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Seasonal Changes in the Trade-off Among Fig-supported Wasps and Viable Seeds in Figs and Their Evolutionary Implications

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Abstract: What the real trade-off is among fig-supported wasps and the viable seeds of figs is heatedly debated in the studies of fig/fig wasp mutualism. In the present study, we collected wasp offspring (galls) and the viable seeds of premature fruits, and determined the foundress number in receptive fruits and all the types of wasps supported by *Ficus racemosa* L. during both the rainy and dry seasons in Xishuangbanna, China. The data show that the galls were positively correlated with viable seeds ($n = 32$; $r = 0.74$; $P < 0.001$) when the proportion of vacant female flowers (PVFF) was high, in April (68.0%), and were negatively correlated with viable seeds ($n = 48$; $r = -0.59$; $P < 0.05$) when PVFF were limited (PVFF = 42.6%) during a colder month (January). The mean foundress number per fruit during the colder months is significantly lower than during the warmer months ($F_{5, 603} = 27.9$; $P < 0.001$) and pollinator wasps can live longer during the colder months. During the colder months, the proportions of non-pollinators and wasp offspring are higher than those found during other months, whereas the proportion of viable seeds is not different compared with that of other months. Non-pollinator wasps tend to oviposit the female flowers that have been oviposited by pollinator wasps. The non-pollinators only negatively affect pollinator wasps and there is no obvious negative effect of non-pollinator wasps on viable seeds, so ovipositing by non-pollinator wasps will not result in the extinction of the figs during the process of evolution. The results of the present study indicate that figs can allow less foundresses to be in fruit cavities when PVFF are limited, which provides supporting evidence for the previous assumption that the plants have developed a mechanism to maintain a stable system because of the conflicts between the parties involved.

Key words: *Ficus racemosa* L.; mutualism; non-pollinator; pollinator; seasonal change; trade-off; Xishuangbanna.

In the obligate mutualism between figs and their pollinator wasps, the figs provide part of their female flowers to their pollinator wasps to oviposit and the larvae of the pollinator wasps develop adults in the ovaries of the female flowers (Wiebes 1979; West and Herre 1994). As reward for the figs, the pollinator wasps carry pollen to the receptive figs, the pollen is dispersed to the female flowers by the pollinators during the process of oviposition, and the fertilized female flowers develop viable seeds (Janzen 1979; Chen *et al.* 1997; Herre and West 1997; Yang *et al.* 2000). For monoecious figs, because both wasp offspring (galls) and viable seeds are developed from the same resource (i.e. female flowers), a conflict should also exist between them while cooperation obviously exists between them (West and Herre 1994; Anstett *et al.* 1996; Herre and West 1997; Weiblen *et al.* 2001). What the trade-off is between the wasp offspring and the viable seeds

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is of central importance in understanding how this system maintains its stability and the strategies of both the figs and their species-specific pollinators (Anstett *et al*. 1997; Herre and West 1997; Herre *et al*. 1999; Weiblen 2002).

Not only must the figs allocate their female flowers to their pollinator wasps, but they must also support non-pollinator wasps that use the same resource, namely the female flowers (Kerdelhue *et al*. 2000; Weiblen 2002). Most previous studies have shown that the non-pollinators have significant negative effects on pollinators because they compete for the same resource with the pollinators or directly parasitize the pollinator wasps (West and Herre 1994; West *et al*. 1996; Kerdelhue *et al*. 2000). In fact, most of the non-pollinators can live independently of the pollinators and can directly use the female flowers or the viable seeds of figs, which has resulted in a heated debate as to whether the non-pollinators use more of the female flowers at the expense of viable seeds, which may then result in the extinction of the figs during the process of evolution because the non-pollinators do not provide any benefits to the figs (Janzen 1979; West and Herre 1994; West *et al*. 1996; Kerdelhue *et al*. 2000). The trade-off among the wasps that the figs support and the viable seeds will directly affect the population size of both figs and wasps, which may provide important information for the conservation efforts for this keystone species of tropical forests (Janzen 1979; McKey 1989; Bronstein *et al*. 1990; Nason *et al*. 1998). In addition, such information may also disclose how the fig/fig wasp system maintains its stability while conflict exists among the various parties involved (Janzen 1979; West and Herre 1994; West *et al*. 1996; Kerdelhue *et al*. 2000).

