



Original article

A switch from mutualist to exploiter is reflected in smaller egg loads and increased larval mortalities in a ‘cheater’ fig wasp



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ARTICLE INFO

Article history:

Received 20 November 2012

Accepted 21 April 2013

Available online 13 July 2013

Keywords:

Agaonidae

Ficus

Galls

Mutualism

Sanctions

Species coexistence

ABSTRACT

The interaction between the hundreds of *Ficus* species and their specific pollinating fig wasps (Agaonidae) presents a striking example of mutualism. Foundress fig wasps pollinate fig flowers, but also lay their eggs in (and gall) some of them. Only two cases of cheating fig wasps (that fail to pollinate) have been reported, from two continents, suggesting that there is a cost to abandoning pollination. Reasons for the rarity of cheating are a major question in fig biology, because persistence of the mutualism depends on fig wasps continuing to pollinate. A cost in terms of reduced reproductive success among cheaters could be one explanation. Here we compare the behavior and reproduction of an undescribed *Eupristina* sp., a cheater that coexists with the pollinator *Eupristina altissima* on *Ficus altissima* in southern China. Adult females of both species fought with conspecifics when they were seeking entry through the ostiole into receptive figs, but there was no fighting with heterospecifics. Despite a similar body size, female pollinators contained more eggs than female cheaters. Pollinators and cheaters produced similar number of galls, and although almost twice as many flowers were galled in figs entered by two compared to one foundress, larval mortality was greatly increased when two foundresses were present. Larval mortality was also significantly higher for cheaters compared to pollinators, independent of the number of foundresses. Ovules galled by the cheater were thus significantly less likely to result in adult offspring, suggesting that there are significant costs associated with abandoning the mutualism.

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1. Introduction

Ficus (Moraceae) is one of the largest genera of plants, with more than 750 included species (Berg, 1989), all of which depend on fig wasps (Hymenoptera: Chalcidoidea: Agaonidae) for pollination. The mutualistic relationship is both ancient and diverse, having originated roughly 70–90 Mya (Rønsted et al., 2008; Compton et al., 2010). Both morphological and molecular studies broadly support the proposition of co-adaptation and co-evolution between genera of pollinating wasps and their respective sections of figs, though colonization events and host switching also occur (Wiebes, 1979; Berg and Wiebes, 1992; Machado et al., 2001; Cruaud et al., 2012).

The fig is an urn-shaped inflorescence lined with numerous tiny uniovulate female flowers. Adult female fig wasps carry pollen from their natal figs into receptive figs, entering through a narrow ostiole. Once inside, the foundresses actively or passively pollinate the flowers, some of which can also be galled and have eggs laid in them (Ramírez, 1970a; Wiebes, 1979; Weiblen, 2002). Pollination of figs is either passive, as in most plant-pollinator systems, with dehiscent anthers depositing pollen on the surface of adult female wasps as they emerge from their galls, or more commonly it is active, with the females collecting pollen into thoracic pollen pockets and subsequently placing the pollen on the stigmas of flowers in the figs where they are ovipositing (Kjellberg et al., 2001). Active pollination has clear benefits for the host plants, because they need to produce far less pollen (Kjellberg et al., 2001; Cook and Rasplus, 2003).

Although once thought to be always strictly species-specific, increasing numbers of morphological (Berg and Wiebes, 1992; Michaloud et al., 1996; Rasplus, 1996) and genetical studies

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(Molbo et al., 2003; Machado et al., 2005; Su et al., 2008; Sun et al., 2011; Cornille et al., 2012) have reported examples of fig tree species that are pollinated by two or more species of fig wasps. These findings undermine the long-held assumption of one to one fig tree–pollinator interactions and add previously unsuspected levels of complexity to the mutualism (Herre et al., 2008). Only one species of pollinator is required to maintain host plant populations and situations where a *Ficus* species is actively pollinated by more than one fig wasp species (Rasplus, 1996; Compton et al., 2009a), provide opportunities for the evolution of ‘cheating’ behavior, where agaonids fail to pollinate their hosts and there is a transition in their relationship from mutualism to antagonism. However, cheating agaonid wasps are very rare.

Among the 400 or so described species of agaonids, only two cases of a loss of pollination behavior have been confirmed among trees that have retained the need to be actively pollinated (Galil and Eisikowitch, 1968; Peng et al., 2008). The African *Ceratosolen galili* is associated with *Ficus sycomorus*, an African fig tree pollinated by *Ceratosolen arabicus*, an active pollinator. *C. galili* has pollen pockets, confirming its evolution from an actively-pollinating species (Compton et al., 1991), but phylogenetic analyses have shown that it is not closely related to *C. arabicus* (Kerdelhué et al., 1999). Cheating behavior therefore followed a host shift involving colonization of *F. sycomorus*. The evolution of cheating behavior followed a different path in the undescribed species of *Eupristina* (referred to here as *Eupristina* sp.) associated with *F. altissima* distributed in southern China (Peng et al., 2008). This cheater also has reduced pollen pockets, again pointing to an active-pollination ancestry, but morphological and molecular evidence suggest that it is the sister species of the tree’s pollinator, *Eupristina altissima* (Peng et al., 2008; Peng, unpublished data) and cheating may therefore have evolved *in situ* on *F. altissima*, though other scenarios are possible.

