Ecology of parasite *Sycophilomorpha* sp. on *Ficus altissima* and its effect on the fig-fig wasp mutualism

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SUMMARY

Figs and their pollinating wasps are a classic example of an obligate mutualism. In addition, figs are parasitized by a suite of non-mutualistic wasps whose basic ecology is largely undescribed. *Sycophilomorpha* (subfamily Epichrysomallinae) fig wasps are ovule gallers and the genus contains only 1 described species. An undescribed *Sycophilomorpha* species parasitized *Ficus altissima* at Xishuangbanna, Southwestern China. The wasp was observed ovipositing on the tiny immature figs that were still concealed beneath the involucre bracts. A *Sycophilomorpha* wasp oviposited on more than 1 fig and spent long time-periods to lay large clutches on a single fig. The wasps naturally occurred on all 7 sampled trees, but the occurrence of wasps was significantly different among trees, crops and months. These wasps were able to prevent unpollinated figs from being aborted, and their offspring were able to develop in the figs that otherwise had no pollinator wasps or seeds. The *Sycophilomorpha* wasp had a detrimental effect on the fig-fig wasp mutualism. Figs in which *Sycophilomorpha* wasps were present, produced significantly fewer seeds, pollinators and cheaters. However, the abundance of *Sycophilomorpha* in a fig was only significantly negatively correlated with pollinator production and not seed or cheater production. Our study illustrates a previously unknown fig wasp niche and expands our understanding of factors that can affect the fig-fig wasp interaction.

Key words: parasitism, coevolution, galler, mutualism, syconia.

INTRODUCTION

Parasites typically depend upon their hosts for shelter, nutrition, and reproduction. Parasites can acquire these needs by 2 alternative strategies: exploitation and cooperation. Parasites exploit hosts to advance their own reproduction at the cost of host fitness. In contrast, mutualists increase their reproductive output by increasing host fitness (Herre, 1995; McBride *et al.* 2008). Parasites reduce host fitness and so can also affect that of a host's mutualists (Compton *et al.* 1994; Kerdelhué *et al.* 2000).

A majority of the 750 *Ficus* species (Moraceae, see Berg, 1989) is involved in a species-specific obligate mutualism with its pollinator chalcid wasp (Hymenoptera: Agaonidae), which also strictly depends on its host fig for reproduction. The system forms a remarkable plant-insect obligate mutualism (Ramirez, 1970; Galil, 1977; Wiebes, 1979). Figs also support a diverse community of non-mutualistic wasps (Compton *et al.* 1994; Kerdelhué *et al.* 2000). Both morphological and molecular data suggest an ancient association between these wasps and their hosts.

Despite providing no pollinating services, and so having no apparent benefit to the fig, these non-mutualistic wasps are ubiquitous (West and Herre, 1994; Kerdelhué and Rasplus, 1996; Jousset *et al.* 2006; Marussich and Machado, 2007). These wasps include gallers, inquiline, kleptoparasites, parasitoids of the pollinators, and parasitoids of other nonpollinating wasp species (Kerdelhué *et al.* 2000; Peng *et al.* 2005a,b). Up to 32 species have been described in association with a single fig species (Bronstein, 1999). In every study that has examined the relationships in detail, non-pollinating fig wasps have been found to have a negative impact on pollinator production, and sometimes also on seed production (Compton *et al.* 1994; West and Herre, 1994; West *et al.* 1996).

Non-pollinating fig wasps belonging to different families and subfamilies have in some cases exhibited ecological convergence in fig utilization (van Noort and Compton, 1996; Rasplus *et al.* 1998). Each particular species oviposits at a specific stage of fig maturation (Elias *et al.* 2008). 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 (Kerdelhué *et al.* 2000; Peng *et al.* 2005a). Among non-pollinating fig wasps, all the species of subfamily Epichrysomallinae are gall-makers. They oviposit in

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very young syconia prior to pollinator arrival, and induce very large galls that protrude in the fig cavity (Kerdelhué *et al.* 2000; Niu *et al.* 2009). They usually gall the flowers (Galil and Copland, 1981), but also apparently the fig wall (J. Y. Rasplus, unpublished data) or on twigs (Ferrière, 1929). In Africa, the subfamily Epichrysomallinae is well represented with nearly 40 species. It is also distributed in the Indo-Australasian region, but most species are undescribed (Boucek, 1988). Unlike the pollinators, epichrysomallinae wasps attack the flowers by piercing the outside of the receptacle. During oviposition, epichrysomalline females inject the contents of their acid gland reservoirs in the ovaries, which stimulates parthenogenetic nucellar development to provide food for the offspring (Galil and Copland, 1981).

