

# WHAT'S IN A FIG? THE INTERACTIONS BETWEEN FIGS, FIG WASPS, AND FIG WASP PARASITIDS

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*Abstract:* Many plants provide consistent and predictable fruit rewards to obtain reliable services from seed dispersers. Fig fruit production, however, is unpredictable in time and space. This behavior creates a scramble for resources in the fruit foraging community. I evaluated one hypothesis that could explain this fruiting behavior. Parasitoids of the obligate fig pollinator wasp (Hymenoptera: Agaonidae) can exert selection pressure on fig fruiting period by increasing the rate of parasitism on late-developing fruits. I sampled sequentially ripening fig fruits from one tree (probably *Ficus obtusifolia*) over 48 hours near the Sirena Biological Station in Corcovado National Park, Costa Rica. I assessed parasitism levels by counting parasitoids directly (Hymenoptera: Torymidae) and also by examining ovules for irregularly shaped exit holes presumably made by parasitoids. The probability of fruits containing parasitoids increased by 3-times over time (although the number of parasitoids within parasitized fruits remained constant at ~ 120 per fruit). This suggests that fig wasps in later figs are more likely to be parasitized, which presumably decreases the fitness of the fig tree. Therefore, increased parasitism may have contributed to selection for the strikingly synchronous fruiting behavior of neotropical fig trees.

*Keywords:* Figs, *Ficus obtusifolia*, fig wasp, fig wasp parasitism, fruiting synchrony

## INTRODUCTION

Many plants provide consistent and predictable fruit rewards that promote the development of specialist seed dispersers. These dispersers in turn increase plant fitness by supplying reliable dispersal. One such example is the interaction between *Piper* species (Piperaceae) and bats in a tropical dry forest (Fleming, 1985). Most individual *Piper* plants produce new flowers continuously for 3-4 months and therefore tend to have flowers and fruits of all developmental stages at all times. This continuous supply of food attracts bats to the same plant every

day, which ensures the continued service of bats to plants and avoids the problem of disperser satiety. Although many other plants also utilize this fruiting strategy, it is not universal. Fig trees are conspicuous fruit producers in tropical forests that behave very differently. Individual fig trees occasionally produce large quantities of flowers that develop synchronously, leading to fruiting events that are localized (a single tree), unpredictable, and highly ephemeral (Janzen 1983). This results in associations with frugivores that lack recognizable community structure (Alexander et al. 2002). Arboreal and ground animals ranging

from spider monkey to red brocket deer, crested guan to white-nosed coati, and scarlet macaw to tapir, have been seen feeding simultaneously and unpredictably at fruiting fig trees.

Synchronous fruiting in figs may be adaptive with respect to seed dispersal. Because food resources are limited, large concentrations of high quality fruits are more likely to attract diverse dispersers than smaller concentrations. Fruiting synchrony may also be an adaptation to selectively attract generalist seed dispersers. Because figs are themselves generalists (Janzen 1983), they may generally benefit from being dispersed into diverse environments by an assortment of animals with varied behaviors.

However, it is also possible that synchronous fruiting behavior in figs is suboptimal and reflects constraints arising from other community interactions. For example, fruiting synchrony could be an evolutionary response to minimize the deleterious effects of fig wasp parasitoids. Every fig species has a species-specific obligate mutualism with a fig wasp species. These wasps are the sole pollinators of fig trees, and fig trees are the only host plants of fig wasp larvae. One problem for the fig wasps, and therefore the fig trees, is the deleterious effect of fig wasp larvae parasitoids. These insect parasitoids are often as abundant as fig wasps (Janzen 1983), and have the potential to exert strong selection

pressure on fig wasps and their fig mutualists. Assuming that female fig wasps are more attracted to higher concentration of fig flowers, and that fig flower abundance increases over the flowering period, fig wasp oviposition and larval abundance should increase over time. And if parasitoids are more likely to aggregate in fig trees containing more fig larvae (possibly identified by stronger chemical signals), parasitism should also increase over fruiting period. If so, fig wasp reproduction, and therefore fig tree fitness, should decrease over time, selecting for a shorter flowering and fruiting period in figs.

