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 sub-family 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
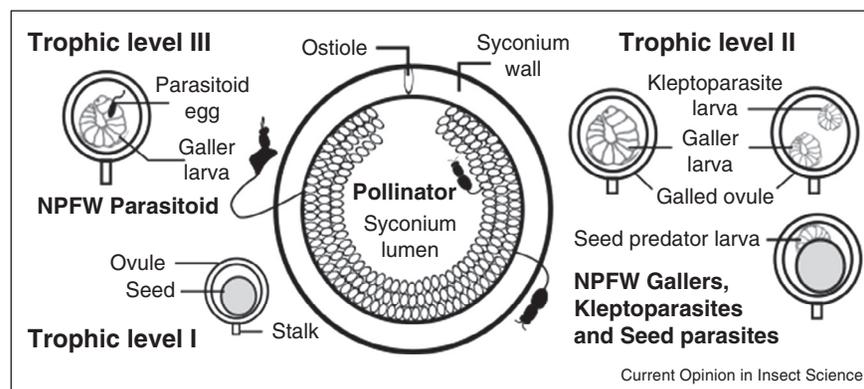
There are at least three trophic levels in the microcosm supported by the mutualism between figs and fig wasps. At the first trophic level are the seeds and other plant tissues that can be utilised by NPFW gallers, kleptoparasites and seed parasites in the second trophic level. At the third trophic level 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.

Figure 2
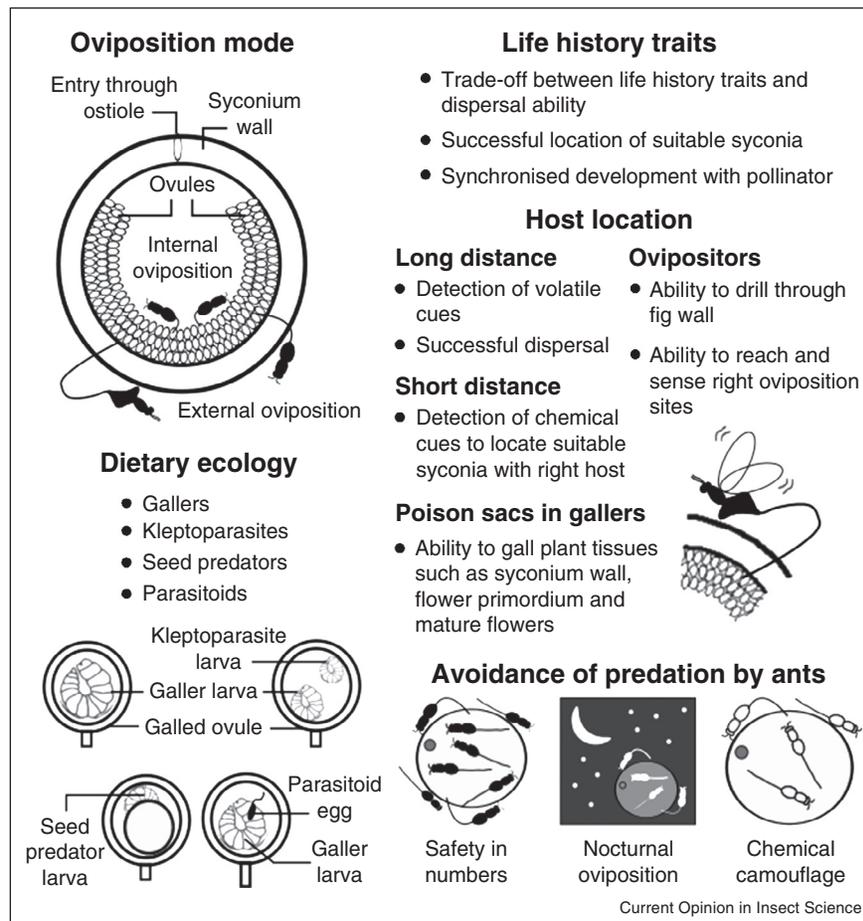
The mutualism between figs and fig wasps can be characterised as a brood-site or a nursery pollination mutualism in which the seeds of figs and the offspring of pollinating wasps develop within an enclosed globular inflorescence, the syconium, which is the nursery or brood-site. Life in this microcosm requires particular biological traits. Invasion of this nursery by parasitic fig wasps is correspondingly facilitated by certain biological features. The figure illustrates some of the many ways in which a non-pollinating fig wasp can exploit the mutualism between figs and fig wasps, and the traits that may facilitate the parasitic lifestyle.

seeds are not an adequate developmental resource. In another fig species which sustains a functional pollinator and a closely related cheater non-pollinator, obligate seed-eating NPFWs developed mostly within syconia occupied by the functional pollinator since only those syconia produced seeds [30].

