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Original article

Relative investment in egg load and poison sac in fig wasps: Implications for physiological mechanisms underlying seed and wasp production in figs

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ABSTRACT

Fig pollinating wasps and most non-pollinator wasps apply secretions from their poison sacs into oviposited flowers that appear necessary to the formation of the galls that their developing offspring consume. Thus, both eggs and poison sac secretions appear to be essential for wasp reproduction, but the relative investment in each is unknown. We measured relative investment in poison sac and egg production in pollinating and non-pollinating wasps associated with seven species of monoecious Panamanian figs representing both active and passive pollination syndromes. We then collected similar data for four fig hosts in China, where some wasp species in the genus *Eupristina* have lost the ability to pollinate ("cheaters"). All wasps examined possessed large poison sacs, and we found a strong positive correlation between poison sac size and absolute egg production. In the Panamanian species, the relative poison sac to egg investment was highest in the externally ovipositing non-pollinator wasps, followed by active pollinators, then by passive pollinators. Further, pollinator wasps of fig species with demonstrated host sanctions against "cheating" wasps showed higher investment in the poison sac than wasps of species without sanctions. In the Chinese samples, relative investment in the poison sac was indistinguishable between pollinators and "cheaters" associated with the same fig species. We suggest that higher relative investment in poison sac across fig wasp species reflects higher relative difficulty in initiating formation of galls and subsequently obtaining resources from the fig. We discuss the implications for the stability of the fig–wasp mutualism, and for the ability of non-pollinators to exploit this mutualism.

1. Introduction

For over 60 million years, fig trees (*Ficus*, Moraceae) and the fig wasps (Agaonidae Chalcidoidea, Hymenoptera) that pollinate them have constituted one of the most complex and interdependent insect–plant mutualisms known (Corner, 1958; Ramirez, 1974; Wiebes, 1979; Berg, 1989; Machado et al., 2001a; Herre et al., 2008; Cruaud et al., 2011; Xu et al., 2011). All *Ficus* species are taxonomically united by their distinctive, enclosed inflorescence, known as a syconium, that ultimately develops into the fig fruit. Nonetheless, figs are taxonomically and functionally diverse, with over 750 species (Harrison, 2005; Cruaud et al., 2011). Reproductively, figs can be either functionally monoecious or functionally dioecious, and the pollination syndrome can be either active or passive (Kjellberg et al., 2001; Machado et al., 2001b; Jousselin et al., 2003; Harrison, 2005; Herre et al., 2008; Jandér and Herre, 2010).

Within a receptive syconium, tens to hundreds of uniovulate flowers are pollinated by female wasps (foundresses). Generally, one or a few species of wasps pollinate any fig species (Michaloud et al., 1996; Molbo et al., 2003; Cornille et al., 2012; Cruaud et al., 2012). When a foundress wasp enters a receptive fig, she inserts her ovipositor into the style of the flower and attempts to deposit an egg between the inner integument of the flower's ovule and the

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maternally derived diploid nucellus (Verkerke, 1986, 1989; Jansen-González et al., 2012). The foundress also deposits several drops of a maternal secretion that is produced and stored in the wasp's poison sac (see Fig. 1). This secretion, possibly in concert with larval secretions, appears to be essential in transforming the oviposited flowers into galls that, in turn, are essential for the wasp larvae to feed and develop (Verkerke, 1986, 1989; Jansen-González et al., 2012). The maternal secretion is associated with gall growth because only inflorescences that receive the maternal secretion develop into galls and the gall tissue rapidly grows after the drops are delivered; often several hours or days before the wasp's egg hatches (Jansen-González et al., 2012). Thus, both eggs and poison sac secretions seem to be essential for pollinator wasp reproduction. Pollinating wasp species exhibit large poison sacs relative to overall body size (Grandi, 1938), consistent with the importance of poison sac function.

Importantly, without pollen-bearing foundress wasps, fig inflorescences cannot produce fertile seeds under natural circumstances. Without the flowers within fig inflorescences, the pollinator wasps cannot reproduce, and the pollinators' female offspring are essential for a fig to disperse its pollen to other receptive figs (Wiebes, 1979; Herre, 1989, 1996). Individual fig flowers within a syconium can support the development of either an intact viable seed, or the development of a single adult wasp (Herre, 1996; Jandér and Herre, 2010). Generally, seeds develop in flowers with longer styles in which the ovules are located closer to the syconium wall and the galls containing the wasp offspring develop from shorter styled flowers in which the ovules are located toward the interior of the syconium (see references in Herre et al., 2008; Wang et al., 2012). Figs benefit reproductively from both seed production and female wasp production; wasps, however, only benefit directly from the production of more wasps (Herre, 1989). This underlies a conflict of interest between the figs and their wasps that would appear to threaten the stability of mutualism (Herre and West, 1997; Herre et al., 2008; references within).