#### *Natural history of figs*

Fig flowers are pollinated by fig wasps in the family Agaonidae. Bearing pollen grains from another fig tree, a female wasp enters a very small, developing fig (known as a synconium) through a natural opening (ostiole). The insides of the fig are lined with hundreds of fully developed and receptive female flowers. Once inside, the female wasp moves from stigma to stigma and pollinates each floret while probing down the style with her ovipositor. If the style is short, she contacts the single ovule and lays an egg. If the style is too long, she cannot reach the ovule and lays no egg. Wasp eggs subsequently develop inside their fig ovule, feeding on and killing the seed. At the same time, parasitoid wasps

(Hymenoptera: Torymidae) may locate the fig synconia and oviposit through the synconium wall, parasitizing the developing fig wasp larvae. As the male fig wasps emerge from fig ovules, they copulate with the females within the fig (chiefly sisters) and die. When the newly mated females emerge within the synconia, they collect pollen from the recently matured male fig florets and exit to pollinate another fig tree, completing the fig wasp life cycle (Janzen 1983).

## METHODS

I located a fruiting fig tree ~ 80 m inland from the coastal end of the Rio Claro trail. It was 25 – 30 m tall with a dbh of 1.5 – 2 m and was probably *Ficus obtusifolia*, based on the size of the fruit, the size of the fruit sepals, and the lack of white spots on the skin (Quesada et al. 1997). I collected freshly fallen fig fruits from this tree on 5 occasions: 08:00 and 17:00 on 8 and 9 February, 2008, and again at 08:00 on 10 February.

I chose 10 - 15 freshly fallen undamaged green figs from each of the five samples and opened the fruits with an exactor knife in the laboratory. If adult parasitoids were present (black with an extremely long ovipositor), I waited for them to leave the fruit (seconds) and counted them on the lab bench. I then examined the inside of each fruit under a dissecting scope and counted developing

parasitoids (ones that were still inside the ovules), and fig wasps (brown with a slim body and lacking a conspicuous ovipositor). To study the fate of ovules and fig wasps within fruits, I randomly chose two subsets of 10 adjacent ovules within each fig, and classified each into one of the three following categories: seed, ovule with circular exit holes presumably made by a fig wasp (Janzen 1983), or ovule with irregular exit holes presumably made by a parasitoid. I also selected five figs representing a range of sizes to look for effects of fruit size on flower provisioning (number of flowers and proportion intended for fig wasps). I measured the two diameters of these fruits, and divided each fruit into 4 - 16 equal-sized sections. For one randomly selected section in each fruit, I counted the total number of male flowers, female flowers, and female flowers with exit holes. I then multiplied these numbers by the number of sections to estimate the totals for each fruit.

## RESULTS

Diameters of fig fruits ranged from 2 - 4 cm. Of the 64 study fruits, 15 had fig wasps and 32 had fig wasp parasitoids. When fruits were opened, fig wasps stayed inside and appeared to continue collecting pollen from male florets. In contrast, parasitoids quickly hopped out and away from the fig fruit (Figure 1).



Figure 1. Fig wasp parasitoids hopping out of a *Ficus obtusifolia* fig fruit near Sirena Biological Station in Corcovado National Park, Costa Rica.

Within figs, I observed developing and mature seeds, ovules with circular exit holes (presumably made by fig wasps), ovules with irregular exit holes (presumably made by fig wasp parasitoids), and male florets (Figure 2). Most mature seeds seemed to have shorter styles than ovules with exit holes, and appeared to be non-randomly concentrated near the synconia wall.

