This is a repository copy of *Interactions between pollinator and non-pollinator fig wasps: correlations between their numbers can be misleading*.

White Rose Research Online URL for this paper:
http://eprints.whiterose.ac.uk/115327/

Version: Accepted Version

Article:

Raja, S, Suleman, N, Quinnell, RJ orcid.org/0000-0003-1557-7745 et al. (1 more author) (2015) Interactions between pollinator and non-pollinator fig wasps: correlations between their numbers can be misleading. Entomological Science, 18 (2). pp. 230-236. ISSN 1343-8786

https://doi.org/10.1111/ens.12100

© 2014 The Entomological Society of Japan. This is the peer reviewed version of the following article: Raja, S., Suleman, N., Quinnell, R. J. and Compton, S. G. (2015), Interactions between pollinator and non-pollinator fig wasps: correlations between their numbers can be misleading. Entomological Science, 18: 230–236. doi: 10.1111/ens.12100, which has been published in final form at https://doi.org/10.1111/ens.12100.This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for Self-Archiving.

Reuse
Unless indicated otherwise, fulltext items are protected by copyright with all rights reserved. The copyright exception in section 29 of the Copyright, Designs and Patents Act 1988 allows the making of a single copy solely for the purpose of non-commercial research or private study within the limits of fair dealing. The publisher or other rights-holder may allow further reproduction and re-use of this version - refer to the White Rose Research Online record for this item. Where records identify the publisher as the copyright holder, users can verify any specific terms of use on the publisher's website.

Takedown
If you consider content in White Rose Research Online to be in breach of UK law, please notify us by emailing eprints@whiterose.ac.uk including the URL of the record and the reason for the withdrawal request.

eprints@whiterose.ac.uk
https://eprints.whiterose.ac.uk/

Interactions between pollinator and non-pollinator fig wasps
: correlations between their numbers can be misleading

Shazia Raja[1,2], Nazia Suleman[1,3], Rupert J. Quinnell[1] and Stephen G. Compton[1,4]

[1] School of Biology, Faculty of Biological Sciences, University of Leeds, Leeds, LS2 9JT, UK and [4]Department of Zoology and Entomology, Rhodes University, Grahamstown 6140, South Africa.

[2] Present Address: The Institute of Plant and Environmental Protection, National Agriculture Research Centre (NARC), Park Road, Islamabad 44000, Pakistan.

[3] Present Address: Plant Protection Division. Nuclear Institute for Agriculture and Biology (NIAB), Jhang Road, Faisalabad 38000, Pakistan

Correspondence: Dr. Nazia Suleman, Principal Scientist, Plant Protection Division, Nuclear Institute for Agriculture and Biology (NIAB), Faisalabad, Pakistan.

Email: nazianasir2002@yahoo.co.in

Abstract

Ficus and their species–specific pollinator fig wasps represent an obligate plant-insect mutualism, but figs also support a community of non-pollinating fig wasps (NPFWs) that consist of gall makers and parasitoids/inquilines. We studied interactions between Kradibia tentacularis, the pollinator of a dioecious fig tree species Ficus montana, and an undescribed NPFW Sycoscapter sp. Sycoscapter sp. oviposited 2-4 weeks after pollinator oviposition, when host larvae were present in the figs. No negative correlation was found between the numbers of the two wasp species emerging from figs in a semi-natural population, which might suggest that the two species do not interact. However, in experiments where the numbers of pollinator foundresses entering a fig were controlled, Sycoscapter sp. significantly reduced the numbers of pollinator offspring. Consequently, it can be concluded that Sycoscapter sp. is a parasitoid of K. tentacularis (that may also feed on plant tissue). Sycoscapter females concentrate their oviposition in figs that contain more potential hosts, rendering invalid conclusions based on simple correlations of host and natural enemy numbers.

Key words: Agaonidae, Ficus, inquiline, Kradibia, NPFW, parasitoid, Sycoscapter

INTRODUCTION

Insect parasitoids have long been popular subjects for ecological studies, because of their importance as natural enemies and biological control agents and because they are ideal for developing relatively simple population models (Hassell 2000). Features that influence the susceptibility of herbivores to parasitoids, such as the plants where they are feeding, and where on the plants they feed, have also received considerable attention (Askew 1961; Cornell & Hawkins 1993). Parasitoids are characterized by their method of feeding, which typically involves a single host individual (usually another insect) and results in the death of their host.