The community of wasps associated with figs also include species in the third trophic level, that is, parasitoids, which feed on developing pollinator or galler larvae, and oviposit early or late in syconial development [20]. Very little is known about the biology of parasitoids, whether they are ectoparasitoids or endoparasitoids, koinobionts or idiobionts. Idiobionts are parasitoids that immobilise and kill the host on which their larvae will develop, while koinobionts feed on hosts that are continuing their development. Presumably idiobionts that kill or paralyse their hosts, and whose larvae develop

using existing host tissue, would parasitise more fully developed host stages, and would therefore utilise syconia at later stages of development compared to koinobionts that allow their hosts to grow and develop after parasitism [28••].

In dioecious figs, NPFWs also occur in syconia of male trees (containing pollinator larvae) and female trees (without pollinator larvae). This NPFW community comprises non-pollinating gallers which support kleptoparasites and parasitoids [31,32] indicating that pollinators are not necessary for multitrophic parasitism of dioecious figs, since the developing stages of non-pollinating gallers can be used as hosts for parasitism.

Oviposition from the external surface of syconia is fraught with the risk of predation by ants that are major predators of fig wasps [33,34]; ants learn to associate pulses of

arriving and departing fig wasps with VOCs emitted by syconia at those times [35•]. Some NPFWs avoid ant predation by nocturnal oviposition [33], or chemical camouflage [36], or dilute predation risk by ovipositing in large congregations on syconia [37].

Sensory ecology of parasitism

The long-distance attraction of pollinators, as well as NPFW gallers and parasitoids to syconia is mediated by fig VOCs [38]. VOCs emitted by fig trees probably rise in plumes that might spread at different heights depending on the heights of the trees and the prevailing wind conditions. Although wind-blown pollinators have been trapped above tree canopies in forests and cities [39•,40], fewer NPFWs were trapped at such heights or lower [39•], making inferences about heights at which NPFWs encounter fig-specific VOCs difficult, especially since information about fig VOC plumes is non-existent. The syconial VOC profile changes throughout development [41]; syconia into which gallers have oviposited emit green leaf volatiles (GLVs) and herbivore-induced plant volatiles (HIPVs) [41]. The pollinator-attracting signal is likely mixed with HIPVs [41] or oviposition-induced plant volatiles (OIPVs). These VOCs may attract parasitoids as in other plant–herbivore–parasitoid systems [42].

Having reached a suitable fig tree, NPFWs would need short-range cues to select syconia for parasitism. In the only published study on the sensory features of the ovipositors of an entire community of fig wasps, pollinator ovipositors had the fewest sensilla [18••]. Pollinators use antennal olfactory sensilla to locate suitable syconia, and once within syconia, do not require complex ovipositor guidance mechanisms. Whether internally-ovipositing NPFWs also have few ovipositor sensilla is not known. Externally-ovipositing NPFWs rely on cue perception by ovipositor sensilla to find oviposition sites within syconia. Sensilla diversity and density increased in NPFWs ovipositing late in syconium development compared to those ovipositing earlier [18••]. All sensilla were concentrated at the tip of the ovipositor, and being situated within pits also avoided damage while penetrating latex-filled syconial tissues [18••]. Parasitoids specialised on specific larval stages may require greater sensilla diversity to find suitable oviposition sites. Since the force required to penetrate the syconium increases with syconial development stage, ovipositors of NPFWs in this community also exhibited increasing sclerotisation and elaboration of ovipositor drilling structures with stage of syconium penetration [18••]. Pollinators and early gallers had smooth ovipositors, whereas all late-arriving gallers and parasitoids had well developed serrations on their ovipositors for syconium penetration [18••]. Penetration of harder figs was facilitated by the presence of metals, such as zinc, in the ovipositors [43,44] as was also found for cynipid gall wasps [45]. Some parasites use oviposition channels drilled by other NPFWs [37]; these may be hyperparasites ovipositing in locations where other eggs were laid or with ovipositors that are unable to independently penetrate the syconium.