Obviously, the trade-off between figs and the wasps they support depends on the production of both viable seeds and wasp offspring (galls), and factors that may affect the production of viable seeds and wasp offspring may also indirectly affect the trade-off between the viable seeds and wasp offspring (Bronstein 1988; Bronstein and Hossaert-McKey 1996; Herre and West 1997). In seasonal areas, the climate is different during different seasons and it has an obvious impact on the production of viable seeds and wasp offspring in the fig/fig wasp system (Janzen 1979; Yang *et al*. 2000). However, until now, it has not been clear how climate changes affect the production of viable seeds and wasp offspring and whether these changes have any impact on the trade-off between them.

In the present study, we used *Ficus racemosa* L. and its wasp community as a model system to investigate the following questions: (i) do the figs have a different production of viable seeds and wasp offspring in different seasons; (ii) does greater wasp offspring production result in greater or less production of viable seeds; (iii) are there any differences resulting from seasonal changes in the fig-supported wasp community and, if so, do these changes affect the trade-off between the wasps that the figs support and the viable seeds of the figs?

1 Materials and Methods

1.1 Study sites

The present study was performed in Xishuangbanna, Yunnan, China (21°41' N, 101°25' E), where the altitude is approximately 600 m and the climate presents a rainy season (May to October) and a dry season (November to the following May). In Xishuangbana, the rainy season lasts from May to October, whereas from April the temperature increases a little. The temperature becomes lower from November to January and January is the coldest month, with a monthly average temperature of 12.5 °C. Approximately 79%–82% of the total yearly rainfall is during the rainy season (Yunnan Weather Bureau 1984; Yang *et al*. 2001). The sample site was in the Xishuangbanna Botanical Gardens and the samples trees are in a fragmented forest of approximately 1 km^2. The sample trees are in a group and can still bear large amount fruits in the dry season, whereas the trees that are not in groups bear very few fruits during the dry season.

1.2 Study species

The monoecious fig *Ficus racemosa* L. is distributed from India to Australia (Corner 1965). *F. racemosa* is a large tree that can reach up to 30 m high and bears large numbers of cauliflorous syconia synchronously within the tree. The trees grow mainly in moist valleys or along rivers. The trees of *F. racemosa* usually occur in groups, with each group consisting of 5 to 10 individuals in primary forest (Yang *et al.* 2000). The density of the fruits during the dry season is much less than that during the rainy season. The trees of *F. racemosa* can fruit within the same trees asynchronously, and produce fewer fruits or do not bear fruits during the dry season. However, the trees that are in groups in the highly fragmented forest can bear very large amount fruits during the dry season and show no obvious differences in fruiting during the rainy season. From the end of April or early May, most trees begin to fruit in large amounts and trees that do not bear fruits in the dry season also begin fruiting during this period. In Xishuangbanna, the fruits of *F. racemosa* need no more than 2 months to complete their fruiting cycle in the rainy season. In the dry season, trees may need 2 or 3 months to complete their fruiting cycle.

F. racemosa is pollinated by *Ceratosolen fusciceps* (Agaoninae). With regard to the non-pollinators of *F. racemosa*, there are three species of *Apocryptphagus* (Sycophaginae) and two species of *Apocrypta* (Sycoryctinae). These non-pollinators can develop independently in fruits without pollinators in *F. racemosa* and the *Apocryptphagus* wasps are resource competitors with pollinators, whereas the *Apocrypta* wasps are parasites of the other wasps (Kerdelhue *et al.* 2000; Weiblen 2002). The non-pollinators do not enter the cavities of the receptive fruits to lay eggs and oviposit the female flowers from outside of the fruit wall.

1.3 Methods

At the time that the cavities of premature fruits are very small or have no cavities (D phase), it is easy to count the flowers, because the seeds and the galls are easy to distinguish at this time (the seeds have just developed to have their distinctive shape). It is also possible to count the number of foundresses and to measure the fruit diameter in the same fruits, because the remains of the foundresses are still easy to distinguish and the fruit diameter stops increasing during this period. In the present study, we counted all the female flowers per fruit in 50% of fruits sampled. In another 50% of the sampled fruits, we only counted all types of female flowers in about 25% part of the each sample fruit, while all of the viable seeds and galls in each fruit were counted. Using data from this 25% part of sample fruits, we calculated the proportion of the developed female female flowers in the total female flowers (the proportion of developed female flowers in total female flowers in 25% part of the each fruit = (seeds + galls)/(seeds + galls + vacant flowers)). Then, we can use data of the total number of galls and viable seeds in each fruit and the proportion of developed female flowers in the total flowers in 25% part of the fruit to estimate the total female flowers per fruit (total female flowers per fruit = (total seeds + total galls)/proportion of developed female flowers). The number of total female flowers per fruit was estimated in half the fruits sampled, whereas in the other half, all types of female flowers were counted.