The relationship between pollinating wasps (Agaonidae) and their host fig trees (Ficus) is a classic example of obligate mutualism (Galil 1977; Janzen 1979) and dates back tens of millions of years (Compton et al. 2010). Each fig tree depends upon one or a small number of host specific pollinating wasp species to provide pollination services and in turn fig trees provide breeding sites for pollinator offspring, which develop inside galled ovules within the figs (Weibes 1979; Yu & Compton 2012).

Figs are also hosts to a number of other fig wasps that do not have any role in pollination (non-pollinating fig wasps, NPFWs). Fig wasp communities (comprising species belonging to several families of Chalcidoidea, in addition to Agaonidae, Heraty et al. 2013) can be diverse, with up to 30 or more species associated with a single tree (Compton & Hawkins 1992; Segar et al. 2013) and several species sharing a single fig (Compton et al. 2009a). NPFW offspring are often abundant and can outnumber pollinator offspring (Bronstein 1991; Bronstein & Hossaert-McKey 1996). NPFWs generally have larvae that develop inside galled ovules, like pollinator larvae, though some species also develop inside galls that form inside the outer wall of figs. Ovule-feeding NPFWs are traditionally classified as gallers, parasitoids or inquilines that destroy other fig wasps and also feed on plant tissues, but the detailed biology of most species is unknown (Compton & van Noort 1992; West & Herre 1994; Kerdelhue & Rasplus 1996). Seed-feeding species, secondary gallers and specialist hyper-parasites have also been described (Pereira et al. 2007; Chen et al. 2013; Compton et al. 2009b) and the utility of separating inquiline and parasitoid species has recently been questioned, because they have the same impact on host population dynamics (Chen et al. 2013). NPFW communities vary greatly between fig species (Compton & Hawkins 1992) in terms of wasp species richness, but there is evidence of some convergence in community structure (Segar et al. 2013). Some NPFWs appear to be host tree specific, like most pollinators (Ulenberg 1985) but the extent of their host specificity is variable (Zhou et al. 2012). Fig trees with dioecious breeding systems (with male trees with figs that support pollinator offspring and female trees with figs that usually only produce seeds) have less species rich NPFW communities than monoecious fig trees, where fig wasps and seeds develop in the same figs (Weiblen 2002; Kerdelhue & Rasplus 1996).

Unlike the pollinators, most NPFWs oviposit from outside of the figs, at a specific stage of fig development, but regardless of oviposition timing all fig wasp species usually emerge from galls inside the figs at the same time and often use a shared exit hole chewed mainly by male pollinating wasps (Compton et al. 1984; Kerdelhue et al. 2000; Suleman et al. 2012). Kerdelhue et al. (2000) identified three ecological groups of non pollinators on the basis of their timing of oviposition**.** Ovule-galling NPFWs oviposit at or shortly before the time of pollinator entry, while parasitoids/inquilines oviposit later (Compton 1993b; Peng et al. 2005). Gallers that oviposit early in fig development often induce large galls and are independent of the pollinators. They act as competitors of the pollinating species, occupying individual ovules and sometimes making the figs unsuitable for entry by pollinators (Kerdelhue 2000). Parasitoids/inquilines oviposit later, feeding in galls induced by other species and killing their larvae. These NPFWs potentially have a negative impact on pollinator populations, though some species target other NPFWs rather than pollinators (Compton 1993a; Compton et al. 1994; Herre & West 1997; Kerdelhue et al. 2000).

Despite their ubiquity, the impacts of NPFW on the fig tree pollination mutualism are not well understood (Galil et al. 1970; West & Herre 1994; Cook & Power 1996, Segar et al. 2013) and studies are generally based on comparisons of the contents of naturally-occurring figs, rather than experiments. Ficus montana Blume is a small SE Asian dioecious fig tree, with a small associated fig wasp fauna that usually comprises just two species, the pollinator (Kradibia tentacularis Grandi) and an undescribed species of Sycoscapter NPFW (Pteromalidae) (Zavodna 2004). Sycoscapter species are generally assumed to be parasitoids of pollinator larvae (Compton 1993b; Cook & Power 1996; Kerdelhue & Rasplus 1996; Kerdelhue et al. 2000), but conclusive evidence is lacking. Utilizing glasshouse populations of K. tentacularis and Sycoscapter sp. we addressed the following questions: at what stage of fig development does Sycoscapter sp. oviposit? Are the numbers of pollinator and Sycoscapter offspring in naturally-pollinated figs negatively correlated? And is the relationship between pollinator and NPFW offspring numbers the same in figs where pollinator foundress numbers are controlled experimentally?