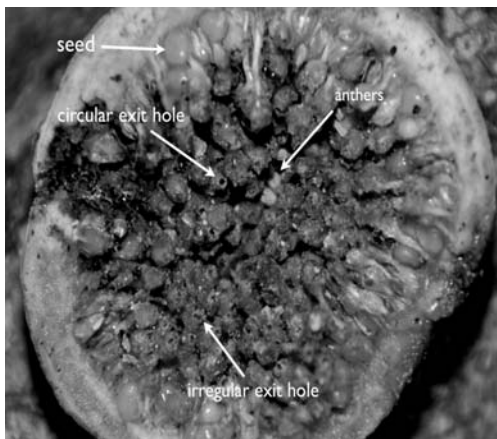


Figure 2. Inside of a *Ficus obtusifolia* fruit near Sirena Biological Station in Corcovado National Park, Costa Rica.

Fruits that ripened later were about 3-times more likely to be parasitized than fruits that ripened earlier (Figure 3). The probability of any fig fruit containing visible parasitoids increased over 48 hours from about 30% to about 90% ( $\chi^2 = 11.61$ ,  $df = 1$ ,  $P = 0.0007$ ). However, among the figs that were parasitized, the number of parasitoids per fig did not vary over time ( $F = 0.44$ ,  $df = 1, 33$ ,  $P = 0.51$ ,  $r^2 = 0.013$ , Figure 4). This suggests that the numbers of parasitic females and eggs were similar between fruits.

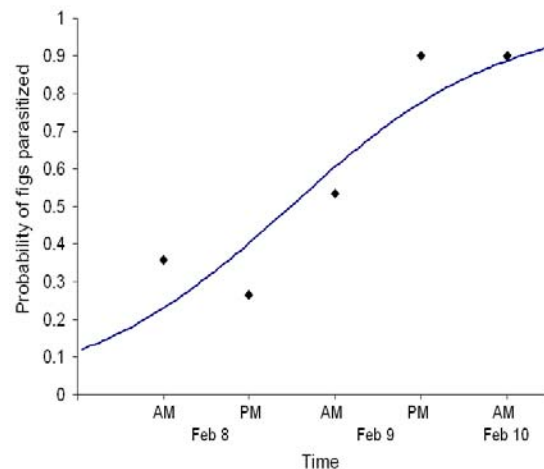


Figure 3. Proportion of figs that contained fig wasp parasitoids as a function of the time ripened fruit dropped to the ground. Data from a single *Ficus obtusifolia* tree near Sirena Biological Station in Corcovado National Park, Costa Rica:  $y = 1 - 1 / (1 + e^{-2.023 + 0.817x})$ .

Contrary to the direct counts of parasitoids, examination of exit holes in ovules revealed no relationship with time: number with irregular exit holes (putative parasitoids) vs. time ( $F = 1.96$ ,  $df = 1, 62$ ,  $P = 0.17$ ); number with regular exit holes (putative fig

wasps) vs. time ( $F = 3.26$ ,  $df = 1, 62$ ,  $P = 0.076$ ); and number of seeds per fig vs. time ( $F = 0.11$ ,  $df = 1, 62$ ,  $P = 0.74$ ; Figure 5). It was not easy to classify exit holes as made by fig wasps vs. parasitoids. Since the exit hole data was not at all consistent with the direct counts of parasitoids, I don't believe that the exit hole data can be reliably interpreted as measures of parasitoid abundance.

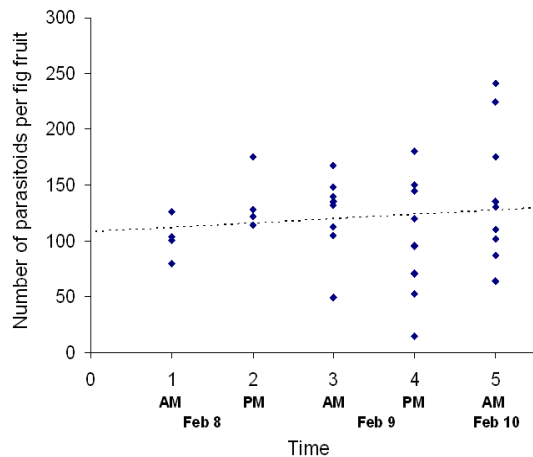


Figure 4. Number of parasitoids per parasitized fig fruit over time of a *Ficus obtusifolia* tree near Sirena Biological Station in Corcovado National Park, Costa Rica.