Life history strategies

Parasite life history strategies should match their parasitic strategy. The life history and parasitic strategies of one fig wasp community occupying a single fig species has been investigated [20,28••]. Gallers exhibited the life history trait of pro-ovigeny, eclosing with a full complement of matured eggs, while parasitoids exhibited synovigeny eclosing with only a few mature eggs. Synovigenic parasitoids continue to develop mature eggs throughout their lifespan. The synovigeny of the parasitoids was coupled with a much longer lifespan (up to 27 days on a sucrose diet) compared to the lifespan of a single day for some gallers, and it is possible that the ability of parasitoids to feed on nectar or other exudates under natural conditions may contribute to their longevity [28••]. Galler lifespan, on the other hand, could not be greatly lengthened by laboratory feeding, possibly because they do not rely extensively on feeding in the wild [28••]. Parasitoids also had the largest eggs and the shortest pre-adult (egg to eclosion) lifespan compared to gallers [28••]. Since all wasps leave the syconium more or less concurrently, early-ovipositing gallers have a longer pre-adult lifespan compared to those wasps, especially parasitoids, that oviposit later into the syconium. Early gallers accelerate the development time of the syconium presumably to pass quickly through larval stages vulnerable to parasitoids while late-arriving parasitoids retard syconium development, possibly to allow their offspring enough time to complete development [46]; successful parasitoid development at that late stage may also be facilitated by nutrition stored in their large eggs [28••]. The mechanism by which syconium development time is influenced by syconium occupants is unknown. Syconium ontogeny is likely a compromise between opposing selection pressures from gallers, parasitoids, and seeds [46].

Many NPFWs rely on pollinator males to cut syconial exit holes to release fully matured wasps [47]. It would be interesting to ask whether the presence of developing pollinator males influences which syconia are parasitised since the sex ratio of pollinators developing within fig syconia is strongly female-biased [2]. It is also possible that externally ovipositing NPFWs distribute eggs between syconia to ensure that at least some syconia will contain sufficient pollinator males. However, information about the presence of male pollinators cannot be employed by galler NPFWs that oviposit before the pollinators; moreover, since unpollinated syconia are usually aborted, distributing eggs between many syconia would be an appropriate bet-hedging strategy [20]. Although the developing offspring of some early gallers are able to prevent the abortion of unpollinated syconia and complete their

development [20], they may remain entombed, unable to exit the syconium owing to the lack of male pollinators (A Krishnan, M Ghara, unpublished data).

Community organisation of fig wasp parasites

Globally, across fig distributions, there is convergence in the structure of multitrophic communities of fig wasps inhabiting fig syconia [22,48]. The species richness of gallers strongly influences the diversity of parasitoids [12] as in other systems [49]. Fig species with larger syconia and larger numbers of flowers may provide greater opportunities for niche specialisation, supporting greater NPFW species diversity. There may be trade-offs between life history traits such as fecundity (eggs matured at eclosion) and dispersal ability assuming that wing loading (ratio of body mass of the insect to wing area) correlates with intrinsic dispersal ability [50] which is the distance that wasps can fly fuelled by their own reserves. Since fig wasps can also be wind-dispersed, their realised dispersal distance would be the combined effect of intrinsic dispersal ability and wind-aided movement. Therefore, proovigenic wasps with higher numbers of mature eggs at eclosion may be expected to have lower intrinsic dispersal ability compared to synovigenic wasps. These tradeoffs between life history strategies and intrinsic dispersal ability might therefore affect the realised dispersal distance of NPFWs with different egg maturation strategies, which when coupled with the spatiotemporal variation in availability of syconia suitable for parasitism and the physiological tolerance of wasps may structure local NPFW communities [50,51]. Parasites vary in their costs on the fig–fig wasp mutualism [52–54] and such costs may also contribute to NPFW community structure.

Do parasites keep pace with the mutualism?

