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## Host–parasitoid development and survival strategies in a non-pollinating fig wasp community

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### ABSTRACT

In a tritrophic system, parasitoid development and galler host survival strategies have rarely been investigated simultaneously, an approach crucial for a complete understanding of the complexity of host–parasitoid interactions. Strategies in parasitoids to maximize host exploitation and in gallers to reduce predation risk can greatly affect the structure of tritrophic communities. In this study, the developmental strategies of galler hosts and their associated parasitoids in the tritrophic fig–fig wasp system are experimentally investigated for the first time. In this highly co-evolved system, wasp development is intrinsically tied with the phenology of the wasp brood sites that are restricted to the enclosed urn-shaped fig inflorescence called the syconium which can be regarded as a microcosm. Wasp exclusion experiments to determine host specificity, gall dissections and developmental assays were conducted with non-pollinating fig wasps in *Ficus racemosa*. Our results provide evidence for exceptions to the widely accepted koinobiont–idiobiont parasitoid dichotomy. This is also the first time fig wasps were raised *ex situ* from non-feeding stages onwards, a technique that enabled us to monitor their development from their pre-pupal to adult stages and record their development time more accurately. Based on variation in development time and host specificity, the possibility of a cryptic parasitoid species is raised. The frequency of different wasp species eclosing from the microcosms of individual syconia is explained using host–parasitoid associations and interactions under the modulating effect of host plant phenology.

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### 1. Introduction

In communities built on tritrophic interactions, gallers and parasitoids are engaged in strategies and counter-strategies. Species at higher trophic levels such as parasitoids can play an important role in maintenance of community structure by controlling the abundance of other species (Lawton and Strong, 1981; Hassell, 2000). In host–parasitoid interactions, the reproductive strategy of the parasitoid can further affect community dynamics (Kraaijeveld and Godfray, 1997; Ishii and Shimada, 2012). Based on development strategy, parasitoids are classified into koinobionts and idiobionts. A koinobiont allows its hosts to develop after parasitism, attacks the early, usually more abundant stages of its developing host (Askew and Shaw, 1986), and is predicted to have higher fecundity (Mayhew and Blackburn, 1999; Pennacchio and Strand, 2006). An idiobiont paralyzes/kills its host immediately, attacks the later and static stages of host development (Askew and

Shaw, 1986) and is predicted to have lower fecundity (Mayhew and Blackburn, 1999; Pennacchio and Strand, 2006). Nearly all koinobionts are endoparasitoids whereas idiobionts attacking larval host stages are almost always ectoparasitoids (those attacking pupal stages may be endoparasitic) (Quicke, 1997). Ectoparasitoids generally do not face significant host immune defense although they often immunosuppress their hosts (Pennacchio and Strand, 2006) whereas endoparasitoids face a strong host immune defense response and have varied evasion mechanisms (Schmidt et al., 2001). From the host's perspective, risk of parasitism, i.e. predation, may increase with length of developmental stages as predicted by the slow growth–high mortality hypothesis (Clancy and Price, 1987) and therefore a host may accelerate through vulnerable stages to avoid predation. However, there is a trade-off between development rate and adult size. A host may develop rapidly but with reduced size or grow larger at the cost of longer development time (Harvey and Strand, 2002); a larger host may also serve as a high quality host in terms of nutrition available for the developing parasitoid (Mohamed et al., 2003) and may therefore carry the extra risk of being preferred for oviposition. The

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optimal developmental strategies of galler hosts and parasitoids to achieve maximum fitness with minimum predation risk and suitable offspring size will be dictated by a trade-off between such factors. A host–parasitoid association may be further complicated by a third species such as in tritrophic interactions where both host and parasitoids can be affected directly or indirectly by plant traits such as phenology and the possibility of plant sanctions (Pages et al., 2012; Borges, 2015a,b; Krishnan et al., 2015). A comprehensive study on the development and survival strategies of parasitoids and their hosts in a tritrophic system where a third interactant can act as a restricting factor can help us understand the dynamics of host–parasitoid interactions within a wider framework and in a natural context.