Data for adult wasps were collected in the same crops as data for seeds and galls. When fruits were mature and still had no exit holes cut by male pollinator wasps, they were collected and taken back to the laboratory. The fruit was cut quickly, put immediately into a funnel, and the mouth of the funnel enclosed with organdie under strong light. Thus, the insects fell into alcohol through the funnel. All insects per fruit were collected separately. Because the male wasps of *Apocryptphagus* are very small and difficult to distinguish, although the sex ratios of wasps in *F. racemosa* are approximately equal (Herre 1985; Kerdelhue *et al.* 2000; Weiblen 2002), we only used data on female wasps in the data analysis.

Because the climate in Xishuangbanna obviously presents a rainy season and a dry season and the fruiting cycle of *F. racemosa* takes 2–3 months, or even longer, we collected two crops in each season over an entire year in 2002. In order to reduce differences from different habitat sites, we only collected these datasets at one sample site.

2 Results

The results show that wasp offspring production differs greatly during the different months of the year (Table 1). Obviously, gall production in the dry season (January and November) is higher than that of the rainy season, whereas seed production is rather stable. Tables 1 and 2 show that the proportion of galls in the total of female flowers increases with a decrease in the average monthly temperature and that the greater gall production in different months is not necessarily at the expense of viable seed production (and even that a higher proportion of galls results in a higher proportion of viable seeds among the crop).

We then separately analyzed the relationships between the viable seeds and wasp offspring (galls) among different crops. In May, vacant female flowers are plentiful, the greater number of wasp offspring (galls) is not necessarily at the expense of viable seeds and there is a positive correlation between the number of galls and viable seeds (Table 3), because pollen dispersion must occur during the process of oviposition. However, in January, the number of wasp offspring is negatively correlated with viable seeds and the proportion of vacant female flowers is very low. The greater number of wasp offspring (galls) must be at expense of viable seeds when vacant female flowers are limited.

The observations show that pollinator wasps can live longer during times with a lower temperature. In May, the pollinator wasps usually live approximately 2 or 3 d and there are no cases in which pollinator wasps lived longer than 3 d. However, pollinator wasps can live longer than 3 d (even up to 4 d) in January (Fig. 1). The longer lifespan of pollinator wasps means that they can oviposit more female flowers, and the greater production of galls in the colder months may be a result of the longer lifespan of the pollinator wasps (Table 1; Fig. 1).

The lower temperature also results in a longer fruiting cycle of the figs and the fruits usually need approximately 2 or 3 months to develop to maturity

Table 1 Mean number galls and viable seeds and their proportion intotal female flowers per fruit in different crops

Month	Sample size	Galls (*n*)	Galls (%)	Seeds (*n*)	Seeds (%)
January	48	3 423 ± 580	50.0 ± 8.1	1 885 ± 672	28.8 ± 12.6
April	32	2 247 ± 1 138	25.7 ± 1.2	1 956 ± 816	23.3 ± 9.2
July	42	1 966 ± 829	30.4 ± 10.5	1 815 ± 754	28.0 ± 10.0
November	20	3 209 ± 1 235	48.9 ± 22.1	1 894 ± 1 006	27.8 ± 10.5

The proportions of galls and viable seeds in total female flowers are calculated on the basis of 25% of female flowers of each fruit.

Table 2 Comparison of the mean numbers of galls and viable seeds and their proportion in the total female flowers of *Ficus racemosa* between the rainy and dry seasons by Student's *t*-test

Types	Crops	Sample size	Galls (*t*)	Seeds (*t*)
Proportion in total female flowers	2	148	67.50^{***}	1.45 (NS)
Mean number	2	148	61.35^{***}	1.85 (NS)

***, $P < 0.001$; NS, not significant at $P = 0.05$.

Table 3 Relationships between viable seeds and wasp offspring (galls) at different mean proportions of vacant female flowers per fruit

	Month			
	January	April	July	November
Sample size	48	32	42	20
PVFF (%)	20.4 ± 2.8	68.0 ± 2.8	54.8 ± 11.0	42.6 ± 13.8
r (Pearson correlation)	-0.59^{*}	0.74^{***}	0.14 (NS)	0.30 (NS)

The analysis was performed with the total number of all types of female flowers. *, $P < 0.05$; ***, $P < 0.001$; NS, not significant at $P = 0.05$. PVFF, the proportion of vacant female flowers per fruit.