MATERIALS AND METHODS

Study site and species

The work was carried out under controlled conditions at the Experimental Gardens of the University of Leeds. The fig wasps and trees originated from the Centre for International Forestry Research (CIFOR) plantation, West Java and from Rakata, Krakatau islands, Indonesia (Moore 2001).

Ficus montana is a small gynodioecious (functionally dioecious) shrub or scrambler found along rivers or in distributed forest in S.E. Asia (Berg & Corner 2005). The developmental stages of figs are generally subdivided according to the terminology devised by Galil & Eiskowitch (1968) for monoecious figs that was later modified by Valdeyron & Lloyd (1979) for dioecious species. The stage before wasp entry is called the A or ‘pre floral’ phase. The receptive or B phase is the time when the pollinator wasps enter the fig through the ostiole, losing their wings and part of their antennae. The subsequent phase is the C or ‘inter floral’ phase, in which the wasps develop within male figs and seeds develop in the female figs. At the D or ‘male’ phase the next generation of wasps emerges, the anthers open, and the female wasps leave the figs, loaded with pollen. Female fig plants lack a male phase and have only one extended ‘post receptive’ phase (E), during which the figs ripen and become attractive to seed dispersers.

Like many other dioecious figs, F. montana has asynchronous fruiting within plants (Suleman et al. 2011a), allowing pollinators and NPFW to cycle among a small number of trees or even on an individual plant. There is also significant variation in flower numbers within the figs produced by different individuals growing under uniform conditions (Suleman et al. 2013a). Pollinating females of K. tentacularis seek out figs at the receptive stage, enter, attempt to oviposit and pollinate and then either die or leave in an attempt to oviposit in another fig (Suleman 2007). These (wingless) foundresses are able to locate and enter figs up to 60 cm from the first fig they enter (Suleman et al. 2013c). The NPFW Sycoscapter sp. needs figs that have already been entered by pollinators (Raja 2007). Females oviposit from the outside of the figs and their larvae develop into adults inside the ovules. As with pollinators, one larva develops in each galled ovule. Male Syscoscapter are apterous and, unusually for NPFW mating occurs inside the female's galls as well as the fig lumen. Both species complete their development at the same time, hatch and mate. At this time the male fig flowers have mature pollen and the adult female pollinator offspring actively collect the pollen that they will transport to new receptive figs. Intersexual mimicry enables this pollination to take place by deceit (Suleman et al. 2011b). Both Sycoscapter and pollinator males can produce the exit holes through the fig wall that allow their females to escape, but only pollinator males co-operate to achieve this (Suleman et al. 2012). Sycoscapter males have large jaws and aggressively fight each other.

Timing of oviposition of Sycoscapter sp.

Sequential bagging of male figs was used to time when oviposition by Sycoscapter sp. takes place (Compton 1993b). One female pollinator was introduced into each fig and the figs were enclosed in fine cotton bags afterwards to prevent entry by more pollinators. Three figs from the first replicate group were exposed to Sycoscapter sp. after one week and they remained open for that whole week. At the end of the week these three figs were bagged again and three others were exposed. The same process was repeated till the end of the seventh week so that some figs were exposed to Sycoscapter sp. throughout C phase, when pollinator larvae are developing. The experiment was repeated six times on different dates to control for any variation in Sycoscapter sp. abundance over time.

The impact of Sycoscapter sp. on pollinators in the general glasshouse population

Male figs at early C phase were selected, labeled and tagged. After about 3-4 weeks, when these fig fruits were mature and had reached early D phase, they were dissected to determine the numbers of K. tentacularis and Sycoscapter sp. adult offspring present.

Impact of Sycoscapter sp. in figs with a controlled number of pollinator foundresses

Nineteen receptive B phase male fig fruits were selected and divided into two groups. In both groups one pollinator foundress was introduced to each fig using a fine paint brush and then enclosed in fine mesh bags to prevent further entry of foundresses. Subsequently, some of the figs had at least eight female Sycoscapter sp. introduced into each bag on four consecutive days. The timing of their introduction was based on the results of the sequential bagging experiments described above. The remaining figs represented a Sycoscapter-free control group. When the figs were mature (early D phase), they were dissected to determine the numbers of adult pollinator and NPFW offspring, un-pollinated (and un-oviposited) flowers and bladders (empty galled flowers, which mostly will have had fig wasps egg laid in them, Ghana et al. 2012).

