Male and female reproductive success in the dioecious fig, *Ficus hirta* Vahl. in Guangdong Province, China: Implications for the relative stability of dioecy and monoecy

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Abstract

We studied components of male and female reproductive success in the fig, *Ficus hirta* from Guangdong Province, China. Specifically, we analyzed the composition and sex ratio of both pollinating (*Blastophaga javana*) and the two species of non-pollinating wasps associated with functionally male figs, as well as seed production in the functionally female figs. In male figs, a mean of 799 flowers produced a mean of 234 wasps (mean proportion of flowers developed in each fruit is ~31%). Female pollinating wasps (the only vectors for fig pollen) comprised the majority of all wasps in male syconia (~62.8%), indicating a relatively high fitness for the pollinator and the fig. The median sex ratio of the pollinators was 0.16 (mean ~24% males) and roughly reflects estimates of average foundress number (1.7). There are two common non-pollinators in male syconia of *F. hirta*: one, *Sycoscapter hirticola*, also exhibited a strongly female biased sex ratio, while the other, *Philotrypesis josephi*, was male biased. In female figs, a mean of 858 flowers produced a mean of 433 viable seeds (mean of flowers developed in each fruit is ~50%). Thus, similarly to other studies of dioecious species in which detailed data on wasp and seed production have been reported, female inflorescences (figs) generally appear to initiate more flowers than male inflorescences, and produce more seeds than male inflorescences produce female pollinator wasps. Compared with published studies of seed and wasp production in monoecious figs, *F. hirta* appears more efficient on a per syconium basis at both seed and female pollinator wasp production than monoecious species characterized by large numbers of flowers, high average foundress numbers, and high non-pollinator wasp loads. These comparisons suggest conditions that favor selection for (and stability of) either the monoecious or dioecious breeding system in figs.

Keywords: *Ficus hirta*, dioecious, monoecious, breeding system stability, sex ratio, fig wasps

1. Introduction

There are approximately 750 fig species (*Ficus*, Moraceae) distributed pan-tropically, pollinated by highly specific chalcidoid wasps (Agaonidae) (Berg, 2003; Molbo et al., 2003). In monoecious fig species, approximately half of the fig species described, trees produce individual inflorescences that perform both female (seed production and dispersal) and male (pollen production and dispersal) functions. In these systems, mated, pollen-bearing female pollinators enter syconia (inflorescences), pollinate the tiny female flowers inside and oviposit in some of them (Galil and Eisikowitch, 1968; Herre, 1989, 1996, 1999). The pollinator offspring develop by consuming the contents of one would-be seed each.

They then emerge, mate, and the winged female either actively or passively gather pollen, leave the natal syconium, and fly off in order to attempt to find a receptive syconium and begin the cycle anew. The fruit then undergo a final ripening and are usually consumed by vertebrate frugivores that also disperse the seeds (Kalko et al., 1996; Shanahan et al., 2001).

In dioecious fig species, some individual trees produce only seed-bearing fruit and are functionally female, while others produce pollen and pollen-carrying wasp progeny and are functionally male. The female pollinators that enter syconia on female trees, which contain only long-styled female flowers, usually fail to oviposit because their ovipositors are too short, and hence only seeds are produced. For the female trees, seed production represents the major component of reproductive success. Those entering syconia on male trees, which contain male and

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"gall" flowers (short-styled female flowers), can oviposit in any of the flowers, but in most species no seeds develop (Galil, 1970; Weiblen et al., 2001; Harrison and Yamamura, 2003). The mature female wasp offspring, having mated inside the inflorescences, disperse carrying pollen and eggs to another receptive inflorescence to start the cycle anew. If the wasps enter a syconium on a male tree, they will be able to reproduce, but the natal tree receives no benefit in terms of ovules pollinated with the pollen the wasp was carrying. However, if the wasps enter a syconium on a female tree, the wasps do not reproduce, but the natal tree benefits via the production of seeds fertilized with its pollen (Kjellberg, et al., 1987; Patel and Hossaert-McKey, 2000; Machado et al., 2001). Thus, the number of female pollinators represents major components of fitness for both the parent wasp(s) and the male fig tree (Herre, 1989; Patel, 1998; Machado et al., 2001).