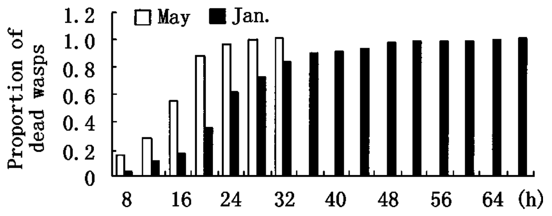

Fig. 1. Proportion of dead pollinator wasps (*Ceratosolen fusciceps*) at different times after exiting mature fruits in May and January (n = 200).

during the rainy season compared with more than 3 months, or even 4 months, to complete their fruiting cycle in the dry season. The longer fruiting cycle of figs results in a longer oviposition time for non-pollinator wasps because the non-pollinators oviposit the female flowers from outside the fruit wall. During the rainy season, only a few fruits have galls (oviposited only by non-pollinators) before pollinators enter the receptive fruits, and the mean number of galls per receptive fruit is 7 (n = 120; the oviposition of non-pollinators occurs mainly after the pollinators have entered the receptive fruit). However, in the dry season, it is very common that the receptive fruits have galls before the pollinators enter the fruits and the mean number of galls per receptive fruit is 17 (n = 105). Obviously, the time for the non-pollinators to oviposit is much longer during the dry season compared with the rainy season.

The structure of the fig-supported wasp community differs considerably among different months. Owing to the rainy season, the proportion of pollinator wasps is much higher than during dry season, whereas in the dry season, the proportion of non-pollinator wasp is much higher than that during the rainy season, especially in January, which has the lowest monthly average temperature in Xishuangbanna (Table 3). During the dry season, the figs support more non-pollinators, and the greater number of non-pollinators is not at the expense of viable seeds, the non-pollinators do have a significant negative impact on the pollinator wasps (Tables 4, 5).

The foundress abundance per fruit also differs considerably in different months ($F_{5,\,603}$ = 27.9; $P <$ 0.001). Figure 2 shows that the mean foundress number per receptive fruit is much lower in cold months (November to January), whereas the number of both wasp offspring and viable seeds is not lower than that in other months, and it is even the case that the number of both the galls and viable seeds in total female flowers is a little higher than that during other months (Tables

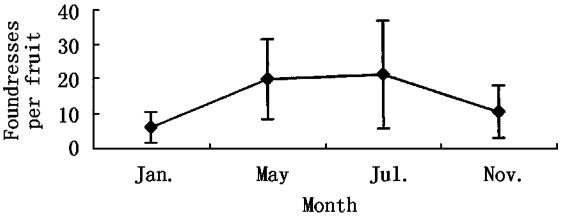

Fig. 2. Seasonal changes in the mean foundresses number per fruit of *Ficus racemosa* in different months (sample size in each crop > 50).

Table 4 The proportions (%) of all kinds of adult female wasps in mature fruits (*Ficus racemosa*) in different months (mean ± *SD*). The non-pollinators include both *Apocryptophagus* wasps and *Apocrypta* wasps.

Seasons	Sampled trees	Sampled fruits	Pollinators	*Apocryptophagus* wasps	*Apocrypta* wasps	Non-pollinators
January	7	70	36.1 ± 29.3	41.3 ± 24.9	22.6 ± 14.9	63.9 ± 29.3
April	4	65	65.9 ± 25.5	24.7 ± 18.5	9.4 ± 11.2	34.0 ± 25.5
July	6	58	54.8 ± 25.0	26.1 ± 18.1	9.1 ± 11.2	45.2 ± 25.0
November	4	64	46.9 ± 28.3	36.1 ± 22.4	18.0 ± 13.9	53.1 ± 28.3

Table 5 Comparison of the mean numbers and proportions of all types of wasps between the rainy and dry seasons in *Ficus racemosa* fruits by Student's *t*-test

Types	Pollinators	*Apocryptophagus*	*Apocrypta* wasps	Non-pollinators
Proportion of total wasps	2.67^{*}	2.90^{**}	3.42^{**}	3.84^{***}
Mean number	3.41^{**}	2.20^{**}	1.97^{*}	5.41^{***}

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

1, 2). In order to determine whether the greater number of galls is a result of the higher proportion of non-pollinators, we compared the proportion of both galls and viable seeds in total female flowers with data from the controlled fruits in which non-pollinators were prevented from ovipositing by the organdie (in November). The results showed that both the proportion of galls (d.f. = 39; $t = 0.83$; $P < 0.05$) and viable seeds (d.f. = 39; $t = 0.06$; $P < 0.05$) in total female flowers was not significantly different between natural fruits and controlled fruits, which indicates that the increased number of galls in the colder months is mainly a result of the longer lifespan of the foundresses rather than due to longer oviposition by non-pollinators.

