syconium using the method described above. Next, the three species of non-pollinators were collected from mature syconia of other male trees, and different non-pollinator numbers were introduced respectively to these syconia. Each species was introduced at their normal time of oviposition. *Philotrypesis pilosa* oviposited on the same or the following day of the entry of *Ceratosolen*. Therefore, they were introduced 2 h after the pollinators. *Philotrypesis* sp. was introduced on the eighth day, and *A. bakeri* introduced on the 17th day. Every species of non-pollinator was awarded the same treatment so that one, three, and five female non-pollinators were introduced to the syconium with three pollinators respectively. From beginning to end, nylon bags were kept on the branches to protect the experimental syconia. When these figs were close to maturity, each fig was sliced open and placed in emergence bags until the winged wasps exited. The insects were then removed from the bag, the males being collected carefully because they were all wingless, and all wasps were killed in 70% ethanol. The number of males and females was then recorded. The number of galls was also counted.

Results

The characteristics of oviposition between pollinator and non-pollinators

In *F. hispida*, four species of wasps with different feeding patterns and oviposition times inhabited the ovaries in coexistence in a small syconium. The reproduction of three non-pollinating wasp species depended on the pollinators that first entered the syconia. Oviposition characters of every fig wasp are shown in Table 1. Two *Philotrypesis* species utilised the galls made by the pollinators, but *P. pilosa* oviposited within the same or the following day of the pollinators' entry; *Philotrypesis* sp. oviposited from the sixth to the 13th day; *A. bakeri* is a parasitoid and oviposited last.

Quantitative relationships of pollinator and non-pollinators in the natural community

A path coefficient was used to determine the direct and indirect relationships among four species of fig wasps of *Ficus hispida*. The results are summarised in Table 2. Though the coexistence percentage between *C. solmsi marchali* and *Philotrypesis* genus was high, and the two *Philotrypesis* species decreased pollinator numbers, no significant impact on pollinators was found (Fig. 1, dashed lines). In contrast, *A. bakeri* showed a low coexistence percentage with the other three species of wasps, but there was a significant effect on the production of the other three species of wasps (Fig. 1, solid lines). In addition, the impact on the *Philotrypesis* species is larger than on *C. solmsi marchali* (Fig. 1, solid lines).

Reproductive success and number of foundresses

When different number of foundresses were introduced to a single syconium, the gall numbers varied. Larval numbers were not the same, which affected the mortality of larval development. The foundress density showed a significant effect on the gall numbers (ANOVA, $F_{2,130} = 31.866$, $P < 0.01$) and on larval mortality (ANOVA, $F_{2,130} = 26.694$, $P < 0.01$). In addition, one-, three-, and five-foundress broods resulted in different percentages of galls, and larval mortality increased with increasing number of foundresses (see Table 3). Three-foundress broods produced the highest percentage of galls and moderate larval mortality, so this level of reproduction is thought to be the most successful. Where only one foundress reproduced in a single syconium, female flowers were not fully utilised, but when there were five foundresses, oviposition competition was apparent, and this led to a decreasing percentage of galls.

The impact of various non-pollinator numbers on pollinator production

Different numbers of non-pollinators were introduced to a syconium with three pollinators. Their rates of parasitism were compared, and the results are shown in Table 4. The rate of parasitism suffered by every non-pollinator species should increase with increasing numbers of females, and the latter has an obvious impact on the former. Moreover, the same number of females of different non-pollinator species produced different parasitism rates. Regardless of the number of non-pollinator foundresses, the rates of parasitism of *P. pilosa* were highest in the three species of non-pollinators studied, whereas the rates of parasitism of *Philotrypesis* sp. were the lowest. In all cases, parasitism by non-pollinators reduced pollinator numbers, and in the case of the three foundresses of *P. pilosa* a significant impact on pollinator numbers in three-pollinator broods was observed, so did one and five foundresses of *Philotrypesis* sp. However, three treatments of *A. bakeri* had a non-significant impact on pollinator production (see Table 4).