Sycophilomorpha genus belonging to subfamily Epichrysomallinae is distributed in the Asian continent, and only 1 species (*Sycophilomorpha sapta-purensis* Joseph and Abdurahiman, 1969) has been described. The fig host is *Ficus bengalensis* in India (Joseph and Abdurahiman, 1969). Nothing about the biology and ecology of this genus has been reported. *Sycophilomorpha* sp. was found to parasitize *F. altissima* at Xishuangbanna, South-western China. Both *F. bengalensis* and *F. altissima* belong to Subgenus *Urostigma* and Section *Conosycea*, and their pollinators are *Eupristina* wasps (Priyadarsanan, 2000). However, *F. altissima* presents an interesting case for studying factors affecting the stability of the fig–fig pollinator interaction, because of the presence of a cheater – a species congeneric with the pollinator that does not pollinate (Peng *et al.* 2008). Hence, in this study we observed the ecology of *Sycophilomorpha* sp. and investigated its effect on this tripartite interaction.

MATERIALS AND METHODS

Study site

The study was carried out around Menglun town, Xishuangbanna in tropical Southwest China (21°55'N, 101°15'E, at about 555 m asl). Temperature and rainfall data collected for 40 years at Xishuangbanna Forest Ecology Station, less than 3 km from the research area, show that annual temperature averages 21.8 °C, with means of 25.7 °C in the hottest month (June) and 16.0 °C in the coldest month (January). Average annual relative humidity is 85.0% and rainfall is variable, with distinct rainy (May–October) and dry (November–April) seasons.

Study species

Ficus altissima (Subgenus *Urostigma*, Section *Conosycea*; Berg and Corner, 2005) is distributed across Asia (Corner, 1965). At Xishuangbanna, the

species occurs naturally in tropical forest, but is frequently planted in cities, villages or near temples both as an ornamental and as a sacred plant. The twigs renew leaf and initiate syconia simultaneously. Figs are produced in synchronous crops with asynchrony between trees. At the time they release their fig wasps they are yellow and average 14.0 mm in diameter (S.E. = 0.99 n = 679). Large crops can number many thousands of figs. *Ficus altissima* is actively pollinated by the agaonid *Euptistina altissima*, but also supports an undescribed congener (*Eupristina* sp.) that has reduced pollen pockets and there is no coxal comb. This species has evolved into a cheater that fails to pollinate, it represents 1 of only 2 known cases in which a fig species harbours a species congeneric with the pollinator that has ceased to pollinate (Peng *et al.* 2008). In addition to the 2 agaonids, *F. altissima* also locally supports at least 25 further species of non-pollinating fig wasps (NPFW) belonging to families other than the Agaonidae (Gu *et al.* 2003). Their detailed biology is largely unknown, but they include ovule gallers and parasitoids. *Sycophilomorpha* sp. is an ovule galler and oviposits prior to pollinator arrival. Males are winged and mating occurs outside of the fig. The mean body size of the *Sycophilomorpha* wasp is 1.96 ± 0.02 (n = 7) and it is larger than the pollinator (mean 1.85 ± 0.01 mm, n = 96).

Observation of oviposition behaviour

The twigs renewed leaf and initiate syconia simultaneously in *F. altissima*, and *Sycophilomorpha* sp. is an early ovipositing species. So, once new leaves appeared, the development of the syconia was tracked. When *Sycophilomorpha* sp. was found to oviposit, we took photographs using a Nikon 995 camera to record the oviposition site and posture of the wasp, and opened the fig to record the developmental status of female flowers using a camera installed in a microscope (Olympus SZX12). The figs with *Sycophilomorpha* sp. eggs were tracked on the twigs until the pollinator entry. Figs were also opened to check the galls in the post-pollination phase.