3 Discussion

Previous theoretical analyses and some empirical data showed that both cooperation and conflict exist in reciprocal mutualism (Axelrod and Hamilton 1981; Pellmyr and Huth 1994; West and Herre 1994; Herre and West 1997), but under what conditions mutualists cooperate or conflict has not been clear until now (Bronstein 2001a, 2001b). Our dataset shows that wasp offspring were positively correlated with viable seeds during the rainy season. The galls are not negatively correlated with the viable seeds in most crops over the year (Wang 2005) and, even, the greater number of wasp offspring can contribute to more viable seed production among different crops, which is in accord with the results of most previous reports that wasp offspring and viable seeds ranged from being weakly to strongly positively correlated in most cases (Bonstein 1988; Bronstein and Hossaert-McKey 1996; Herre and West 1997). The data of the present study show that wasp offspring are positively correlated with viable seeds when the vacant female flowers are plentiful. Many galls are not developed from fertilized female flowers and the increase in the number of wasp offspring is not necessarily at expense of viable seeds (Jousselin *et al.* 2003; Kjellberg F 2003, personal communication). In fact, pollen dispersion to the female flowers must occur during the process of oviposition by the pollinators and, thereby, more oviposition by the pollinators can contribute to more pollen dispersion to the vacant female flowers when vacant female flowers are plentiful. Wang's unpublished data on *F. racemosa* show that the foundresses are positively correlated with viable seeds when vacant female flowers are plentiful. To allow more foundresses to be in the fruit cavities can contribute to a greater production of viable seeds when vacant female flowers are plentiful and, in such cases, cooperation exists.

During the colder months, the pollinator wasps can live longer and thereby oviposit in more of the female flowers and disperse more pollen to the vacant female flowers, which results in a limitation of vacant female flowers (Bronstein 1988; Anstett *et al.* 1996, 1997; Anstett 2001). The non-pollinators can also use more of the female flowers in the colder months, because they can oviposit over a longer time than during the warmer months, which can also result in a limitation on the availability of vacant female flowers. When vacant female flowers are in limited supply, the greater number of galls must be at the expense of viable seeds and, thus, conflict exists during the colder months. In fact, the cold temperature seldom occurs in the tropical rain forest and there are many ecological and evolutionary factors that can constrain the mutualists to maximize the female flowers (Wang 2005) and, thereby, conflict seldom occurs in the fig/fig wasp system and the conflict is of a very elusive nature (Herre and West 1997; West SA and Herre EA, 2004, personal communication). Whether mutualists cooperate or conflict may depend on the availability of the common resource (female flowers), and mutualists will cooperate when the public resource is plentiful, whereas they will be in conflict when the public resource is limited.

There is considerable debate as to why the non-pollinators do not exploit more of the female flowers at the expense of viable seeds and result in the local extinction of figs during the process of evolution (Janzen 1979; West and Herre 1994; West *et al.* 1996; Wang 2005). Our data for *F. racemosa* show that non-pollinators only have negative effects on pollinators, whereas there is no obvious negative impact on viable seeds. In the dry season, the non-pollinators can oviposit for a longer time because of the longer developmental time of the fruits and it results in a much larger proportion of non-pollinators in the fig-supported wasp community during the dry season. The data in Tables 1 and 4 show that the larger proportion of non-pollinators only results in a lower proportion of pollinators and a negative effect on the viable seeds is not obvious; thereby, non-pollinators will not overexploit viable seeds and result in the extinction of figs during the process of evolution.