In addition to pollinating wasps, many non-pollinating wasp species are also associated with figs (Compton and Van Noort, 1992; Compton and Hawkings, 1992; Kerdelhue and Rasplus, 1996). Most of these oviposit from outside of the syconium, by inserting their ovipositors through the wall. Studies in monoecious species show that some non-pollinator species potentially have a negative impact on the fig-fig pollinator interaction through competition for oviposition sites or by killing pollinator larvae or by using fertilized ovules and thus eating a certain proportion of the potential seeds (West and Herre, 1994; West et al., 1996; Kerdelhué et al., 2000). However, in most dioecious studies, successful development of non-pollinators appears to be completely or largely restricted to fruits on male trees and often comes at the expense of pollinator wasp production (Kerdelhué and Rasplus, 1996; Patel and Hossaert-McKey, 2000; Weiblen et al., 2001; Harrison and Yamamura, 2003; Peng et al., 2005).

Phylogenetic analyses suggest that the monoecious breeding system is basal in figs, that dioecious lineages have evolved at least twice from monoecious lineages and further that there has been at least one reversion from dioecy to monoecy (Machado et al., 2001; Rønsted et al. 2005). These patterns imply that during the course of the evolution of the genus *Ficus,* selection at different times has favored one or the other of these two breeding systems. Quantitative studies in monoecious fig systems show that conditions that might favor the fig's female success (seed production) are not necessarily those that favor the fig's male success (production of female pollinator wasps). Specifically, there is an inherent negative relationship between seed and wasp production in monoecious figs (Herre 1989, 1996, 1999; Herre and West 1997).

Further, factors that reduce relative or total female wasp production (e.g., higher foundress numbers within pollinator broods, or increases in certain groups of non-pollinators) can greatly reduce fig "male" fitness while increasing or not affecting fig "female" success. These observations suggest a series of functional hypotheses predicting the conditions that can provide relative advantages for either dioecy or monoecy in figs (Herre, 1989, 1999; West and Herre, 1994; Kerdelhué and Rasplus, 1996; West et al., 1996; Weiblen et al., 2001; Harrison and Yamamura, 2003). However, few studies have presented detailed data on seed and pollinator wasp (especially female pollinators) production in dioecious figs, and fewer still have compared the efficiency of figs of monoecious and dioecious breeding systems in producing these major components of female and male reproductive success (Patel, 1998; Patel and Hossaert-McKey, 2000; Weiblen et al., 2001; Harrison and Yamamura, 2003).

In this study, we measured major components of the reproductive success of male and female trees in the dioecious fig species *Ficua hirta.* By assessing total numbers of flowers in male and female inflorescences, and relating that to ultimate wasp composition and sex ratio in the former, and seed production in the latter, we are able to estimate the relative efficiency of the figs realizing male and female fitness. We then can compare those efficiencies on a per syconium basis with published figures from monoecious figs to infer conditions that provide relative advantages to each breeding system.

2. Material and Methods

Species

Ficus hirta Vahl (subsection *Eriosycea*, subgenus *Ficus*) is an understory dioecious fig tree that grows to a height of approximately 1–3 m. Male and female syconia can be produced year-round, although there are peaks at certain times of the year (Yu et al., 2006).

Blastophaga javana Hilli (Agaoninae, Agaonidae, Chalcidoidea) is the pollinator of *F. hirta.* Three species of non-pollinators (Sycoryctinae, Agaonidae, Chalcidoidea) have also been recorded on *F. hirta* at Guangdong (South of China): *Sycoscapter simplex* Mayr, *Philotrypesis josephi* Balakrishnan and *Sycoscapter hirticola* Balakrishnan. Both females and males of these species can be recognized from morphological characters. In Guangdong, *P. josephi* and *S. hirticola* were relatively common, but *S. simplex* was very rare. Females of all non-pollinating species oviposit from outside the syconium, so they cannot contribute to pollination.

Study sites and collections

Between July 2002 and June 2003, we collected syconia from both male and female figs at the South China Botanical Garden (SCBG), Guangdong Province, China (E113°11′, N23°11′, elevation 20–327 m), and assayed their contents.

Table 1. The contents of 107 D-phase male syconia of *Ficus hirta* Vahl. collected in South China Botanical Garden (Guangdong Province, China) from July 2002 to June 2003.