Collection of *Sycophilomorpha* sp. in natural fig

Seven *F. altissima* trees were selected to collect figs at the male (wasp releasing) stage. The sampled trees were checked weekly from 13 January 2003 to 6 December 2005. When present, 30 nearly mature D-phase figs that were producing wasps per crop were collected. Each fig was placed individually in a fine-mesh bag (20 × 20 cm), and the fig wasps were allowed to emerge. All fig wasps, including those remaining inside the figs, were carefully collected and preserved in 70% ethanol. The sexes of *Sycophilomorpha* sp. were identified and their numbers

Fig. 1. Oviposition behaviour of *Sycophilomorpha* sp. (A) When *Sycophilomorpha* sp. was ovipositing the fig was still covered by hood-like involucral bracts and the stipule. (B) The blue arrow indicates the position of the hidden fig. (C) The ovipositor pierced the fig wall and left a small black scar (red arrow). (D) The flowers in such young figs had not yet differentiated into ovule, style, and stigma.

were counted. During the 3 years, a total of 679 figs were collected from 23 crops.

Statistical analyses

We used binomial models to examine variation in the occurrence of *Sycophilomorpha* sp. among trees, crops (nested within trees) and months. We also used binomial models to examine the effect of *Sycophilomorpha* sp. on the occurrence of pollinators, seeds and cheaters. Next, to examine the effect of the presence of *Sycophilomorpha* sp. on the contents of a fig, we used t-tests to compare fig diameter, the number of female flowers, male flowers, pollinators, seeds and cheaters between figs with and without *Sycophilomorpha* sp. In the latter tests we selected only those figs that had pollinators, seeds and cheaters, respectively. Finally, we used general linear models, with a negative binomial distribution of the error term, to

examine the effect of the number of *Sycophilomorpha* sp. present on the numbers of pollinators, seeds and cheaters, using only those figs that had *Sycophilomorpha* sp. and pollinators, seeds and cheaters, respectively. We elected to analyse occurrence and quantitative effects separately because of the large number of zero values (absences) in our dataset. All analyses were performed in R v2.9.2 program.

RESULTS

Oviposition behaviour of *Sycophilomorpha* sp. in *Ficus altissima*

Sycophilomorpha sp. oviposited very early, when the new twigs appeared and the new leaves were still covered by their stipules (Fig. 1A). At this stage the new figs were covered by hood-like involucral bracts (Fig. 1B), and only approximately 1.43 mm in

Fig. 2. A frequency distribution of the number of *Sycophilomorpha* wasps per sampled fig.

diameter. This is the only reported case of fig wasps ovipositing so early in the development of the syconia. *Sycophilomorph* sp. oviposited for several hours to 1 day on the same fig. When *Sycophilomorph* sp. finished ovipositing and left, a small black spot representing the scar left by the ovipositor could be seen on the fig under the microscope (Fig. 1C). *Sycophilomorph* sp. moved among a small number of figs to oviposit. When oviposited figs were opened, there was no discernible structure to the female flowers (i.e. ovary, style, stigma, pedicel and petal) under the microscope (Fig. 1D). The development of the figs with and without *Sycophilomorph* wasps was very long. For example, on 21 September 2009 *Sycophilomorph* sp. was observed ovipositing on one tree but the pollinators did not enter the figs on the same tree until 10 January 2010 or over 3 months later. Figs with and without *Sycophilomorph* sp. developed in synchrony. The galls made by *Sycophilomorph* had long pedicels and protruded into the fig cavity, but the gall flower had no style or stigma.