Data analysis

The relationship between numbers of pollinator and NPFW in the general glasshouse population was analysed using Pearson's correlation. Differences in the numbers of fig wasps and bladders between control figs and those experimentally exposed to Sycoscapter were analysed using Poisson GLMs; to take into account any possible effect of differing numbers of female flowers between figs, analyses were also carried out on the proportion of female flowers that contained wasps or bladders, using binomial GLMs. In all GLMs, over-dispersion was accounted for by including figs as a random effect. Analyses were performed in Stata 11.0.

RESULTS

Oviposition timing

Sycoscapter sp. only oviposited during a period of 2-4 weeks after the pollinators had laid their eggs in the figs (Table 1). At this time host larvae are available to attack, but plant material is still present inside the galled ovules alongside the pollinator larvae.

The impact of Sycoscapter sp. on pollinators in the general glasshouse population

Out of 114 figs, only seven had no Sycoscapter sp. present. The numbers of pollinator progeny and Sycoscapter sp. progeny averaged 18.85 ± 1.03 (± SE) and 12.31± 0.71 (± SE) respectively. The maximum numbers of progeny present were 55 K. tentacularis and 36

Sycoscapter sp. Pearson product correlation detected no association between the numbers of pollinators and Sycoscapter sp. sharing figs (r^2 = 0.004, P= 0.97).

The impact of Sycoscapter sp. in figs with a single foundress

In contrast to the results from the general population, Sycoscapter sp. significantly reduced the numbers of pollinator progeny inside figs that had been entered by a single foundress (Wald χ^2=9.53, P =0.002, Table 2). A similar reduction was seen in the proportion of female flowers that contained pollinators (Wald χ^2= 22.7, P <0.001). This fall in pollinator numbers was not due to the killing of pollinator larvae during Sycoscapter sp. oviposition, as we did not find a significant influence of Sycoscapter sp. on the numbers or proportions of empty galls (numbers: Wald χ^2 1.05, P = 0.31; proportions: Wald χ^2=0.42, P=0.52, Table 2). This conclusion is reinforced by comparing the combined number of Sycoscapter sp. and pollinator progeny in figs exposed to the parasitoid, compared with the other figs where only pollinators were present (Table 2). The total numbers of wasps in the figs, and the overall proportion of flowers that contained wasps, were similar in the two groups (numbers: Wald χ^2=1.25, P=0.26; proportions: Wald χ^2=0.03, P=0.87)

DISCUSSION

Sycoscapter sp. oviposits into figs about 2-4 weeks after pollinator entry, when pollinator larvae are present in the figs. In the natural community, where variable numbers of foundresses entered the figs, there was no correlation between the numbers of adult offspring of the two fig wasp species. This could be interpreted as an indication that the two species do not interact, with the two species utilizing ovules that are different distances from the fig wall, for example. However, in experiments where the numbers of pollinator foundresses entering a fig were controlled, Sycoscapter sp. significantly reduced the numbers of pollinators, with the combined numbers of offspring of the two species the same as that of pollinators alone in those figs where Sycoscapter sp. was absent. The contrast between these conclusions probably results from Sycoscapter females preferring to oviposit in figs that initially contained larger numbers of pollinator larvae (Suleman et al. 2013b). Its negative impact was only evident after controlling the numbers of pollinator foundresses entering figs and the presence or absence of Sycoscapter.

Comparisons with other studies of pollinator-NPFW interactions reinforce the impression that non-experimental studies can underestimate or fail to detect the impact of NPFW. As in our study, Patel (1998) found no correlation between the numbers of pollinating and NPFW offspring sharing figs, and Peng et al. (2005) even recorded a positive correlation between the numbers of NPFW and pollinators in figs of F. hispida. Kerdelhue et al. (2000) nonetheless were able to detect a significant negative relationship between the numbers of offspring of pollinators and a different Sycoscapter sp. in figs of Ficus sagittifolia. A positive relationship between the numbers of pollinator and NPFW offspring can be generated if there is sufficient variation between figs in the number of flowers (and therefore potential oviposition sites). Conversely, if parasitoid NPFW do not strongly aggregate in figs containing more initial pollinator offspring, then negative correlations between their numbers are to be expected. Even so, only by controlling for initial pollinator numbers, and taking into account variation in flower numbers, can a more accurate picture be obtained.

