OVIPOSITION STRATEGIES IN NON - POLLINATING FIG WASPS (HYMENOPTERA, CHALCIDOIDEA)

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INTRODUCTION

Ficus plants are characterised by their peculiar urn - shaped inflorescences, called figs or syconia. Pollination of the pistilate flowers is performed by tiny chalcid wasps belonging to the Agaonidae family, which also deposit their eggs in some of the flowers, inducing a gall in which their offspring will develop (11). This intricate association that opened new evolutionary opportunities for both associates is regarded as a mutualism. However, it is common in mutualistic associations the occurrence of opportunistic species, known as parasites of the mutualism, which take advantage of the resources involved in the interaction without providing any service in return (14). The fig-fig wasp interaction is exploited by non - pollinating fig wasps (parasites of mutualism), which deposit their eggs in pistilate flowers or galls but do not provide any pollination service, since they oviposit from the outside of the fig, through the fig wall (11).

According to the proposed phylogeny for these wasps, the pollinating Agaonidae appears as a monophyletic group, basal to the other Chalcidoidea. Pollination by agaonid wasps apparently appeared only once in the evolutionary history of the mutualism. On the other hand, each group of non - pollinating fig wasps (NPFW) probably evolved independently (9).

NPFW present different biologies, in that they can be gallers, such as the pollinators, colonising figs at the same time as the latter; inquilines, whose larvae are phytophagous but the wasps are incapable of inducing galls; or parasitoids, whose larvae feed directly on gallers' larvae (6). Most of the studies on NPFW biology are speculations based on indirect data on community structure (4, 5, 12, 13). Detailed studies on NPFW biology are rare and comprise only a few host *Ficus* species (1,3).

Fig wasp species biologies have been assumed regular within species lineages (e.g. within fig wasp genera) (7). However, recent data showed accentuated differences in biology between species of the same genus (*Idarnes*) (1).

Since gallers and non - gallers use different substracts (namely, pistilate flowers and galls) for oviposition, they are subject to different selective pressures and may present different strategies on resource exploitation, involving the oviposition mode, the local of ovipositor insertion and egg deposition. Therefore, NPFW biology allows us to study the evolution of larval feeding habits, oviposition strategies and resource utilization in these groups of wasps.

OBJECTIVES

Assess, by means of experimental studies, the resource exploitation strategies in non - pollinating fig wasps belonging to two different subfamilies and associated to host species from different *Ficus* sections.

MATERIAL AND METHODS

Study area and study species

The study was carried out in urbanised areas at São Paulo University campus, Ribeirão Preto city, Brazil ($21^0$10'S; $47^0$48'W) and Xishuangbanna Tropical Botanical Garden, China ($21^0$41'N, $101^0$25'E) during the years of 2006 to 2009. In Brazil, we studied *Ficus citrifolia* (section *Americana*), which host *Idarnes* (*flavicollis* species group) and *Idarnes* (*carme* species group) wasps (*Sycophaginae*). In China we studied NPFW associated with three *Ficus* species: *Philotrypesis pilosa* and *Philotrypesis* sp. (Sycoryctinae, Pteromalidae) on *Ficus hispida* (section *Sycocarpus*); *Platyneura* sp. (Sycophaginae) and *Sycoscapter* sp. (Sycoryctinae, Pteromalidae) on *Ficus semicordata* (section *Hemicardia*); and *Platyneura* sp. 2 (Sycophaginae) on *Ficus auriculata* (section *Sycomorus*).

Data collection

We studied the sequence of colonisation by NPFW to assess the overall strategy of fig utilisation. To standardise

fig development, we control - pollinated syconia, and we expressed the colonisation sequence in "days after pollination" (DAP). Five branches with young figs (before colonisation by any wasp species) were bagged with "voil" cloth, preventing access from any wasp. When figs reached the receptive phase, the cloth bags were removed and one foundress wasp was introduced per fig (five to 10 figs per branch). The experimental syconia were daily monitored in relation to other wasps' visits.

