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How to be a fig wasp parasite on the fig–fig wasp mutualism

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The nursery pollination mutualism between figs and pollinating fig wasps is based on adaptations that allow wasps to enter the enclosed inflorescences of figs, to facilitate seed set, and to have offspring that develop within the nursery and that leave to enter other inflorescences for pollination. This closed mutualistic system is not immune to parasitic fig wasps. Although the life histories and basic biology of the mutualists have been investigated, the biology of the fig wasp parasites has been severely neglected. This review brings together current knowledge of the many different ways in which parasites can enter the system, and also points to the serious lacunae in our understanding of the intricate interactions between gallers, kleptoparasites, seed eaters and parasitoids within this mutualism.

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For the Snark *was* a Boojum, you see.
From: The Hunting of the Snark, Lewis Carroll, 1876

Introduction

Interactions between plants and insects vary from antagonistic (resource–consumer relationships) to mutualistic (resources in exchange for pollination and defence). In some systems, the interaction has evolved into an obligatory or mutualistic one such as the relationship between ants and obligate myrmecophytes and that between pollinating wasps and figs. These highly intimate relationships often require sophisticated adaptations in both partners to secure the interaction. Yet these interactions are often exploited by 'cheaters'. In this review, I present novel ways in which the mutualistic interaction between figs and fig wasps is exploited by parasites.

The biology of the fig–fig wasp mutualism

The mutualism between figs and their pollinating fig wasps is ancient, originating ca 75 mya in Eurasia [1•]. *Ficus* (Moraceae) has an enclosed globose inflorescence, the syconium, with a single opening, the ostiole. Figs have two breeding systems [2••,3••,4••]. In monoecious figs, uniovulate female flowers line the syconium cavity. Pollen-bearing female fig wasps enter the syconium, oviposit into flowers producing galls, and subsequently die. Male offspring eclose first, mate with and release females from their galls. In actively pollinated figs, females collect pollen from male flowers and store it in pollen pockets. Pollen-bearing females enter another pollen-receptive fig syconium to continue the cycle. In gynodioecious figs, female trees bear syconia with long-styled female flowers; male trees bear syconia with short-styled female flowers that develop first, male flowers develop later. Pollen-bearing wasps entering female syconia are unable to oviposit into flower ovaries since their ovipositors are shorter than the styles; syconia on female trees therefore produce only seeds, while those on male trees produce mostly wasps. Inter-sexual mimicry of floral scents between syconia on male and female trees contributes to pollination by deceit in dioecious figs [5].

The fig–fig wasp mutualism was considered the quintessential example of co-evolution and co-speciation, each fig species interacting with a unique pollinator species [2••]. This view has changed with the discovery of many fig species being pollinated by multiple fig wasp species [6,7]. Although co-speciation does occur, co-phylogenetic analyses reveal considerable host shifts and wasp lineage duplications [1•,6]. Still, the mutualism between figs and wasps is characterised by several adaptations or co-adaptations [8••]. For example, ostiole shape and size are mechanical filters limiting syconial access to pollinators [9]. Wasps and seeds have similar development times [2••]. Pollinator ovipositor lengths match flower style lengths. Pollinators are attracted by volatile organic compounds (VOCs) emitted by pollen-receptive figs [10••]. Females leave the syconium through an exit hole cut cooperatively by male pollinators. Given this intricate biology, how might a non-pollinating fig wasp parasitise such a closed system that requires unusual adaptations?

Non-pollinating fig wasp parasites of the fig–fig wasp mutualism

Figs harbour many kinds of fig wasp parasites [2••]. Pollinating fig wasps occur within the monophyletic agaonid clade of chalcid wasps, and are closely related to non-pollinating fig wasp (NPFW) gallers of the subfamily Sycophaginae [11]. Another chalcid family Pteromalidae contains the majority of other NPFWs within several subfamilies such as Sycoecinae and Sycoryctinae [11] suggesting several independent origins of parasitism. NPFW assemblage size varies from 3 to 30 species on a single fig species [12]; many closely related NPFWs parasitise the same fig species and the same fig tree [13]. NPFWs are mostly primary gallers, secondary gallers, kleptoparasites or parasitoids [14] and oviposit by entering the syconium or oviposit from the syconium exterior through the syconium wall (Figures 1 and 2).