NPFWs are much less ancient than pollinators, exhibiting delayed phylogenetic tracking of their hosts [55•,56–58], much less close co-cladogenesis with the figs and much more host shifting than exhibited by pollinators and figs [55•,56]. The same parasites were found on more than one fig species [59], suggesting less specificity than previously believed.

How opportunistic or how generalist are parasites? Since NPFWs are attracted by fig VOCs, gallers or parasitoids could exploit a set of fig species that produce similar key VOCs even if they are embedded in the overall volatilome emitted by the figs. Generalist gallers must be able to induce galls in a variety of fig species, and generalist kleptoparasites or parasitoids must be able to exploit the larval stages of a variety of hosts. More importantly, since emergence times of gallers, pollinators and parasitoids should coincide so that all wasps leave the syconium concurrently, it is conceivable that life history traits such as body sizes and other correlated traits must match within a set of fig wasps that can successfully occupy a syconium. These correlations must be established for fig and fig wasp communities.

Future prospects

Successful parasitism of the fig–fig wasp mutualism is clearly a challenge. Although many aspects of the fig–pollinator association have been examined, the biology of NPFWs has been severely neglected. Explaining the patterns that are emerging on the presence or absence of co-diversification between figs, their pollinators, and their parasites will only be possible when dietary ecology, life history traits and sensory ecology are investigated. The fig system is not readily amenable to yielding information because much of the action occurs within the closed confines of the fig syconium. Despite these difficulties, the fig system offers myriad surprises at every turn. Is the Snark a Boojum? We'll see.

Acknowledgements

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- • of special interest
- •• of outstanding interest

1. Cruaud A, Rønsted N, Chantarasuwan B, Chou LS, Clement WL,
• Couloux A, Cousins B, Genson G, Harrison RD, Hanson PE *et al.*: **An extreme case of plant–insect codiversification: figs and fig-pollinating wasps**. *Syst Biol* 2012, **61**:1029-1047.
Dates the fig–fig wasp mutualism to 75 mya with an origin in Eurasia.

2. Cook JM, Rasplus J-Y: **Mutualists with attitude: coevolving fig**
•• **wasps and figs**. *Trends Ecol Evol* 2003, **18**:241-248.
Presents several important research ideas to be investigated.

3. Kjellberg F, Jousselin E, Hossaert-McKey, Rasplus J-Y: **Biology,**
•• **ecology, and evolution of fig-pollinating wasps (Chalcidoidea, Agaonidae)**. In *Biology, Ecology, and Evolution of Gall-Producing Arthropods.* Edited by Raman A, Schaefer CW, Withers TM. Enfield (NH) USA: Science Publishers, Inc.; 2005:539-572.
An outstanding compilation of information on the biology of the fig mutualism including material from older, hard to acquire literature sources.

4. Herre EA, Jandér KC, Machado CA: **Evolutionary ecology of figs**
•• **and their associates: recent progress and outstanding puzzles**. *Annu Rev Ecol Evol Syst* 2008, **39**:439-458.
Presents many unanswered questions that deserve investigation.

5. Soler CCL, Proffit M, Bessière J-M, Hossaert-McKey M, Schatz B: **Evidence for intersexual mimicry in a dioecious plant**. *Ecol Lett* 2012, **15**:978-985.

6. McLeish MJ, van Noort S: **Codivergence and multiple host species use by fig wasp populations of the *Ficus* pollination mutualism**. *BMC Evol Biol* 2012, **12**:1.

7. Darwell CT, al-Beidh S, Cook JM: **Molecular species delimitation of a symbiotic fig-pollinating wasp species complex reveals extreme deviation from reciprocal partner specificity**. *BMC Evol Biol* 2014, **14**:189.

8. Weiblen GD: **How to be a fig wasp**. *Annu Review Entomol* 2002,
•• **47**:299-330.
A comprehensive review of known and potential fig wasp strategies.

9. van Noort S, Compton SG: **Convergent evolution of agaonine and sycoecine (Agaonidae, Chalcidoidea) head shape in response to the constraints of host fig morphology**. *J Biogeogr* 1996, **23**:415-424.