Sycoscapter sp. is either a parasitoid of K. tentacularis that kills its host after it has consumed all the contents of each galled ovule, or an inquiline that kills the pollinator larvae and subsequently feeds on some plant tissue. No plant material remains inside the galled ovules after pollinator and Sycoscapter sp. adults emerge and dissections of figs at varying ages only detected single larvae inside each gall. This suggests that Sycoscapter sp. is not an ectoparasitoid. It is likely to be either an endoparasitoid that allows host larvae to consume all the contents of the ovules before killing them, or an endoparasitoid which also feeds on plant material after emerging from its host larva. Whether or not any plant material is directly consumed by Sycoscapter sp. larvae does not modify the extent of its negative interactions with the pollinator and indirectly with the pollinator's host plant.

NPFWs are ubiquitous associates of figs, but their biology has received relatively little attention, compared with that of pollinator fig wasps (Bronstein 1991; Cook & Power 1996; Kerdelhue & Rasplus 1996). Experimental manipulations of predators have nonetheless demonstrated the extent of NPFW impact in a monoecious fig tree species (Compton & Robertson 1988) and Weiblen et al. (2001) showed similarly large effects in dioecious figs. The study of oviposition behavior and feeding habits is important for developing an understanding the role of NPFW in natural fig wasp communities (Morris et al. 2003). Pollinators and NPFWs oviposit at specific stages during fig maturation, but regardless of the timing of oviposition, all fig wasp species usually emerge from the galls at the same time as the pollinators and often use the same exit hole, made by male pollinators, to escape (Weiblen 2002). As the timing of oviposition is rarely determined precisely, most studies have emphasized qualitative differences in the timing of fig wasp oviposition (West & Herre 1994; West et al. 1996). This allows NPFWs to be classified according to the times when female wasps oviposit in the figs (Kerdelhue et al. 2000) and the timing to be related to the lengths of their ovipositors and the diameters of figs and thickness of walls of figs at those times (Compton et al. 1994; Kerdelhue & Rasplus 1996; Peng et al. 2005). Experimental manipulations nonetheless remain important if the strengths of interactions between fig wasp species are to be quantified.

ACKNOWLEDGEMENTS

Funding to S. Raja and N. Suleman for this research was provided by the Ministry of Education, Govt. of Pakistan. Martin Lappage provided the most helpful service of maintaining the population of fig trees at the University of Leeds Experimental Gardens.

REFERENCES

Askew RR (1961) On the biology of the inhabitants of oak galls of Cynipidae (Hymenoptera) in Britain. Transactions of the Society for British Entomology **14,** 237–268.

Berg CC, Corner EJH (2005) Moraceae, Ficus. Flora Malesiana 17, Ser. I, part 2. Leiden: Nationaal Herbarium Nederland.

Bronstein JL (1991) The non-pollinating wasp fauna of Ficus pertusa: exploitation of a mutualism? Oikos **61,** 175–186.

Bronstein JL, Hossaert-McKey M (1996) Variation in reproductive success with a sub tropical fig–pollinator mutualism. Journal of Biogeography **23,** 433–446.

Chen HH, Yang DR, Gu D, Compton SG, Peng YQ (2013) Secondary galling: a novel feeding strategy among 'non-pollinating' fig wasps from. Ecological Entomology **38**, 381–389.

Compton SG (1993a) An association between epichrysomallines and eurytomids (Hymenoptera: Chalcidoidea) in Southern African fig wasp communities. African Entomology **1**, 123–125.

Compton SG (1993b) One way to be a fig. African Entomology **1,** 151–158.

Compton SG, Ball AD, Collinson ME, Hayes P, Rasnitsyn AP, Ross AJ (2010) Ancient fig wasps indicate at least 34 million years of stasis in their mutualism with fig trees. Biology Letters **6**, 838–842.

Compton SG, Grehan K, van Noort S (2009a) A fig crop pollinated by three or more species of agaonid fig wasps. African Entomology **17**, 215-222.

Compton SG, Hawkins BA (1992) Determinants of species richness in Southern African fig wasp assemblages. Oecologia **91,** 68–74.

Compton SG, Rasplus J, Ware AB (1994) African parasitoid fig wasp communities. In: Hawkins BA, Sheehan W(eds.), Parasitoid community ecology, Oxford University Press, Oxford.