N=number of sample syconia (N=107)		Number of different elements in syconiun		Production (%) of different elements vs. female flowers in syconium		Sex ratio ($\male/\male+\female$) percentage (%) of pollinators and non-pollinators vs female flowers in syconium	
Number of syconia occupied		Mean±SD	Range	Mean±SD	Range	Mean±SD	Range
107	Female flowers	799±362	160–1852	–	–	–	–
105	Pollinator	190±179	0–997	24.4±18.4	0–85.9	24.2±22.0	0–98.5
	Female pollinator	146±149	0–852	18.3±15.7	0–65.7	–	–
60	*Sycoscapter hirticola*	25.6±39.8	0–192	4.9±8.4	0–42.4	9.5±15.6	0–66.7
61	*Philotrypesis josephi*	18.7±26.5	0–100	2.8±4.5	0–23.6	67.1±33.5	0–100

Table 2. The contents of 139 late C-phase female syconia of *Ficus hirta* Vahl. collected in South China Botanical Garden (Guangdong Province, China) from July 2002 to June 2003

N=number of sample syconia (N=139)	Number of different elements in syconiun		Production (%) of seeds vs. female flowers in syconium	
Number of syconia occupied	Mean±SD	Range	Mean±SD	Range
139 Female flowers	858±413	210–2747	–	–
139 Seeds	433±347	36–2524	50.0±26.0	4.2–97.9

For male figs, we randomly collected 4–20 D-phase male syconia monthly. In total, 107 male syconia in D-phase from at least 30 trees were examined. In order to count numbers of symbiotic wasps in each fruit, we placed individual male fruit with un-emerged wasps into separate muslin bags. After the exit of the winged wasps was completed, we removed them from the bag and then sliced the fruit open to collect the entrapped males and the galls in which the wasps have not exited. All wasps found in these fruit were thus counted and identified, as were the number of undeveloped female flowers in a randomly selected section that represented one-quarter of each fruit. The total number of female flowers in each fruit was the sum of developed female flowers and four times undeveloped female flowers in that section. Production (%) of different elements (such as pollinators and non-pollinators) vs. female flowers in each fruit was estimated by dividing the number of them by the total number of female flowers. Results are presented as means ± SD (Table 1).

For female figs, we collected 9–14 late C-phase syconia monthly. In total, 139 female syconia in late C-phase from at least 40 trees were examined. The key syconia parameters, such as number of flowers and seeds were counted under a dissecting microscope (SZ-CTV, Olympus, Japan). The number of female flowers and seeds in a randomly selected section that represented one-quarter of

each fruit were multiplied by 4 to estimate production in the entire fruit. Production (%) of seeds vs. female flowers in each fruit was estimated by dividing the number of them by the total number of female flowers. Results are presented as means ± SD (Table 2).

As sex ratio and production of fig wasps are generally adjusted for different foundress number, it is important to know foundress distribution in our samples. But in most of them, we could not find remains of foundress. Re-emergence of foundress after pollination and egg deposition have been reported in some fig species (Gibernau et al., 1996; Bronstein and Hossaert-McKey, 1996; Moore et al., 2003) and which may also exist in pollinator of *F. hirta*. In order to estimate the foundress distribution and re-emergence of *F. hirta* in SCBG, syconia in B-phase (60 male and 54 female) and in former C-phase (208 male and 182 female) were collected randomly from September 2004 to June 2006 in SCBG. In the laboratory, each fruit was split open and the number of pollinators trapped inside (either in the fig cavity or in the ostiole) was noted.

3. Results

Male fig brood composition and sex ratios

We found that in 107 male syconia examined the mean number of flowers was 799±361. Of the 107 D-phase male syconia, 32% were found to contain no parasites, 11% only contain *S. hirticola*, 12% only contain *P. josephi*, and 45% contain both. Out of all the observed syconia, just two contained only non-pollinators: one had only *S. hirticola*, the other contained both *S. hirticola* and *P. joseph*. The most likely explanation is that the galls contained pollinator larvae previously had all been predated by non-pollinators which parasite in them. In the 107 figs, *Blastophaga javana*, there was a mean of 190±179 pollinator wasps, of which the mean number of females was 146±149. The mean sex ratio (proportion of males) in the broods was 0.24±0.22. The median sex ratio was ~0.16. In the samples in which the species occurred, *Sycoscapter hirticola*

showed a mean of 25.6±39.8 individuals per syconium. The mean brood sex ratio was 0.095±0.156. For *Philotrypesis jospehi*, a mean of 18.7±26.5 was encountered. The mean brood sex ratio was male biased, 67.1±33.5 (see Table 1). As a proportion of total flowers, pollinator production ranged from 0 to 85.9%, and the mean 24.4%; female pollinator production was from 0 to 65.7%, and the mean 18.3%; *Sycoscapter hirticola* was from 0 to 42.4%, and the mean 4.9%; *Philotrypesis josephi* was from 0 to 23.6%, and the mean 2.8%. In total, mean production of wasps was nearly 31%.