10. Hossaert-McKey M, Soler C, Schatz B, Proffit M: **Floral scents:**
•• **their roles in nursery pollination mutualisms**. *Chemoecology*
2010, **20**:75-88.
A comprehensive review of volatile organic compounds in nursery polli-
nation systems such as that of the figs and fig wasps.

11. Heraty JM, Burks RA, Cruaud A, Gibson GAP, Liljeblad J, Munro J,
Rasplus J-Y, Delvare G, Janšta P, Gumovsky A *et al.*: **A**
phylogenetic analysis of the megadiverse Chalcidoidea
(Hymenoptera). *Cladistics* 2013, **29**:466-542.

12. Compton SG, Hawkins BA: **Determinants of species richness in**
southern African fig wasp assemblages. *Oecologia* 1992,
91:68-74.

13. Cruaud A, Underhill JG, Huguin M, Genson G, Jabbour-Zahab R,
Tolley KA, Rasplus J-Y, van Noort S: **A multilocus phylogeny of**
the world Sycoecinae fig wasps (Chalcidoidea: Pteromalidae).
PLoS ONE 2013, **8**:e79291.

14. Chen H-H, Yang D-R, Gu D, Compton SG, Peng Y-Q: **Secondary**
galling: a novel feeding strategy among 'non-pollinating' fig
wasps from *Ficus curtipes*. *Ecol Entomol* 2013, **38**:381-389.

15. Zhao J-B, Peng Y-Q, Quinnell RJ, Compton SG, Yang D-R: **A**
• **switch from mutualist to exploiter is reflected in smaller egg**
loads and increased larval mortalities in a 'cheater' fig wasp.
Acta Oecol 2014, **57**:51-57.
Explores the costs of developing a cheating strategy in a lineage of
pollinating wasps.

16. Peng Y-Q, Duan Z-B, Yang D-R, Rasplus J-Y: **Co-occurrence of**
two Eupristina species on *Ficus altissima* **in Xishuangbanna,**
SW China. *Symbiosis* 2008, **45**:9-14.

17. Weiblen GD, Bush GL: **Speciation in fig pollinators and**
parasites. *Mol Ecol* 2002, **11**:1573-1578.

18. Ghara M, Kundanati L, Borges RM: **Nature's Swiss army knives:**
•• **ovipositor structure mirrors ecology in a multitrophic fig wasp**
community. *PLoS ONE* 2011, **6**:e23642.
The first investigation of the sensory ecology of fig wasp ovipositors with
detailed information on sensilla, ovipositor drilling apparatus, and mea-
surement of penetration forces.

19. al-Beidh S, Dunn DW, Power SA, Cook JM: **Parasites and**
mutualism: measuring enemy-free space in a fig–pollinator
symbiosis. *Oikos* 2012, **121**:1833-1839.

20. Ghara M, Ranganathan Y, Krishnan A, Gowda V, Borges RM:
Divvying up an incubator: how parasitic and mutualistic fig
wasps use space within their nursery microcosm. *Arthropod-*
Plant Interac 2014, **8**:191-203.

21. Conchou L, Ciminera M, Hossaert-McKey M, Kjellberg F: **The non-**
pollinating fig wasps associated with *Ficus guianensis*:
community structure and impact of the large species on the
fig/pollinator mutualism. *Acta Oecol* 2014, **57**:28-37.

22. Cruaud A, Jabbour-Zahab R, Genson G, Kjellberg F, Kobmoo N,
van Noort S, Yang D-Y, Peng Y-Q, Ubaidillah R, Hanson PE *et al.*:
Phylogeny and evolution of life-history strategies in the
Sycophaginae non-pollinating fig wasps (Hymenoptera,
Chalcidoidea). *BMC Evol Biol* 2011, **11**:178.

23. Jansen-González S, Teixeira SP, Pereira RAS: **Mutualism from**
• **the inside: coordinated development of plant and insect in**
an active pollinating fig wasp. *Arthropod-Plant Interac* 2012,
6:601-609.
The first detailed histological investigation of the galling process in a
pollinating fig wasp.

24. Jansen-González S, Teixeira SP, Kjellberg F, Pereira RAS: **Same**
•• **but different: larval development and gall-inducing process of**
a non-pollinating fig wasp compared to that of pollinating fig-
wasps. *Acta Oecol* 2014, **57**:44-50.
The first histological investigation of the galling process in a non-pollinat-
ing fig wasp.