Pollination is the key service that fig wasps provide to their hosts, and the stability of the mutualism depends on this service (Kjellberg et al., 2001; Herre et al., 2008). Previous studies have shown that un-pollinated figs of species that are normally actively-pollinated may be selectively aborted by the trees, and pollinator reproductive success is improved in figs where pollination has taken place (Jousselin et al., 2003; Tarachai et al., 2008; Jandér and Herre, 2010). This suggests that any agaonid wasps that cheat and do not pollinate their host figs can suffer fitness costs. Improved nutrition for larvae developing in pollinated ovules is a likely benefit of maintain pollen-carrying, and the smaller size of *C. galili* adults, relative to *C. arabicus*, has been suggested as a possible consequence of poorer nutrition for its larvae (Compton et al., 1991). Moreover, a recent study reported that higher larval mortalities in unpollinated figs is likely to be due to the lack of endosperm in unfertilized flowers (Jansen-González et al., 2012).

In this study, the behavior and reproductive biology of the pollinator and cheater agaonids associated with *F. altissima* were compared in order to discover whether costs associated with a loss of active pollination could be detected. We addressed the following questions: (i) Do the pollinator and cheater have similar body sizes and egg loads? (ii) Do adult females of the two species compete when attempting to enter the same figs? (iii) Do they produce similar numbers of offspring? and (iv) How does their reproductive success respond to intraspecific and interspecific competition?

2. Materials and methods

2.1. Study site and species

The study was conducted at the Xishuangbanna Tropical Botanical Garden (101°15'E, 21°55'N, at about 555 m a.s.l.), located in SW China at the northern margin of tropical SE Asia.

F. altissima Blume (subgenus *Urostigma*, section *Conosycea*: Berg and Corner, 2005) has a wide natural distribution across Asia. It is also regularly planted in cities and villages or near temples as an ornamental or sacred plant. The figs are axillary and paired (rarely solitary) and produced throughout the year in synchronous crops, but with asynchrony between trees. Large crops can number many thousands of figs. Mature figs are sub-globose, measure about 14 mm in diameter, and contain on average 585 female flowers and 53 male flowers (Peng et al., 2008).

F. altissima is actively pollinated by the agaonid *Eupristina altissima*, but also supports an undescribed congener (*Eupristina* sp.) which has reduced pollen pockets and does not actively pollinate. The females of *E. altissima* and *Eupristina* sp. are easily distinguished by their body coloration and shape of their antennae. *E. altissima* has seven funicular segments and clava is unisegmented, whereas *Eupristina* sp. has six funicular segments, with the last atrophied and the clava is besegmented (Figure S1). *Eupristina* sp. can be the only agaonid developing in a fig, or even a whole crop of figs, showing that it does not require figs to be pollinated by *E. altissima* to complete its development. Under natural conditions, 57% of the sampled figs contained one foundress, and an average of 1.8 foundresses entered a fig. Females of the two *Eupristina* species fly to and locate receptive figs at the same times of day, so they potentially compete for entry into shared figs, though only 9% of the figs were found to contain foundresses of both species (Peng et al., 2008).

2.2. Body sizes and egg loads of the two *Eupristina* species

Head size (length and width) is considered to be a good indicator of wasp body size (Herre, 1989; Liu et al., 2011). Freshly emerged adult females were collected from 20 D-phase figs on one tree, about 10 wasps per fig were selected and the head lengths of 96 pollinators and 100 cheaters were measured using an eyepiece graticule mounted on a binocular microscope. Measurements were made to the nearest 0.0025 mm. Dry body weights of the two species were compared, 200 pollinators and 200 cheaters were dried for three hours in 40 °C drying oven. Due to their very small size, groups of 20 individuals were weighed to the nearest 0.0001 g. In total, 10 groups were weighed per species.

Agaonids are pro-ovigenic and freshly-emerged adults contain their full complement of mature eggs. 18 female pollinators and 23 female cheaters were dissected under a microscope to count the number of eggs in their ovaries (Dunn et al., 2011).

2.3. Observations of foundress behavior on receptive figs

Pre-receptive *F. altissima* figs were bagged to prevent any fig wasps from entering them. When they became receptive, we placed freshly emerged pollinators from figs on other trees onto the figs. Firstly, one pollinator or one cheater was put on the surface of a fig, away from the ostiole. Their behavior while searching and during ostiole entry was recorded and compared with groups of 2–3 pollinators or 2–3 cheaters similarly put on the surface of other figs. We recorded fighting between females using a Nikon E4500 camera and then collected winners and losers of fights separately and measured their body sizes (head width) as before. In total, the body sizes of 11 pollinator winners and 12 losers were measured, and 32 cheater winners and 30 losers. We also repeatedly placed mixed pairs of cheaters and pollinators on the figs, in an attempt to induce fighting between them.

2.4. Experimental introductions

Pre-receptive figs on one tree were enclosed in fine-mesh nylon bags to prevent oviposition. When the figs became

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