Discussion

The differing characteristics of pollinator and non-pollinator oviposition behaviour

The study of oviposition behaviour and feeding habits is important in developing an understanding of the role of fig wasps in natural communities (Morris *et al.*, 2003). Non-pollinating fig wasps can be classified according to the moment the females arrive on the fig to oviposit (Kerdehué *et al.*, 2000). Previous authors reported that only *P. pilosa* and *A. bakeri* oviposited on *F. hispida*, and they oviposited through the wall of young syconia already infested by the pollinator *C. solmsi marchali* (Abdurahiman & Joseph, 1978; Abdurahiman, 1986; Murray, 1987; Patel & Hossaert-Mckey, 2000). In this study, three species of non-pollinating fig wasps were discerned on *F. hispida*. The oviposition time of *P. pilosa* was determined first. Like *Idarnes*

Table 1. Oviposition characteristics of fig wasps in *Ficus hispida*. The values of fig diameter and fig wall thickness are means (± SD).

Fig wasp species	Coexisting roles	Fig diameter (± SD)	Fig wall thickness (± SD)	Oviposition stage (day)
C. solmsi marchali	Pollinators	18.500 (1.606)	4.071 (0.375)	2 (1–2)
P. pilosa	Inquilines	18.500 (1.606)	4.071 (0.375)	2 (1–2)
Philotrypesis sp.	Inquilines	23.170 (2.856)	4.817 (0.569)	8 (6–13)
A. bakeri	Parasitoids	25.627 (2.754)	5.094 (0.452)	5 (17–21)

Note: means ± SD are given in millimetres. The beginning time of every non-pollinator oviposition was recorded according to the entering time of the pollinator.

Table 2. Path analyses coefficient results.

Relationship between		Coexisting percentage	Path coefficient
C. solmsi marchali	*P. pilosa*	0.570	0.020 NS
	Philotrypesis sp.	0.746	0.050 NS
	A. bakeri	0.159	0.187**
P. pilosa	*Philotrypesis* sp.	0.764	0.079 NS
	A. bakeri	0.279	0.145*
Philotrypesis sp.	*A. bakeri*	0.313	0.312**

*$P < 0.01$; **$P < 0.001$; NS, not significant.

wasps, *P. pilosa* oviposited at the same stage of fruit development as the pollinator wasps and appeared to use the same attractant cues as the pollinators to find receptive trees (Herre, 1989; Bronstein, 1991; West & Herre, 1994). Next in time of oviposition was *Philotrypesis* sp., when it might attack pollinators or *P. pilosa*. The parasitoid *A. bakeri* oviposited last. Abdurahiman and Joseph (1979) suggested that *A. bakeri* only parasitised pollinators. Now it seems that *A. bakeri* has a chance to attack the larvae of pollinators or two *Philotrypesis* species, and the relationship among fig wasps observed in a natural community supports this view.

Though the diameter of figs and the thickness of the fig wall have often been used to quantify the characters of the oviposited fig, the exact oviposition time of the fig wasps had previously not been investigated (Abdurahiman & Joseph, 1979; Abdurahiman, 1986; Kerdehué & Rasplus, 1996) and is reported here for the first time. The accurate assessment of oviposition time should provide an important basis for any quantitative study of pollinator and non-pollinator relationships.

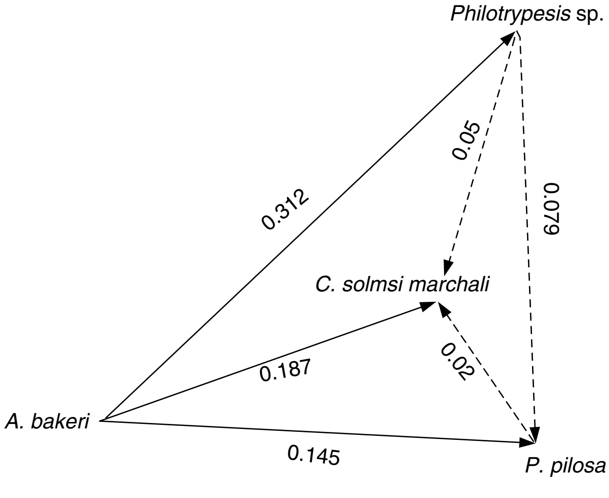

Fig. 1. Path diagrams of four species of fig wasps on *Ficus hispida*. The dashed lines represent non-significant covariance coefficients, whereas the solid lines represent significant covariance coefficients. Results are detailed in Table 2.

Table 3. Multiple comparisons of the mean percentage of galls and larval mortality (see equations 2 and 3) based on three kinds of foundress density.