25. Martinson EO, Jandér KC, Peng Y-Q, Chen H-H, Machado CA,
Arnold AE, Herre EA: **Relative investment in egg load and**
poison sac in fig wasps: implications for physiological
mechanisms underlying seed and wasp production in figs.
Acta Oecol 2014, **57**:58-66.

26. Tooker JF, Helms AM: **Phytohormone dynamics associated**
with gall insects, and their potential role in the evolution of the
gall-inducing habit. *J Chem Ecol* 2014, **40**:742-753.

27. Elias LG, Teixeira SP, Kjellberg F, Pereira RAS: **Diversification in**
the use of *Idarnes* **species: bypassing functional constraints in**
the fig–fig wasp interaction. *Biol J Linn Soc* 2012, **106**:114-122.

28. Ghara M, Borges RM: **Comparative life-history traits in a fig**
•• **wasp community: implications for community structure**. *Ecol*
Entomol 2010, **35**:139-148.
Presents the first comprehensive investigation of life history traits of a fig
wasp community occupying a single fig species.

29. Pereira RAS, Teixeira SP, Kjellberg F: **An inquiline fig wasp using**
seeds as a resource for small male production: a potential first
step for the evolution of new feeding habits? *Biol J Linn Soc*
2007, **92**:9-17.

30. Wang R, Matthews A, Ratcliffe J, Barwell LJ, Peng Y-Q, Chou L-S,
Hu H, Yang H-W, Compton SG: **First record of an apparently**
rare fig wasp feeding strategy: obligate seed predation. *Ecol*
Entomol 2014, **39**:492-500.

31. Weiblen GD, Yu DW, West SA: **Pollination and parasitism in**
functionally dioecious figs. *Proc R Soc B* 2001, **268**:651-659.

32. Wu T, Dunn DW, Hu H-Y, Niu L-M, Xiao J-H, Pan X-L, Feng G, Fu Y-
G, Huang D-W: **The occurrence of fig wasps in the fruits of**
female gynodioecious fig trees. *Acta Oecol* 2014, **46**:33-38.

33. Ranganathan Y, Ghara M, Borges RM: **Temporal associations in**
fig–wasp–ant interactions: diel and phenological patterns.
Entomol Expt Appl 2010, **137**:50-61.

34. Bain A, Harrison RD, Schatz B: **How to be an ant on figs**. *Acta*
Oecol 2014, **57**:97-108.
A comprehensive review of current knowledge about the interaction of
ants with fig wasps and figs.

35. Ranganathan Y, Borges RM: **Predatory and trophobiont-tending**
• **ants respond differently to fig and fig wasp volatiles**. *Anim*
Behav 2009, **77**:1539-1545.

36. Ranganathan Y: *Ants, figs, fig wasps: the chemical ecology of a*
multitrophic system. Bangalore, India: Indian Institute of Science;
2012, PhD thesis.

37. Compton SG, van Noort S, McLeish M, Deeble M, Stone V:
Sneaky African fig wasps that oviposit through holes drilled by
other species. *Afr Nat Hist* 2009, **5**:9-15.

38. Proffit M, Schatz B, Borges RM, Hossaert-McKey M: **Chemical**
mediation and niche partitioning in non-pollinating fig-wasp
communities. *J Anim Ecol* 2007, **76**:296-303.

39. Harrison RD: **Fig wasp dispersal and the stability of a keystone**
• **plant resource in Borneo**. *Proc R Soc London B* 2003, **270(Suppl**
1):S76-S79.
Presents data on trapping fig wasps at different heights above an Asian
rainforest and discusses implications of these findings for long distance
dispersal of fig wasps.

40. Jeevanandam N, Corlett RT: **Fig wasp dispersal in urban**
Singapore. *Raffles Bull Zool* 2013, **61**:343-347.

41. Borges RM, Bessière J-M, Ranganathan Y: **Diel variation in fig**
volatiles across syconium development: making sense of
scents. *J Chem Ecol* 2013, **39**:630-642.