Female fig reproductive composition

We found that in 139 female figs examined the mean number of flowers was 858±413, and there was a mean of 433±347 seeds. Seed production was from 4.2% to 97.9%, and the mean was nearly 50%.

Foundress number

The number of pollinators trapped (foundress number) per B-phase syconium was 1.7±1.6 in the males and 1.3±0.8 in the females. Foundress number per C-phase syconia was 0.4±0.7 in the males and 0.5±0.7 in the females. Fig. 1 (A, B) shows foundress number in B- and C-phase syconia of *F. hirta* from SCBG. Foundress numbers per B-phase syconium (i.e. pollination intensity on a per-syconium basis) ranged from 1 to 9 in the male and from 1 to 6 in the female: a majority of them (70.0% male; 85.2% female) contained just one pollinator; two pollinators were the second commonly sampled: 13.3% male and 9.3% female; one or two pollinators made up 83.3% of the observed case in male syconia, and 94.4% in female syconia. Foundress numbers per C-phase syconium ranged from 0 to 3 in the female and from 0 to 5 in the male: a majority of them (65.9% male; 61.5% female) contained no pollinator; one pollinator was the second most commonly sampled: 29.3% male and 32.4% female; 95.2% of male syconia and 94.0% female syconia contained 0 or one pollinator.

The mean number of foundress in C-phase syconia is much lower than that in B-phase syconia, and many C-phase syconia contain no pollinators but have clearly been pollinated as evidenced by some swollen ovaries. In some C-phase syconia, we also observed pollinators dead in the bracts around the ostiole with heads facing outwards, which imply that they try to escape. So we conclude that foundresses commonly re-emerge in *F. hirta*.

4. Discussion

All else equal, more efficient production of seeds and pollen-carrying pollinator wasps should be at a selective
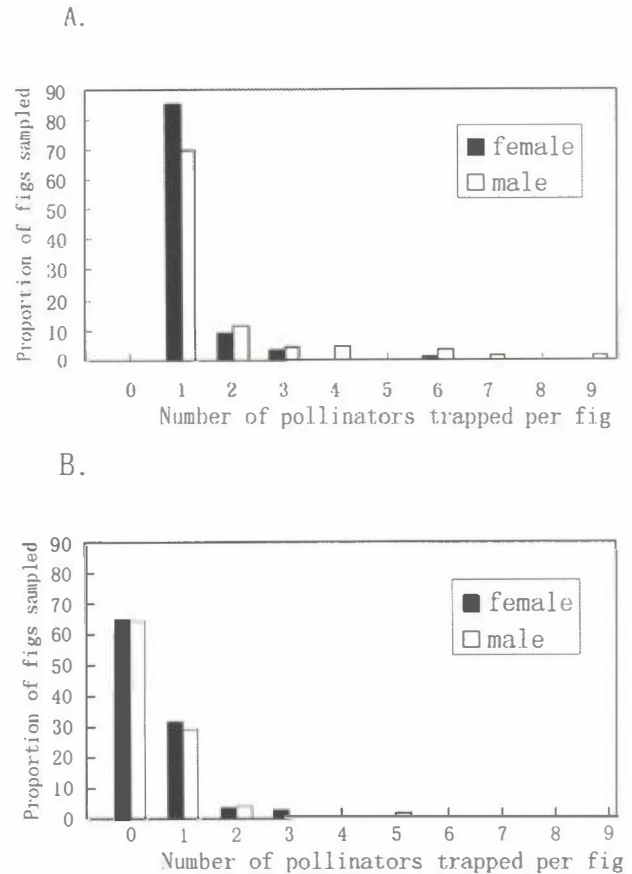
A.

B.