Number of foundresses	Samples	Percentage of galls (mean ± SD)	Larval mortality (mean ± SD)
1	39	17.055 (7.766)^{a}	16.288 (15.004)^{a}
3	80	31.083 (13.589)^{b}	33.235 (23.460)^{b}
5	34	27.285 (12.909)^{bc}	50.410 (25.534)^{c}

Note: same letters represent non-significant variation between means; different letters represent a significant difference between means ($a = 0.05$); mean difference is significant or non-significant at the 0.05 level.

The quantitative relationships of pollinators and non-pollinators

Fig wasps belonging to different families and subfamilies have in some cases exhibited ecological convergence in fig utilisation (van Noort & Compton, 1996; Rasplus *et al.*, 1998). Non-pollinating fig wasps were thought to have a negative effect on the reproductive success of pollinator wasps (Herre, 1989; Kobbi *et al.*, 1996; West *et al.*, 1996). In contrast, the results from the work reported here suggest a positive correlativity between the numbers of non-pollinators and pollinators. A possible factor for this in *F. hispida* is that the primary resources of the non-pollinators are flowers containing pollinators. Three non-pollinator species typically oviposited only after a syconium had been visited by a pollinator, so each non-pollinator population would be restricted by the pollinator population. Interestingly, *P. pilosa* oviposited at nearly the same time as the pollinator. This contrasts with Joseph (1966), who reported that *P. pilosa* oviposited in a syconium already infested by the pollinator, and suggested that the larvae of *P. pilosa* competed more successfully than *C. solmsi marchali* for food reserves in the endosperm. If that were the case, *P. pilosa* should have the highest coexistence percentage with the pollinator and the largest population among the three non-pollinator species, but these results do not support this hypothesis. It is possible that *P. pilosa* wasps are not attracted to every tree and might disappear seasonally on certain trees. Another reason could be that the oviposition of *P. pilosa* is easily disturbed; also, oviposition time is short, lasting only about 4 min (Y. Q. Peng, unpubl. data). Also, ant predation was observed while *Philotrypesis pilosa* probed for oviposition sites and laid eggs, and this could impose a limit on parasitoid search time and egg numbers. However, *Philotrypesis* sp. suffered none of these shortcomings. It reproduced at a high rate and had the highest coexistence percentage with *C. solmsi marchali* and *P. pilosa*. Although both *P. pilosa* and *Philotrypesis* sp. decreased pollinator numbers, no significant impact on pollinators was shown. This paradox could reflect the fact that *C. solmsi marchali* and the two *Philotrypesis* species have undergone long-term cospeciation. The result was similar to the case of *Philotrypesis* and pollinating *Kradibia*, in which *Philotrypesis* was sufficient to stabilise the interaction in

Table 4. Multiple comparisons of the mean of ratios of parasitism of the same non-pollinators derived from three forms of treatment; ANOVA was used to analyse the effects on pollinators of different numbers of non-pollinators.

	Three pollinators + non-pollinators		The effect of non-pollinators in three-pollinator broods		
Wasp species	No. of foundresses of non-pollinators (sample sizes)	The proportion of non-pollinators parasitised (%) Mean (± SD)	d.f.	*F*	*P*
Philotrypesis pilosa	1 (19)	1.120 (1.293)^{a}	97	0.436	0.511
	3 (40)	2.989 (7.168)^{a}	118	15.130	<0.001
	5 (27)	8.813 (16.857)^{b}	105	1.470	0.228
Philotrypesis sp.	1 (22)	0.478 (0.769)^{a}	100	15.582	<0.001
	3 (33)	1.279 (1.499)^{b}	110	17.598	<0.001
	5 (25)	1.493 (1.173)^{bc}	103	1.894	0.172
Apocrypta bakeri	1 (25)	0.931 (1.598)^{a}	102	0.448	0.505
	3 (6)	2.422 (1.050)^{b}	84	0.672	0.415
	5 (9)	2.621 (1.819)^{bc}	87	1.297	0.258

Note: the rate of parasitism = npn/tgn × 100, where npn is non-pollinator numbers and tgn is total gall numbers. Same letters represent non-significant variation between means; different letters represent significant difference between means ($a = 0.05$); mean difference is significant or non-significant at the 0.05 level.

dioecious figs rather than destroying the mutualism of fig and pollinating wasp (Weiblen, 2002). In African fig wasp communities, *Apocrypta* is a galler, and *Ceratosolen* and *Apocrypta* were negatively correlated in *Ficus vallis-choudae* (Kerdehué *et al.*, 2000). Godfray (1988) reported that *Apocrypta* was a hyperparasitoid of *Apocryptophagus*. In this study, *A. bakeri* is confirmed by control experiments to be a parasitoid of *C. solmsi marchali*. The results indicate that larval ecology is not always conserved within fig wasp genera. In the natural community of fig wasps collected from *F. hispida*, *A. bakeri* also parasitised *P. pilosa* and *Philotrypesis* sp., and the effect on *Philotrypesis* is larger than that on *C. solmsi marchali.*