42. Fatouros NE, Lucas-Barbosa D, Weldegergis BT, Pashalidou FG,
van Loon JJA, Dicke M, Harvey JA, Gols R, Huigens ME: **Plant**
volatiles induced by herbivore egg deposition affect insects of
different trophic levels. *PLoS ONE* 2012, **7**:e43607.

43. Kundanati L, Ghara M, Borges RM, Sane S, Gundiah N:
Micromechanics of insect boring during oviposition. *Poster*
*presented at 6*th *World Congress on Biomechanics*; *Singapore:*
2010.

44. Kundanati L, Gundiah N: **Biomechanics of substrate boring by**
fig wasps. *J Expt Biol* 2014, **217**:1946-1954.

45. Polidori C, García AJ, Nieves-Aldrey JL: **Breaking up the wall:**
metal-enrichment in ovipositors, but not in mandibles,
co-varies with substrate hardness in gall-wasps and their
associates. *PLoS ONE* 2013, **8**:e70529.

46. Krishnan A, Borges RM: **Parasites exert conflicting selection pressures to affect reproductive asynchrony of their host plant in an obligate pollination mutualism**. *J Ecol* 2014, **102**:1329-1340.

47. Suleman N, Raja S, Compton SG: **Only pollinator fig wasps have males that collaborate to release their females from figs of an Asian fig tree**. *Biol Lett* 2012, **8**:344-346.

48. Segar ST, Pereira RA, Compton SG, Cook JM: **Convergent structure of multitrophic communities over three continents**. *Ecol Lett* 2013, **16**:1436-1445.

49. Joseph MB, Gentles M, Pearse IS: **The parasitoid community of *Andricus quercuscalifornicus* and its association with gall size, phenology, and location**. *Biodiv Conserv* 2011, **20**:203-216.

50. Duthie AB, Abbott KC, Nason JD: **Trade-offs and coexistence: a lottery model applied to fig wasp communities**. *Am Nat* 2014, **183**:826-841.

51. McLeish MJ, van Noort, Tolley KA: **African parasitoid fig wasp diversification is a function of *Ficus* species ranges**. *Mol Phylogen Evol* 2010, **57**:122-134.

52. Pereira RAS, do Prado AP: **Non-pollinating wasps distort the sex ratio of pollinating fig wasps**. *Oikos* 2005, **110**:613-619.

53. Dunn DW, Segar ST, Ridley J, Chan R, Crozier RH, Yu DW, Cook JM: **A role for parasites in stabilising the fig-pollinator mutualism**. *PLoS Biol* 2008, **6**:e59.

54. Segar ST, Cook JM: **The dominant exploiters of the fig/pollinator mutualism vary across continents, but their costs fall consistently on the male reproductive function of figs**. *Ecol Entomol* 2012, **37**:342-349.

55. Silvieus SI, Clement WL, Weiblen GD: **Cophylogeny of figs,**
  • **pollinators, gallers and parasitoids**. In *Specialization, Speciation, and Radiation: The Evolutionary Biology of Herbivorous insects*. Edited by Tilmon KJ. Berkeley: University of California Press; 2008:225-239.
Presents many ideas on the types of co-diversification or co-speciation patterns that can be expected between fig and their fig wasps.

56. Cook JM, Segar ST: **Speciation in fig wasps**. *Ecol Entomol* 2010, **35(S1)**:54-66.

57. Cruaud A, Jabbour-Zahab R, Genson G, Couloux A, Yan-Qiong P, Yang D-Y, Ubaidillah R, Pereira RAS, Kjellberg F, van Noort S *et al.*: **Out of Australia and back again: the world-wide historical biogeography of non-pollinating fig wasps (Hymenoptera: Sycophaginae)**. *J Biogeogr* 2011, **38**:209-225.

58. Segar ST, Lopez-Vaamonde C, Rasplus J-Y, Cook JM: **The global phylogeny of the subfamily Sycoryctinae (Pteromalidae): parasites of an obligate mutualism**. *Mol Phylogen Evol* 2012, **65**:116-125.

59. McLeish MJ, Beukman G, van Noort S, Wossler TC: **Host–plant species conservatism and ecology of a parasitoid fig wasp genus (Chalcidoidea; Sycoryctinae; Arachonia)**. *PLoS ONE* 2012, **7**:e44804.