Individual fig fruits contained about 400 to 1000 flowers, depending on size. But regardless of size, there were ~10 times more female flowers than male flowers (Figure 6, upper). About 40-50% of female flowers had short styles (Figure 6, lower), presumably allocated by the plant to feed fig wasps.

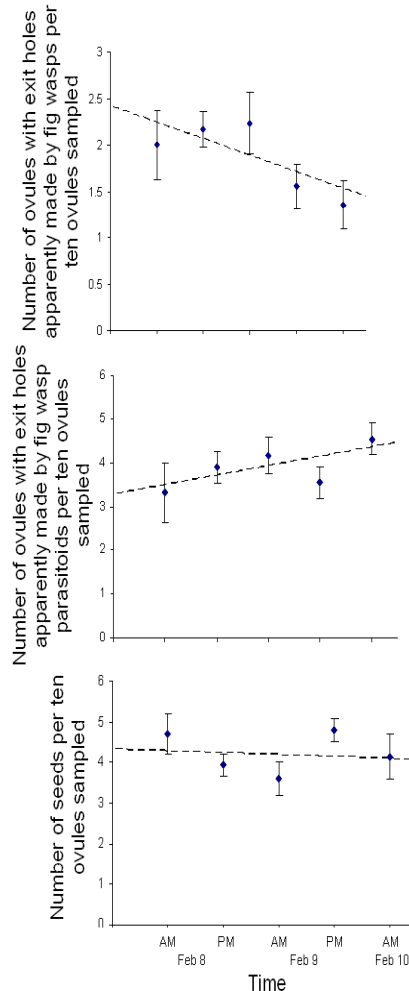


Figure 5. Number of ovules with exit holes apparently made by fig wasps (top), ovules with exit holes apparently made by parasitoids (middle), and seeds (bottom) per subsample of ten ovules over time of *Ficus obtusifolia* fruits near Sirena Biological Station in Corcovado National Park, Costa Rica. Mean  $\pm$  SE; dashed lines indicate insignificant linear regression models.

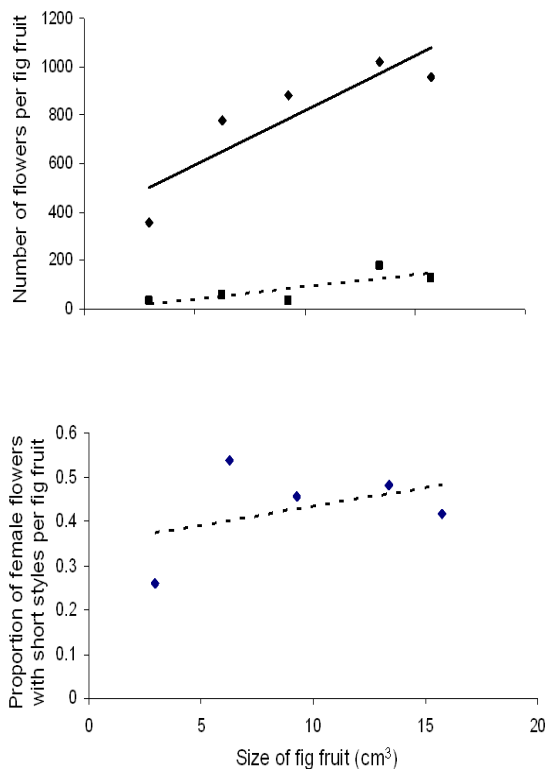


Figure 6. Number of male (top) and female (middle) flowers and proportion of female flowers with wasp exit holes (bottom) inside *Ficus obtusifolia* fruits near Sirena Biological Station in Corcovado National Park, Costa Rica. Solid vs. dashed lines indicate respective significant vs. insignificant regression models ( $\alpha = 0.05$ ).