For the species whose biology could not be elucidated by the colonisation sequence, we carried out experiments to verify whether the wasps were able to induce galls in the absence of the pollinating wasps, being a galler. In each monitored tree, one to three branches with young figs (five to 10 figs per branch) were bagged with "voil" cloth. Experiments consisted in allowing NPFW females oviposit in pollinated (control) or unpollinated figs. We introduced approximately 10 NPFW per bag and kept branches bagged until shortly before offspring emergence. The wasps' offsprings were then identified and counted.

NPFW observed ovipositing non - experimental syconia were killed with a drop of chloroform to observe where their ovipositors were inserted in. Then, the fig was collected and taken to laboratory for dissecation under stereoscope microscope.

RESULTS AND DISCUSSION

Idarnes (*flavicollis* species group) wasps (in *F. citrifolia*) colonised syconia simultaneously with the pollinator up to five days after pollination (DAP), and their offspring could be reared in the absence of pollinators (mean number of wasp offspring $\pm$ SD = 74.8 $\pm$ 34.6, n = 29 syconia), confirming the galler habit in these wasps. These wasps' ovipositors are inserted through the stigma of the flowers. *Idarnes* (*carme* species group) wasps, on the other hand, were observed colonising syconia around the 15th and up to the 25th DAP, and no offspring was observed in unpollinated syconia (n= 52 syconia), suggesting these wasps are not gallers. carme wasps insert their ovipositors directly through the galls' wall.

Philotrypesis pilosa (in *F. hispida*) was observed colonising figs simultaneously with the pollinator up to two DAP, but their offspring could not be reared in unpollinated figs (n=19 figs), suggesting these wasps are not gallers. *Philotrypesis* sp. was observed colonising figs from five to 20 DAP, and also did not develop in unpollinated figs (n=10 figs). Both species were observed inserting their ovipositors through galls' wall or flowers' pedicels and then through the gall wall.

Platyneura sp. (in *F. semicordata*) was observed colonising figs from three to 25 DAP, and did not present offspring when exposed to unpollinated figs (n=13 figs). *Sycoscapter* sp. was observed colonising figs rather late in fig development (20 to 30 DAP) and were clearly non gallers. Both wasps insert their ovipositors through the galls' wall.

In *F.auriculata*, data on previous studies show that *Platyneura* sp. 2 wasps are effective gallers (8), and they were indeed observed colonising figs simultaneously with the pollinator up to five DAP. These wasps were observed inserting their ovipositors through the flower stigma.

Our results suggest that NPFW with different biologies (gallers or non gallers) present different exploitation strategies. Galler NPFWs colonise figs early in their development and have a very precise ovipositor insertion mechanism, inserting their ovipositors through the stigma of flowers, even though they oviposit from the outside of the fig. These wasps have to induce a gall in order to develop their offspring and such precise oviposition strategy is constrained by ovary structure and plant embryology (2, 10).

On the other hand, non gallers seem to be less constrained by plant embryology, and they do not present any specialised ovipositor insertion mode. Indeed, the oviposition mode in these wasps seems to be more linked with the fig structure, e.g. the fig wall thickness (15) and packing structure of galls, as NPFW use plant tissues to conduct their ovipositors into the fig (F. Kjellberg, unpublished data).

Our results shed light on the evolution of resource utilisation in NPFW, showing that oviposition strategies are less phylogenetically conserved than suggested by previous studies (5). Phylogenetically close species such as *Idarnes* (*flavicollis* species group) and *Idarnes* (*carme* species group) present different biologies and different oviposition modes. Moreover, *Platyneura* sp. in *F. semicordata* and *Platyneura* sp. 2 in *F. auriculata* also present different biologies and, therefore, different oviposition modes.

CONCLUSION

Our results strongly suggest that exploitation strategies in NPFW are linked to the wasps' biology, and that both strategies and biologies are influenced by fig structure. For gallers, the flower embryology plays an important role shaping their oviposition strategy and resource utilisation. On the other hand, for non gallers, there is a relaxed selective pressure concerning oviposition strategies, for they do not have to induce galls. Therefore, oviposition strategies seem to be evolutionary labile, responding quickly to selective pressures imposed by the fig structure. (Acknowledgments: FAPESP 04/10299 - 4, 2007/59059 - 3 and Chinese Academy of Sciences. We would like to thank Gang Wang, Wen Juan Ma, Yang Pei and Yi Cui Xi for field support).

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