In the seasonal tropical rain forest, many fig species have considerable different fruit abundance between the rainy and dry seasons. In some figs, such as all the banyans, except for *Ficus superba*, only small retarded crops occur in the dry season or during winter (Janzen 1979), which results in a bottleneck effect on both the viable seeds of figs and the fig-supported wasps. However, because of the negative effect of non-pollinators on the pollinators, the seasonal change in the community structure of the fig-supported wasps may result in a different trade-off among viable seeds and wasps. Usually, the non-pollinators oviposit from outside the fruits and can oviposit for a much longer time than pollinator wasps, whereas the pollinators must oviposit in the fruit cavities and only live 2 or 3 d after exiting from galls (Bronstein and McKey 1989, 1991; Kerdelhue and Rasplus 1996; Nason *et al.* 1998). In the dry season (winter), the developmental time of fig fruits is much longer than that during the rainy season (warmer in climate), which results in more time for non-pollinators to oviposit, whereas the situation for pollinators has not changed compared with that of the rainy season. Obviously, the non-pollinators have negative effects on the production of pollinating wasps (Bronstein 1991; Kerdelhue and Rasplus 1996; West and Herre 1994; West *et al.* 1996). The increase in the proportion of non-pollinators results in a decrease in the abundance of pollinator wasps, which can worsen the pollinator supply during the dry season. Thereby, the bottleneck effect on the pollinator population is more severe than that on non-pollinators and figs.

One remaining question is why the pollinating wasps do not exploit more or even all of the female flowers at the expense of seed production by the fig (Bronstein 1988; Kathuria *et al.* 1995; Herre and West 1997; Kjellberg *et al.* 2001). Although there are many mechanisms involved, the conflict between viable seeds and wasp offspring may be the real hidden dynamic maintaining this obligate system stable (Herre and West 1997; Anstett 2001; Bronstein 2001a, 2001b). The conflict only exists during a certain period and the selective force to maintain this system may only work during the period that the conflict exists between the mutualists, and it may be possible that the fig has developed a mechanism to maintain a stable system (Pellmyr and Huth 1994; Herre and West 1997; Herre *et al.* 1999; Bronstein 2001a, 2001b). In the Yacca/Yacca moth system, the plants maintain a stable system by the selective abortion to the fruits oviposited by non-pollinators or the less effective pollen dispersion pollinators (Pellmyr and Huth 1994). In the fig/fig wasp system, Herre and West also assumed that the plant developed a mechanism to maintain a stable system for the conflict that exists between the wasp offspring and viable seeds (Herre and West 1997; Herre *et al.* 1999). Our dataset shows that the figs allow fewer foundresses to be in their fruit cavities during the colder months. In the controlled experiment with a high pollinator density, the figs obviously allow fewer foundresses to be in their receptive fruits on the colder days, whereas they allow more pollinators to be in their receptive fruits on the warmer days (Wang 2005). During the colder months, because of the longer lifespan of the pollinators and the longer oviposition of non-pollinators, vacant female flowers are in limited supply, meaning that the increased number of wasp offspring must be at the expense of the viable seeds. Thus, allowing fewer foundresses to be in their fruit cavities can prevent the wasps from overexploiting the female flowers at the expense of the viable seeds because the foudress number is positively correlated with the number of galls ($n = 65$; $r = 0.48$; $P < 0.001$). Our data may suggest that figs maintain a stable system by regulating foundress abundance in their fruit cavities. It may be possible that figs regulate foundress abundance by different receptive lengths to pollinators (Khadari *et al.* 1995) and differences in the tightness of bracts during different periods (Wang 2005).

As how the fig/fig wasp system maintains its stability has been debated for many decades (Janzen 1979; West and Herre 1994; Herre and West 1997; Weiblen 2002). Our data showed that the pollinators cannot overexploit the viable seeds because the figs can limit the number of foundresses that are in their fruit cavities, thereby not allowing exploitation of more female flowers at the expense of the viable seeds, which is in accordance with the assumption of Herre and West (1997). The non-pollinators tend to oviposit the female flowers that have been oviposited by pollinators and only have a negative effect on the pollinators, with no obvious negative effect on viable seeds. These data provide an answer to the question why wasps do not utilize more of the female flowers at the expense of the viable seeds, thereby resulting in the extinction of the figs during the process of evolution (Janzen 1979; West and Herre 1994; Herre and West 1997). The remaining question on this topic is why the non-pollinators did not exclude the pollinators in the process of evolution because they utilize the same resource or the non-pollinators directly parasite the pollinators and the negative effect of non-pollinators on the pollinators obviously exist (Janzen 1979; West and Herre 1994; Weiblen 2002). The abortion of unpollinated fruits may be one of the main mechanisms (Herre 1989; Wang 2005, unpublishing data, but there are other more mechanisms that need to be investigated because many fruits can still develop to maturity without pollination (Wang RW 2003, unpublishing data; Herre EA 2004, personal communication) and some non-pollinators are parasites of the pollinators (Kerdelhue *et al.* 2001; Weiblen 2002).

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