## DISCUSSION

The surprisingly strong increase in fig wasp parasitism within fruits that matured 48 hours later than other fruits on the same tree was consistent with the hypothesis that fig wasp parasitoids could select for synchronous fruiting in figs. Because fig wasps are the sole pollinators of figs, the fitness of fig trees must be influenced by figs' success in producing female fig wasps that disperse pollen. If it is general that

late developing figs are more heavily parasitized, natural selection for increasing within-tree fruiting synchrony could be quite strong. However, because I only sampled one fig tree over a single fruiting period, further studies are needed to justify generalizing this pattern.

The skew sex ratio of flowers may result from fact that a female flower can produce only one seed where as a male flower can produce thousands of pollen grains. It could also be that investment in female fitness is more important because it is more certain than male fitness. Once pollinated, a female flower can develop immediately into a seed. In contrast, pollen has to travel long distances to a flowering plant of the same species before a seed can be produced.

Janzen suggested that the number of flowers intended for fig wasp larvae is optimized at 30-80% (1983), which is consistent with the 40-50% that we observed. However, Janzen did not seem to consider potential effects of fig wasp parasitoids on this optimum. In addition to selecting for increased within-tree fruiting synchrony, fig wasp parasitism may also affect the optimum proportion of female flowers allocated to fig wasp larvae. It may be that the optimum proportion would change from the earliest developing flowers to the latest developing flowers (even if fruiting is only over 2-3 days). Since higher

parasitism risk decreases fig wasp reproductive success, perhaps there would be selection for less female flowers to be allocated to fig wasps towards the end of the fruiting period.

Fruit size could also affect the optimal proportion of female flowers intended for fig wasps. It may be that figs can provide only as many ovules as the average number of eggs a female fig wasp lays. If so, the proportion of female flowers with short styles should decrease with increasing fruit size because larger fruits have more flowers. Alternatively, the ratio of short to long styled female flowers is genetically fixed and does not change with fruit size.

I was surprised to observe that most flowers that produced mature seeds had shorter styles than those with exit holes from fig wasps or fig wasp parasitoids. The conventional wisdom is that fig wasps oviposit in fig ovules with short styles (Janzen 1983). One possibility is that parasitism risk decreases towards the center of the fig, where fig wasp larvae are least accessible to female adult parasitoids that oviposit from outside the syconium wall. This gradient in larvae survival is likely to select for pollinator avoidance of outer ovules during oviposition, ensuring that some fig ovules will produce seeds (Dunn et al. 2008).

Fig wasp parasitism could be a significant selective force on the fruiting biology of fig trees. Because

synchronous fruiting in tropical trees is also evident in some non-figs, such as members of the Lauraceae family and *Dipteryx panamensis*, fig wasp parasitism cannot be the only ecological factor that favors this fruiting syndrome. However, selection from fig wasp parasitoids on pollination may be a partial explanation for the fleeting tumults of frugivory that accompany fig fruiting events in tropical forests (Alexander et al. 2002).

## REFERENCES

- Alexander, K. M., E. B. Close, and M. E. Harrison. 2002. An evaluation of community structure in the guild of vertebrates that exploit fruiting fig trees. *Dartmouth Studies in Tropical Ecology* 2002, pp. 89-94.
- Dunn, D.W., S.T. Segar, J. Ridley, R. Chan, R.H. Crozier, D.W. Yu, and J.M. Cook. 2008. A role for parasites in stabilising the fig-pollinator mutualism. *PLoS Biology* 6.3:1-7.
- Fleming, T. H. 1985. Coexistence of five sympatric Piper (*Piperaceae*) species in a tropical dry forest. *Ecology* 66:688-700.
- Janzen, D. H. 1983. Blastophaga and Other Agaonidae. Pages 696 - 700 in D.H. Janzen, editor. *Costa Rican Natural History*. University of Chicago Press, Chicago, Illinois, USA.
- Quesada, F. J. Q., Q. J. Madrigal, N.Z. Villalobos, R. A. Fernandez, and J.G. Ramirez. 1997. *Arboles de la*

Peninsula de Osa. INBio, San Jose,  
Costa Rica.