The fig–fig wasp system, with its species-specific pollinator and non-pollinators whose development is obligately linked with host plant development and therefore restricted in many ways, provides an excellent system to understand the interactions, reproductive strategies and complexity of population dynamics of the members of a tritrophic system (Borges, 2015a; Krishnan et al., 2015). The fig inflorescence or syconium can be considered a microcosm (Borges, 2015a) within which a multiplicity of ecological processes occur. The non-pollinating fig wasps (NPFWs) that oviposit from outside the syconium with their long ovipositors can be gall-inducing species, secondary gallers that modify galls made by primary gallers, inquiline or kleptoparasites of gall inducers, or parasitoids of other fig wasps (Joseph, 1959; Jousselin et al., 2008; Chen et al., 2013; Borges, 2015a). Although NPFWs attack figs at different stages of syconial development (Wang and Zheng, 2008; Ranganathan et al., 2010), they all need to complete their development at the same time in order to exit synchronously and opportunistically with the pollinators, since it is usually pollinator males that cooperate to cut exit holes through the wall of the otherwise sealed syconium allowing pollen-laden females and other fig wasps to escape (Cook and Rasplus, 2003; Herre et al., 2008; Suleman et al., 2012). Once pollinators have left the syconium, it ripens quickly, often within a few hours. Delayed departure from the syconium as a result of delayed eclosion would therefore expose wasps to consumption by frugivores or predation by ants (Bronstein, 1988). This requirement for inter-species congruence in eclosion time sets up an interesting arena for developmental conflict between gallers, parasitoids and host-plant with the earlier arriving gallers attempting to hasten syconium development time and the later-arriving parasitoids attempting to retard it in order to complete their development (Krishnan and Borges, 2014). Arrival of different galler species for oviposition at different stages of the fig development cycle also translates to a range of hosts available for parasitoids. Parasitoids capable of exploiting a wide range of host instars generally exhibit developmental plasticity (Harvey et al., 1994). The fig system provides an excellent system to understand this flexibility in parasitoid development since the development of their galler hosts is coupled with the host plant and more specifically with syconium development which in turn restricts the maximum development duration of parasitoids when parasitizing a later stage of the galler host. On the other hand, gallers are expected to have less intra-species variation in their development owing to their shorter oviposition windows in terms of days available for oviposition during syconium ontogeny (Ghara and Borges, 2010; Ranganathan et al., 2010). Although both gallers and parasitoids arrive for oviposition at specific ontogenetic stages of the syconium (Ranganathan et al., 2010) and gallers exploit specific fig inflorescence structures as oviposition sites (Ghara et al., 2011), the specificity of parasitoids for their galler hosts has not been experimentally investigated. Some predictions about host specificity have been made based on the frequency of wasp species developing within syconia (Wang and Zheng, 2008; Ghara et al.,

2015) and the similarity between gallers and parasitoids in cuticular hydrocarbon profiles (Ranganathan et al., 2015). Such questions are particularly challenging given the enclosed microcosm within which wasp development occurs. Furthermore, syconia that do not receive pollination, and in which an adequate number of developing pollinators and seeds are not present, may be aborted by the fig plant (Jousselin et al., 2003; Wang et al., 2010). Nevertheless, in our study system of *Ficus racemosa*, the role of life history traits, resource partitioning along space and time axes, and tools for resource partitioning between gallers and parasitoids for fig wasp community co-existence have been successfully investigated (Ghara and Borges, 2010; Ghara et al., 2011, 2015).

In the present study, in order to understand host–parasitoid interactions, we asked the following questions using experimental manipulations:

- What are the galler host–parasitoid pairings in *Ficus racemosa*?
- What are the ontogenetic, i.e. developmental stages of parasitoids and their hosts in this system?
- Do non-pollinating galler hosts exhibit any strategies specific to increasing survival against their parasitoids?

We also examine whether the development and survival strategies of parasitoids and host gallers can explain the observed relative abundance of NPFWs that emerge from the microcosms of individual syconia, and whether general rules for assembly of fig wasp communities are deducible.

## 2. Methods and materials

### 2.1. Study system

Experiments were conducted on *Ficus racemosa* trees within the campus of the Indian Institute of Science, Bangalore, India (12°58' N, 77°35' E). The phenology of the monoecious *F. racemosa* can be divided into five stages (Ranganathan et al., 2010; adapted from Galil and Eisikowitch, 1968): A—pre-pollination phase; B—pollen receptive phase; C—interfloral phase; D—pollen donation and wasp dispersal phase; and E—seed dispersal phase (Fig. 1). There is one specific pollinator species, *Ceratosolen fusciceps*, whose progeny develops in some flowers at the expense of seeds. The community has six specific NPFWs (*Sycophaga stratheni*, *Sycophaga testacea*, *Sycophaga fusca*, *Sycophaga agransensis*, *Apocrypta* sp. 2, and *Apocrypta westwoodi*) that attack syconia at different stages of their development (Ranganathan et al., 2010) and differ in their oviposition windows, i.e. length of time during syconium development when oviposition occurs (Fig. 1).

The early arriving gallers (*S. stratheni* and *S. testacea*) develop in larger galls whereas later arriving gallers (*S. fusca* and *C. fusciceps*) develop in smaller galls (Ghara et al., 2015). These species show differential occupancy (different proportional abundances) within and between syconia with the pollinator being the most abundant species (Ghara et al., 2015). Of the galler hosts, *S. stratheni* is the largest (adult mass  $0.85 \pm 0.09$  mg (wet weight)), *S. testacea* is of intermediate mass ( $0.35 \pm 0.08$  mg) with *S. fusca* ( $0.25 \pm 0.08$  mg) and *C. fusciceps* having the smallest mass ( $0.22 \pm 0.06$  mg); of the parasitoids, *S. agransensis* ( $0.24 \pm 0.05$  mg) and *Apocrypta* sp 2 ( $0.25 \pm 0.04$  mg) have equivalent masses while *Apocrypta westwoodi* is 4–5 times heavier ( $1.1 \pm 0.17$  mg) ( $n = 10$  for all species; data from Ghara and Borges, 2010).

In the present study, of the seven fig wasp species in the community, only the abundant pollinator *C. fusciceps* and its putative parasitoid *S. agransensis* (Ghara et al., 2015) have not been investigated owing to the fragile nature of pollinator galls resulting in unsuccessful dissections. Exclusion experiments in which only

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