Compton SG, Robertson HG (1988) Complex interactions between mutualisms: ants tending homopterans protect fig seeds and pollinators. Ecology **69**, 1302–1305.

Compton SG, van Noort S (1992) Southern African fig wasps (Hymenoptera:

Chalcidoidea): resource utilization and host relationships. Proceedings Konijke Nederlands Akademie Wetenschappen **95**, 423–435.

Compton SG, van Noort S, Mcleish M, Deeble M, Stone V (2009b) Sneaky African fig wasps that oviposit through holes drilled by other species. African Natural History **5**, 9–15.

Cook JM, Power SA (1996) Effect of within tree flowering asynchrony on the dynamics of seed and wasp production in an Australian fig species. Journal of Biogeography **23,** 487–493.

Cornell HV, Hawkins BA (1993) Accumulation of native parasitoid species on introduced herbivores: a comparison of hosts as natives and host as invaders. American Naturalist **141,** 847–865.

Galil J (1977) Fig biology. Endeavour **1,** 52–56.

Galil J, Duhlberger D, Rosen D (1970) The effects of Sycophaga sycomorus L on the structure and development of the syconia of the Ficus sycomorus L. New Phytologist **69,** 103–111.

Ghana S, Suleman N, Compton SG (2012) Factors influencing realized sex ratios in fig wasps: double oviposition and larval mortalities. Journal of Insect Behavior **25**, 254–263.

Hassell MP (2000) Host parasitoid population dynamics. Journal of Animal Ecology **69,** 543–566.

Heraty JM, Burks RA, Cruaud A et al. (2013) A phylogenetic analysis of the megadiverse Chalcidoidea (Hymenoptera). Cladistics **29,** 466–542.

Herre EA, West SA (1997) Conflict of interest in a mutualism: documenting the elusive fig wasp-seed trade off. Proceedings of the Royal Society of London Series B **264,** 1501–1507.

Janzen DH (1979) How to be a fig. Annual Review of Ecology and Systematics **10,** 13–51.

Kerdelhue C, Rasplus JY (1996) Non-pollinating afrotropical fig wasps affect the fig-pollinator mutualism in Ficus within the subgenus Sycomorus. Oikos **75,** 3–14.

Kerdelhue C, Rossi JP, Rasplus JY (2000) Comparative community ecology studies on old world figs and fig wasps. Ecology **81,** 2832–2849.

Moore JC (2001) The Ecology and Evolution of Gynodioecious Figs (Ficus: Moraceae) and Their Pollinators (Agaoninae: Agaonidae). Ph.D. Thesis. The University of Leeds, U.K.

Morris WF, Bronstein JL, Wilson WG (2003) Three way coexistence in obligate mutualist-exploiter interaction: the potential role of competition. American Naturalist **161,** 860–875.

Patel A (1998) Wasp composition in inflorescence of two dioecious fig species–implications for the fig wasp mutualism. Biotropica **30,** 477- 480.

Peng YQ, Yang DR, Wang QY (2005) Quantitative tests of interaction between pollinating and non-pollinating fig wasps on dioecious Ficus hispida. Ecological Entomology **30,** 70–77.

Pereira RAS, Teixeira SP, Kjellberg F (2007) An inquiline fig wasp using seeds as a resource for small male production: a potential first step for the evolution of new feeding habitats. Biological Journal of the Linnaean Society **92**, 9–17.

Raja S (2007) Factors Influencing Populations of The Fig Pollinator (Liporrhopalum tentacularis) and Its Parasitoid (Sycoscapter sp.). Ph.D. Thesis. The University of Leeds, UK.

Raja S, Suleman N, Compton SG (2008) Why do fig wasps pollinate female figs? Symbiosis **45,** 25–28.

Segar S, Pereira R, Compton SG, Cook J (2013) Convergent structure of multitrophic communities over three continents. Ecology Letters ELE-00283-2013.R3

Suleman N (2007) Population biology of a fig plant-pollinator and parasitoid system under laboratory conditions. Ph.D. Thesis. The University of Leeds, UK

Suleman N, Raja S, Compton SG (2011a) A comparison of growth and reproduction, under laboratory conditions, of males and females of a dioecious fig tree. Plant Systematics and Evolution **296,** 245–253.