Fig trees also host non-pollinating wasps that belong to at least six subfamilies within the superfamily Chalcidoidea (Boucek, 1993; Rasplus et al., 1998; Jousselin et al., 2008; Cruaud et al., 2011). Many of these species oviposit from the outside of the syconium, thereby initiating gall growth (Ghara and Borges, 2010) but without providing pollination services (also see Van Noort and Compton, 1996). Although less well studied than the pollinators, a wealth of detailed work on the ecology of these wasps indicates that they are generally parasitic on some aspect of the fig–pollinator mutualism or on other non-pollinator wasp species (West and Herre, 1994; West et al., 1996; Pereira and do Prado, 2005; Pereira et al., 2007; Herre et al., 2008). The most common ecological roles are: small, pollinator sized gall-forming wasps that function ecologically as competitors to the pollinators (Compton and van Noort, 1992; West and Herre, 1994; Elias et al., 2008, 2012); large gall-forming wasps that are physically much larger than the pollinators (West et al., 1996); parasitoids of pollinators, small or large non-pollinators (Compton et al., 1994; West et al., 1996; Compton et al., 2000; Dunn et al., 2008; Ghara and Borges, 2010).

As with the pollinators, non-pollinating wasps possess a poison sac and many of them induce galls that appear similar to those induced by pollinating wasps and utilize the same flower tissue. Interestingly, several non-pollinator wasps, like the New World competitors of pollinators (of the genera *Idarnes* and *Critogaster*) also utilize a similar set of short-styled flowers as the pollinators, despite the fact that they oviposit from the exterior of the fig and thus are farther away from the interior ovules (West and Herre, 1994). Non-pollinating wasps appear to cost the fig tree not only by initiating gall growth without providing pollination services, but also by directly competing with the pollinating wasps for potential gall flowers, reducing the number of pollinators that develop (Compton and van Noort, 1992; Compton et al., 2000; West and Herre, 1994; West et al., 1996; and see references in Herre et al., 2008).

Directly or indirectly, all pollinator and most non-pollinator wasp species exploit fig flowers. However, there are many still-unresolved questions (reviewed in Herre et al., 2008; Jandér and Herre, 2010; Jandér et al., 2012; Wang et al., 2012). Concerning fig–pollinator interactions: How does the fig prevent pollinator wasps from galling all of the flowers to rear their offspring? Why are flowers with shorter styles the ones that are predominately galled by pollinators? Concerning non-pollinators there are also many unresolved questions: Why does the fig not prevent gall formation of non-pollinating wasps? Why do the non-pollinator species that most directly compete with the pollinators also predominately gall short-styled flowers? More broadly, what limits the ability of these non-pollinators to exploit and undermine the mutualism?

Despite great progress (reviewed in Herre et al., 2008; also see West and Herre, 1994; Jousselin et al., 2003; Elias et al., 2012; Jandér et al., 2012; Jansen-González et al., 2012; Wang et al.,

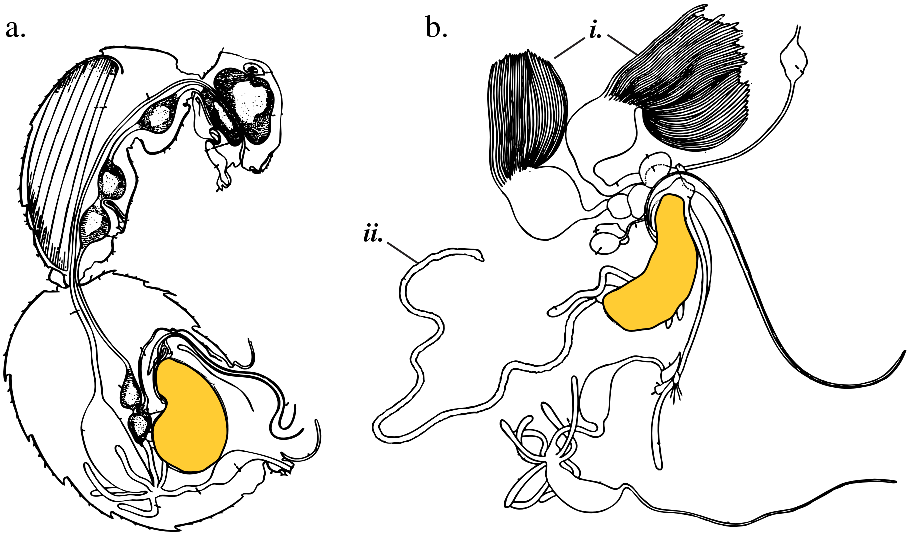

Fig. 1. The poison sac (yellow) (A) *in situ* in the fig wasp abdomen, and (B) when dissected out, attached to other abdominal organs (i. ovaries, ii. acid gland). Modified from Grandi (1938).