Occurrence of *Sycophilomorpha* sp. in *Ficus altissima*

In total, 11.5% of figs were colonized by *Sycophilomorpha* sp. in *F. altissima* in Xishuangbanna, and varied from 0 to 50% among 23 crops. A single gall housed 1 *Sycophilomorpha* wasp. On average, the number of *Sycophilomorpha* wasps per occupied fig was 35.13 ± 4.58 (S.E., $n = 79$), the range was 1 to 172. By comparison, the average number of agaonid wasps per fig was 163.15 ± 5.11 (S.E., $n = 312$). About 40% of figs colonized produced less than 10 *Sycophilomorpha* sp. offspring, 45% of the figs produced 10–90 offspring, and 15% of the figs produced more than 90 offspring per fig (Fig. 2). *Sycophilomorpha* sp. naturally occurred in all 7 sampled trees, but the occurrence of wasps was significantly different among trees ($z = 3.487$, $P = 0.00049$) and crops ($z = 4.628$, $P < 0.00001$). The effect of month on the occurrence of *Sycophilomorpha* was also significant but was relatively weak ($z = -2.079$, $P < 0.05$).

Sycophilomorpha sp. were observed from March to August and the proportion of figs occupied was higher in 2004 (Fig. 3).

The effect of *Sycophilomorpha* sp. on the fig-fig wasp interaction

Figs with *Sycophilomorpha* sp. were small (mean diameter = 11.19 ± 0.23 , $n = 50$), and had significantly fewer female flowers ($t = -6.92$, D.F. = 91.24, $P < 0.00001$; mean = 391.14) than figs without *Sycophilomorpha* sp. (mean diameter = 12.38 ± 0.20 , mean number of flowers = 520.55) (Fig. 4). Therefore, colonization by *Sycophilomorpha* sp. reduced fig size and the flower resources available for oviposition.

Sycophilomorpha sp. had a highly significant negative effect on the occurrence of pollinators ($z = -8.408$, $P < 0.00001$) and seeds ($z = -7.170$, $P < 0.00001$) after controlling for the effect of cheaters, and on cheaters ($z = -8.588$, $P < 0.00001$) after controlling for the effect of pollinators. Thus, figs colonized by *Sycophilomorpha* sp. were less likely to be entered by either a pollinator or cheater.

Figs with *Sycophilomorpha* sp. had significantly fewer pollinators ($t = -3.15$, D.F. = 15.66, $P = 0.0061$, mean with = 72.53 , mean without = 138.07), seeds ($t = -2.73$, D.F. = 28.61, $P = 0.011$, mean with = 84.23 , mean without = 141.03), and cheaters ($t = -5.93$, D.F. = 29.90, $P < 0.00001$, mean with = 26.83 , mean without = 79.07) (Fig. 4).

However, in figs with both *Sycophilomorpha* sp. and pollinators, seeds and cheaters, respectively, *Sycophilomorpha* sp. had a significant effect on the numbers of pollinators ($z = -2.54$, $P = 0.0119$) but not seeds ($z = 0.862$, $P = 0.409$) or cheaters ($z = -1.664$, $P = 0.0962$). Thus, while the presence or absence of *Sycophilomorpha* sp. had a significant effect on seed and cheater production, the abundance of *Sycophilomorpha* did not.

In summary, *Sycophilomorpha* sp. had a substantial detrimental effect on the reproductive success of *F. altissima* and its pollinator. *Sycophilomorpha* sp. occupied 11.5% of figs. Of these, 64% were not entered by a pollinator or cheater and *Sycophilomorpha* sp. was able to prevent these unpollinated fruit from being aborted. In the remaining figs colonized by *Sycophilomorpha* sp. and pollinators or cheaters the production of pollinators, seeds, and cheaters were all approximately half the normal levels. However, in these figs the abundance of *Sycophilomorpha* sp. only had a significant effect on the abundance of pollinators.

DISCUSSION

Sycophilomorpha wasps oviposited earlier in fig development than is reported for any other non-pollinating fig wasps (Weiblen, 2002). At this stage,

Fig. 3. Occurrence of *Sycophilomorpha* sp. among sampled crops (arranged chronologically). The uppercase letters represent the different trees and the number the sequential crop number on a particular tree.

Fig. 4. Comparison of fig contents with and without *Sycophilomorpha* sp. (without, $n=600$; with, $n=79$). (a) number of flowers, (b) the number of pollinators, (c) the number of seeds, and (d) the number of cheaters. The numbers of flowers, pollinators, seeds and cheaters were all significantly reduced in figs with *Sycophilomorpha* sp. (see text for details).

there was no discernible structure to the female flowers. This study also found that the immature phase of fig development is longer than previously

reported. *Sycophilomorpha* wasps also influenced flower development preventing any differentiation into style and stigma.