Suleman N, Raja S, Zhang Y, Compton, SG (2011b) Sexual differences in the attractiveness of figs to pollinators: females stay attractive for longer. Ecological Entomology **36,** 417–424.

Suleman N, Raja S, Compton SG (2012) Only pollinator fig wasps have males that collaborate to release their females from figs of an Asian fig tree. Biology Letters **8,** 344–346.

Suleman N, Quinnell RJ, Compton SG (2013a) Variation in inflorescence size in a dioecious fig tree and its consequences for the plant and its pollinator fig wasp. Plant Systematics and Evolution **299,** 927–934.

Suleman, N, Raja S, Compton SG (2013b) Parasitism of a pollinator fig wasp: mortalities are higher in figs with more pollinators, but are not related to local densities of figs. Ecological Entomology **38,** 478–484.

Suleman N, Raja S, Quinnell RJ, Compton SG (2013c) Putting your eggs in several baskets: oviposition in a wasp that walks between several figs. Entomologia Experimentalis et Applicata **149,** 85–93.

Ulenberg SA (1985) The systematics of the fig wasp parasites of the genus Apocrypta Coquerel. Amsterdam, the Netherlands: North- Holland Publishing Company.

Weibes JT (1979) Co- evolution of figs and their insect pollinators. Annual Review of Ecology and Systematics **10,** 1–12.

Weiblen GD (2002) How to be a fig wasp. Annual Review of Entomology **47,** 299–330.

West SA, Herre EA (1994) The ecology of the New World fig parasitizing wasps Idarnes and implications for the evolution of the fig-pollinator mutualism. Proceedings of the Royal Society of London Series B **258,** 67–72.

West SA, Herre EA, Windsor DM, Green PRS (1996) The ecology and evolution of the New World non-pollinating fig wasps communities. Journal of Biogeography **23,** 447–458.

Weiblen GD, Yu W, West SA (2001) Pollination and parasitism in functionally dioecious figs. Proceedings of the Royal Society of London Series B **268,** 651–659.

Yu H, Compton SG (2012) Moving your sons to safety: galls containing male fig wasps expand into the centre of figs, away from enemies. PLoS ONE **7,** 1.

Zavodna M (2004) On The Biology of Pollinating Fig Wasps and The Maintenance of TheirMmutualism With Fig Plants. Ph.D. Thesis. Universiteit Utrecht.

Zhou MJ, Xiao JH, Bian SN et al. (2012) Molecular approaches identify known species, reveal cryptic species and verify host specificity of Chinese Philotrypesis (Hymenoptera: Pteromalidae) Molecular Ecology Resources **12,** 598–606.

Table 1 The relationship between oviposition by Sycoscapter sp. and the times after pollinator entry when the figs were exposed. Figs were exposed for one week periods at various times after a single pollinator fig wasp had been introduced into each fig.

Days exposed to Sycoscapter sp.	Proportion of figs colonized (n/total)	Number of Pollinators per fig (mean ± SE)	Number of Sycoscapter per fig (mean ± SE)	Proportion Sycoscapter (mean ± SE)
7-13	0 (0/12)	42 ± 6	0	0
14-20	0.85 (11/13)	30 ± 5	11 ± 2	0.32 ± 0.06

21-27	0.67 (8/12)	29 ± 2	10 ± 2	0.24 ± 0.05
28-34	0 (0/14)	30 ± 3	0	0
35-41	0 (0/10)	32 ± 5	0	0
42-48	0 (0/10)	30 ± 5	0	0

Table 2

Summary of the contents of figs entered by a single foundress that were exposed to Sycoscapter sp. (n=9 figs) and those that were not exposed to Sycoscapter sp. (n=10 figs).

	With Sycoscapter sp.		Without Sycoscapter sp.	
	Mean	SE	Mean	SE
Male pollinators	7.3	0.6	8.3	0.8
Female pollinators	26.2	5.9	44.2	3.3
Total pollinators	33.6	5.9	52.5	3.5
Male parasitoids	4.6	0.7	---	---
Female parasitoids	22.0	1.7	---	---
Total parasitoids	26.6	1.9	---	---
Total wasps	60.1	6.0	52.5	3.5
Un-pollinated flowers	13.9	3.8	16.4	4.1
Total bladders	31.6	3.3	27.6	5.7
Total female flowers	105.6	8.3	96.5	9.3
Total male flowers	17.1	2.2	15.4	1.7
Total flowers	122.7	9.1	111.9	9.6