Reproductive efficiency and number of foundresses

Unlike monoecious figs, which contain a mixture of wasps, seeds, and pollen in every fruit, dioecious fig species have a functionally male tree, which harbours wasps and produces pollen, and a female tree, which produces seeds only. Increasing numbers of foundresses would result in increasing proportions of numbers of flowers developing either wasps or seeds, up to a point where the maximum possible flowers develop wasps and seeds. This relationship has been demonstrated in monoecious and dioecious fig species (Herre, 1989; Patel & Hossaert-Mckey, 2000). In India, Patel and Hossaert-Mckey (2000) found that mean pollinator offspring numbers were significantly lower for the one-foundress treatment than for the three- or eight-foundress treatments in *F. hispida*. Moreover, they also reported that there were no significant differences in vacant ovary numbers per fruit between three- and eight-foundress pollinations. In this study, one-, three-, or five-foundress treatments also showed similar results. Also in the work reported here, larval mortality was used to determine the reproductive success of the pollinator. Although egg deposition has been quantified by comparing the number of eggs left in foundress ovaries after oviposition (Kathuria *et al.*, 1999; Moore & Greeff, 2003), the eggs alone represent only part of effective reproduction. In most cases, no distinction can be made between dead eggs and unparasitised flowers. Therefore, it is very difficult to know actual egg numbers per brood. Instead, gall numbers were considered to reflect the number of larvae. Some of larvae will die because they have fewer resources or because their size is limited by competition for space during fig development. Therefore, larval mortality is an important factor in determining reproductive success. By comparing one-, three-, or five-foundress treatments, the results show that larval mortality increased with foundress density. Here, reproductive success was measured by the percentage of galls and larval mortality, because the percentage of galls represented the ability of foundresses to exploit female flowers and larval mortality showed the developmental state of the offspring. Three-foundress broods had the highest percentage of galls and suffered moderate larval mortality, so their reproduction was thought to be the most successful. Moreover, the reproductive success of the pollinator shows weak intraspecific competition.

The effect of the numbers of non-pollinators on pollinator production

In *F. hispida*, the data on community structure indicated that three non-pollinator species showed positive correlations. Only *A. bakeri* showed a significant impact on the pollinator. By contrast, data on the population dynamics of parasitic *Philotrypesis* and pollinating *Kradibia* indicated that heterogeneity in the rate of parasitism is sufficient to stabilise the interaction in dioecious figs; host density dependence and between-crop variation were thought to be the sources of heterogeneity (Weiblen, 2002). However, studies by West *et al.* (1996) and Weiblen *et al.* (2001) showed an inverse relationship between the rate of parasitism and pollinator density. In this study, the experimental focus was changed and attention was paid to other factors that could stabilise the interaction in dioecious figs.

The results showed that the parasitism rate of *P. pilosa* is the highest among the three non-pollinator species. In the natural community, only *P. pilosa* showed a lower coexistence percentage with the pollinator, with *Philotrypesis* sp. showing the opposite pattern. Therefore, the rate of parasitism and the coexistence percentage can inform us of the different reproductive strategies of the two *Philotrypesis* species. Moreover, it was also found that the high parasitism rate of the genus *Philotrypesis* did not obviously affect pollinator reproduction. Developmental mortality of fig wasps could be an important adjusting factor.

Apocrypta bakeri showed a significant effect on the three fig wasp species that had been previously oviposited, and it tended to attract *Philotrypesis* species. When *A. bakeri* was introduced to three-pollinator broods only, the one, three, and five treatments had no obvious impact on pollinator reproduction. It is suspected that not enough individuals of *A. bakeri* were introduced or that there was no *Philotrypesis* present so that the oviposition of *A. bakeri* was restricted. Thus, developmental mortality probably affects the true parasitism rate, with host preference leading to a high, low, or even zero parasitism. However, the impact of the pollinator density on the ratio of parasitism has a more important significance at the sub-population level (single syconium), and the coexistence percentage might thus represent the interaction frequency between two species. In short, these factors may affect each other in a manner which acts to stabilise the interactions between fig wasps.

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