Most of the non-pollinating fig wasps are rare and rarely abundant in any given fig (Weiblen and Bush, 2002). Similarly, *Sycophilomorpha* sp. only occurred in 8 out of 23 crops and overall colonized 11.5% of sampled figs. However, *Sycophilomorpha* sp. sometimes laid large clutches in a single fig. More than 50% of the figs colonized by *Sycophilomorpha* produced more than 10 offspring, and occasionally over 100 offspring. In the figs with *Sycophilomorpha* sp., 64% of the figs only produced *Sycophilomorpha* offspring. This indicates that different non-pollinating wasp genera employ different reproductive strategies, despite having an apparently similar ecology in other respects.

Sycophilomorpha sp. naturally occurred in every tree, but the occurrence of wasps varied significantly among trees, crops and months. Over the 2 years of observation *Sycophilomorpha* sp. occurred from March to August. Our observations indicate that the development of *Sycophilomorpha* wasps can be very slow, approximately 6 months from oviposition in September 2009 to emergence in March 2010. The duration of fig development in *Ficus altissima* varies widely depending on the season, and is longer in the winter when temperatures reach as low as 10 °C at night than in the warm season (Peng *et al.* 2010). It is not clear from our relatively short observation window, whether the absence of *Sycophilomorpha* wasps from September to March is just a stochastic effect of their long development or a strategy to avoid the coldest part of the year.

Non-pollinating parasitoids and gallers are species-rich components of fig wasp assemblages, and have negative impacts on the fig–fig pollinator mutualism through predation of pollinator larvae, through competition with pollinators for seed resources and through use of ovules that might otherwise become seeds (Compton *et al.* 1994; West and Herre, 1994; West *et al.* 1996). Moreover, all non-pollinating fig wasps drain energetic resources from the host plant. If gallers oviposit before the pollinator, they may directly compete with the pollinator by reducing the number of ovules available for oviposition or indirectly by inhibiting the ability of the pollinator to lay eggs. In the case of *F. altissima*, when the pollinator entered a fig that had been colonized by *Sycophilomorpha* sp. they may have found it difficult to oviposit, because the galls of *Sycophilomorpha* protrude into the fig cavity. Inhibited movement by the pollinator within the fig cavity could also have a negative impact on seed production through reduced pollen dispersal, as appears to be the case in *F. altissima*. *Sycophilomorpha* sp., colonized 11.5% of figs, 64% of these figs did not produce any seeds or pollinators, and in those that were entered by an agaonid, figs with *Sycophilomorpha* sp. had significantly fewer pollinators, cheaters and seeds.

Through a differential effect on pollinators and cheaters it is possible that *Sycophilomorpha* sp. could

affect the interaction between these competing species, possibly contributing to stable coexistence. However, in comparing the strengths of the effects of *Sycophilomorpha* sp. on these species, we find limited support for this. *Sycophilomorpha* sp. had an almost identical effect on both species in terms of the occurrence, which was the most important effect we measured. The presence of *Sycophilomorpha* sp. did have a stronger effect on the number of cheaters than on the number of pollinators when comparing figs with and without *Sycophilomorpha* sp. However, the abundance of *Sycophilomorpha* sp. had a significant effect on pollinator but not cheater abundance. Combined, these figures translate into a reduction in pollinator production of 1.92% and in cheaters of 2.70%. Thus, the percentage difference in the effect on pollinators and cheaters is just 0.78%. Given the high mortality rates of agaonids (approximately 99% died without reproducing), it is doubtful that such a small difference could be important.

Our study has shown that, despite their rarity, *Sycophilomorpha* sp. have a significant impact on the fig–fig wasp mutualism in *F. altissima*. Given the ubiquity of non-pollinating fig wasps, many of which are much more abundant than *Sycophilomorpha*, it is perhaps surprising that the fig–fig wasp mutualism is stable across so many species (approximately 800 spp. globally). A greater appreciation of the effects of non-pollinating wasps would enhance our understanding of the factors that have contributed to the evolutionary success of the fig–fig wasp mutualism.

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