Parasites entering syconia for oviposition

Lineages of pollinating wasps can evolve into cheaters [15•] with reduced pollen pockets and without the coxal combs that are essential for active pollination [16]; survival of such parasites is greater when they share syconia with congeneric non-cheating pollinators [15•]. The mechanism behind the facilitative effect of the mutualistic pollinator on the cheater is unknown. Some sycoecine wasps oviposit into galled flowers already containing pollinator eggs; such parasites are larger than the pollinators, emerging from larger galls suggesting their own contribution to galling [14]; this is termed secondary galling. Convergent evolution on head shape has allowed parasites to overcome the ostiolar filter and successfully invade the syconium interior [9].

Parasites ovipositing into syconia from the outside

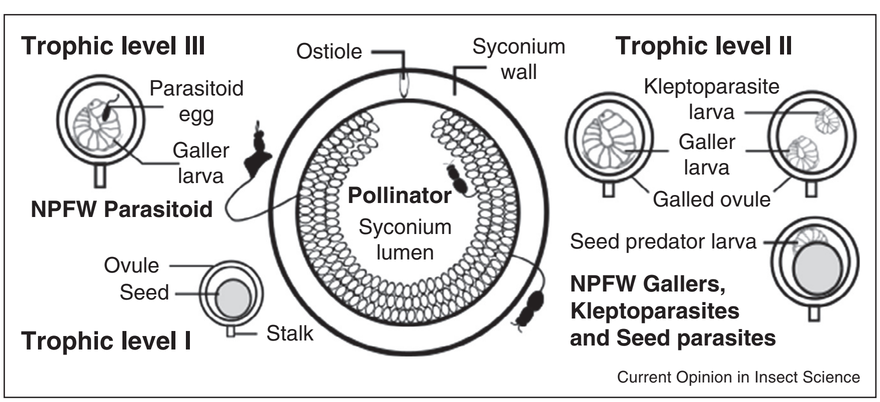
Most parasites oviposit into the syconium from its external surface. Since syconium size increases during development, ovipositor lengths of parasite species match the syconial stage of parasitism [17,18••,19,20].

Gallers are the first to attack a syconium. Gallers can oviposit into very small syconia even before floral primordia develop [20]; they gall tissues lining the young syconial lumen and produce very large, thick-walled galls that fill lumen space. Other early gallers oviposit into floral primordia [20,21]. The large galls of these very early and early gallers impose a much greater cost on the mutualism than the one-flower cost equivalent per gall imposed by pollinators [21]. Yet another group of gallers attacks flowers concurrently with the pollinators [22], producing galls similar in size to those of the pollinators [20] and competing with pollinators for mature female flowers. The galling process has just begun to be investigated. Unlike pollinators, whose larval nutrition mainly derives from hypertrophied seed endosperm [23•], NPFW gallers cause hypertrophy of the ovary nucellus which does not require pollination of the flowers [24••]. The molecular mechanism of galling is completely uninvestigated; secretions of the poison gland may be involved [25]. Gallers, particularly the large gall inducers, may inject cytokine-like compounds that manipulate plant tissue as in other systems [26].

Some NPFWs are kleptoparasites [27] incapable of inducing galls but ovipositing into existing galls; their larvae feed on galled tissue, starving the gall occupant. How such larvae out-compete existing gall inhabitants is unknown but is important to understand because developing fig wasps are confined to their own galls from which they must derive all nutrition [28••].

Some parasites consume seeds. In one fig species where NPFWs were kleptoparasites of pollinator larvae, seed parasitism occurred only under high parasitism pressure, suggesting facultative expansion to the new resource based on competition [29]. Only small-sized parasite males emerged from these seeds [29] indicating that

Figure 1



There are at least three trophic levels in the microcosm supported by the mutualism between figs and fig wasps. At the first trophic level are the seeds and other plant tissues that can be utilised by NPFW gallers, kleptoparasites and seed parasites in the second trophic level. At the third trophic level are the parasitoids which can exploit the developing stages of gallers. The figure illustrates the microcosm of the syconium which is utilised by internally and externally ovipositing fig wasps.