Figure 1. Distribution of pollinator wasps trapped per fig. Data from syconia in B-phase (60 male and 54 female) and in former C-phase (208 male and 182 female) of *Ficus hirta* Vahl. in South China Botanical Garden (Guangdong Province. China). were collected randomly from September 2004 to June 2006. A) Represent the data in B-phase syconia; B) Represent the data in former C-phase syconia.
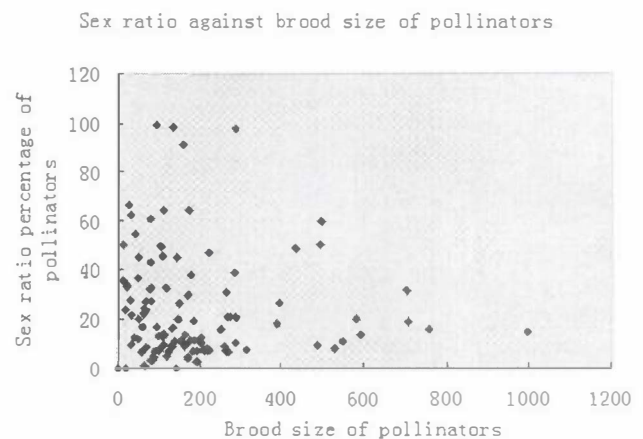

Figure 2. The relationship between the brood sex ratio percentage (proportion of males) and brood size of a fig-pollinating wasp (the wasp that pollinate *Ficus hirta* Vahl.). Data from 107 male syconia in D-phase in South China Botanical Garden (Guangdong Province. China) from July 2002 to June 2003.

advantage in figs. The conditions under which, and the degree to which, either a monoecious or a dioecious system is more efficient at producing these major components of reproductive success should be related to relative stability of each system (Kerdelhue and Rasplus, 1996; Herre, 1989; Patel, 1998; Patel and Hossaert-McKey, 2000; Weiblen et al., 2001; Harrison and Yamamura, 2003; see Charnov, 1982).

A series of quantitative studies of factors influencing the production of seeds and female wasps across a community of Panamanian monoecious figs (Herre, 1989, 1996, 1999; West and Herre, 1994; West et al., 1996; Herre and West, 1997) demonstrate how fruit size, flower number, wasp size, foundress number, and non-pollinator wasp number interact to influence seed and wasp production within and across fig species exhibiting a wide range of each of these variables. Specifically, in monoecious figs there is an inherent trade-off between wasp production (largely fig "male" success) and seed production (fig "female" success); each wasp is produced at the expense of one would-be seed (Herre and West, 1997). Further, factors that undermine efficiency of female wasp production (fig male success) by shifting wasp sex ratio away from females (i.e., high levels of local mate competition produced by high foundress numbers) often promote efficiency of seed production (fig "female" success; Herre, 1989). These studies suggest that by having both sexual functions within a single syconium, monoecious species are subject to inherent tradeoffs between and inefficiencies in both female and male function.

In addition, it has been suggested that the negative effects of non-pollinator wasps (that mostly reduce fig male function) have contributed to the evolution of dioecy in figs (Kerdelhue and Rasplus, 1996; Harrison and Yamamura, 2003). However, few studies report seed and total wasp production in dioecious figs (reviewed in Harrison and Yamamura, 2003) and fewer still give sufficient details of wasp production (male and female pollinators, male and female non-pollinators; see Patel, 1998; Patel and Hossaert-McKey, 2000; this study) to allow direct comparison with the monoecious data.

We find that in *Ficus hirta*, as with most dioecious studies (Harrison and Yamamura 2003), the syconia of female dioecious figs generally have more female flowers, and generally produce more seeds than male syconia produce wasps (total) and many more than male syconia produce female pollinator wasps. Compared to the detailed studies of monoecious figs (Herre, 1989) we see evidence for a relatively higher efficiency of producing female pollinators compared to monoecious species in which the average foundress number is high, and in which the proportion of non-pollinators is high. However, monoecious species with low average numbers of foundresses and low incidence of non-pollinators often appear to be more efficient at producing both seeds and

female pollinator wasps (Herre, 1989). Thus, our data and the comparisons that they allow, suggest that we could expect that dioecy arose from a lineage of monoecious figs that were large, had high foundress numbers and showed high levels of non-pollinators (see Kerdelhue and Rasplus 1996; Patel and Hossaert-McKey, 2000; Harrison and Yamamura, 2003). Similarly, we can expect that reversions to monoecy likely occurred in dioecious lineages characterized by small fruit, few foundresses, and low levels of non-pollinator infestation.

Wasp sex ratios

In addition to directly influencing fig male function via affecting proportion of female pollinators produced, knowledge of pollinating wasp sex ratio (proportion of the males) is also valuable in examining general theoretical predictions of local mate competition (LMC). Previous studies on wasp composition and sex ratios have focused mainly on monoecious fig species (Bronstein, 1988; Herre, 1987, 1989; Kerdelhué and Rasplus, 1996; Kerdelhué et al., 2000; Molbo et al., 2003; Pereira and do Prado, 2005), and studies on dioecious figs are relatively few (Patel, 1998; Weiblen, 2002; Peng et al., 2005).

In *F. hirta*, we found mean pollinator sex ratios of 0.24±0.22 (median of 0.16). Thus a male of pollinator from could expect to mate with 3.16 females on average in each syconium (Table 1). This value is higher than observed in many monoecious species with low foundress numbers (Herre, 1987; Pereira and Prada 2006). Reports from other dioecious species, such as *F. exasperata* and *F. hispida*, show similar or lower pollinator sex ratio (Nair and Abdurahiman, 1984; Patel, 1998) most likely according to local wasp abundance. Although the median sex ratio (0.16 males) agrees well with the observed foundress numbers (1.7 foundress per fig in average), the mean sex ratio of pollinators (~0.24) is relatively high given the foundress number. This probably reflects the influence of a relatively few broods with high sex ratio values which could correspond to the relatively few cases we found with high foundress numbers (some cases with 5–9 foundresses). Nonetheless, correlations between brood sex ratios and brood size of pollinators do not suggest that the number of wasp offspring is strongly related to sex ratios (i.e. if larger broods are produced by more foundresses as is the case in several monoecious species (Herre, 1989), larger broods should have more males). We did not observe pollinating males fighting and dispersing in figs of *F. hirta* (see Greef et al., 2003).

Mean production of non-pollinator offspring (2.8% for *P. josephi* and 4.9% for *S. hirticola*) is also lower than many, but not all monoecious fig species (0–59%; Herre, 1989; Patel, 1998; also Herre, unpublished), but similar to other dioecious figs (Patel, 1998; Weiblen et al., 2001; Peng et al., 2005). So, in agreement with other studies the

non-pollinator wasp loads in the dioecious appear generally lower than those in monoecious species. Many non-pollinators can move among syconia and can be expected to oviposit in multiple syconia, so applying LMC theory and sex ratio predictions can be difficult (Patel, 1998; West and Herre, 1998). In *F. hirta*, the two non-pollinators had very different sex ratios: the mean sex ratio of *S. hirticola* was strongly female-biased (9.5% males) implying LMC is high and single- or few-foundress broods are the norm; while that of *P. josephi* was slightly male-biased implying LMC is low and more foundresses commonly oviposit on the same syconium. The males of *S. hirticola* are smaller and with elongate head what supposedly allowed them to manoeuvre and mate in areas of the fig where flowers are tightly packed, whereas *P. josephi* usually show high levels of aggression and lethal combat to challenge for mating opportunities. Careful observational, experimental, and / or genetic studies are needed to determine the precision with which the wasps associated with *F. hirta* conform to LMC predictions (e.g., see West and Herre, 1998; Molbo et al., 2003).

Conclusions

All else is almost never equal, and a focus simply on efficiencies of per fruit production of seeds and wasps leaves out important considerations of crop level pollination success, resource or pollen limitation, differential system capacities to maintain pollinator (or non-pollinator) wasp populations, etc. All of these considerations might be expected to influence relative stability of functionally monoecious and dioecious fig systems (Kjellberg et al., 1987; Herre, 1996, 1999; Patel and Hossaert-McKey 2000; Weiblen et al., 2001; Harrison and Yamamura, 2003). Nonetheless, estimating production the basic currencies of reproductive success for the fig and the wasps (as well as the efficiencies at producing them) is fundamental for informed comparisons of the relative stability of monoecious and dioecious reproductive systems in figs. Combined with other studies, this one suggests that inherent trade-offs between efficient female and male function underlie the observation that over evolutionary time, figs have shifted back and forth between monocious and dioecious breeding systems on more than one occasion.

Acknowledgements

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