

TOP: *Ficus tremula* with figs receptive for pollination (left), cross-section of fig with a fig wasp pollinator female inside the central cavity (centre), and a magnified view of the pollinator 'ovipositing' down the style into the ovary, simultaneously depositing pollen on the stigmas with her forelegs.

Illustration: Simon van Noort.

ABOVE: Underside of the head of the fig wasp pollinator of *Ficus bubu*, *Courtella michaloudi* showing mandibles and mandibular appendages bearing many rows of backward pointing teeth that she uses to facilitate her entry into the fig through the ostiole (a tiny bract-lined opening at the apex of the fig).

Photo: Simon van Noort.

The ultimate challenge

How fig trees are pollinated

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Pollinators of plants can often be predicted, based on flower colour, fragrance and shape. White, fragrant flowers with a long corolla tube, for example, are usually pollinated by hawk moths, which are nocturnal and have a long tongue. Fig trees, however, are unique. Their flowers are completely concealed within the fig with hundreds of tiny florets lining the inside of a central cavity. Attempting to guess what pollinates figs and how the act is carried out would no doubt lead to the conclusion that the pollinator, as for many plant species, must be highly specialized. In fact, fig trees are completely dependent on tiny wasps, a couple of millimeters long, for their propagation and survival. These fig wasps are the sole pollinators of fig trees and in turn, fig wasps can breed nowhere else but inside figs, a relationship that is a classic example of an 'obligate mutualism' where neither party can survive without the other, and which has evolved over ninety million years.

Each species of fig tree is usually pollinated by one fig wasp species that is only associated with that fig species, a host-specific relationship that plays a major role in the prevention of hybridization between different species of fig trees. However, only 300 of a potential 750 fig wasp pollinator species are currently known (there are 750 species of *Ficus* in the world), and already we know that the one-to-one rule between fig tree and wasp does not always hold, so the interaction is not as well defined as initially appears. What the exceptions do tell us, however, is that we are dealing with a continually evolving dynamic system, the intricacies of which

we are only just beginning to understand.

How then do these tiny wasps that only live for a few days manage to perform their amazing task of finding and pollinating flowers that are hidden inside the fig? Female fig wasps, leaving the fig they have bred in, need to fly off in search of another fig tree to continue the reproductive cycle. This is often a long and arduous journey that only a few out of thousands manage successfully. This remarkable feat is achieved by homing in on host tree-specific 'volatiles' (a chemical signal released by the fig when it is receptive for pollination).

Completion of this journey is the first test of endurance, as once the fig wasp has located a receptive fig, she needs to circumvent the next barrier. The only link the fig cavity has to the outside world is through a tiny bract-lined opening at the apex of the fig, called the ostiole, and it is by means of this passage that the pollinating fig wasp gains access to the florets. Negotiating the ostiole is no easy task, with the female wasp having to squeeze and labour her way between the tightly closed bracts. She is, however, remarkably adapted to do so. Her body, in particular her head and thorax, is extremely flattened and elongate. She also has row upon row of backward pointing teeth on her mandibular appendage, situated on the underside of her head, as well as a few

strong teeth on her legs. These teeth assist her progress through the ostiole and also prevent her slipping backwards. Nevertheless, the process of gaining access to the fig cavity is so difficult that her wings and antennae usually break off in the ostiole, but this fortunately does not influence her pollinating or egg-laying ability.

The female wasp then proceeds to lay eggs in the ovules of some of the florets, and to pollinate the stigmas at the same time. This she does by inserting her long ovipositor down the inside of the style. The florets that have styles longer than the wasp's ovipositor are pollinated, but no eggs reach the ovule and hence these florets set seed. The wasp larvae feed on the endosperm tissue in the galled ovary (where the eggs were laid) and the larvae take anything from three to twenty weeks to develop, depending on the season.

Once the wasps have reached maturity they chew their way out of the galls and emerge into the fig cavity at much the same time. The wingless males mate with the females before chewing a hole through the fig wall to the exterior to allow the females to escape - the male's only two functions in life, as he dies soon afterwards! The females either actively load up pollen from ripe anthers into special pollen pockets, or in some species, they passively become covered with pollen, before emerging from the fig in search of young recep-

tive figs to complete the cycle.

Once the female fig wasps have left the fig, it ripens, changing colour and smell, and becomes attractive to seed or fruit eating birds, bats, monkeys and even lizards. Fig trees are considered to be keystone species in many tropical and subtropical ecosystems, because of their all year round production of figs, providing food in seasons when other fruiting trees do not. Fruit eating animals help to disperse the seeds.

Besides the pollinators there is a suite of non-pollinating fig wasps that also breed in figs, but which play no role in the pollination process. From the fig's perspective they are unwanted interlopers. In Africa, as many as thirty species of non-pollinating fig wasp can be associated with a particular fig tree species, as in *Ficus thonningii*, but more commonly three to fifteen species are associated with each fig species. One group of non-pollinators also enter the fig to lay eggs, and exhibit parallel morphological adaptations to those of the pollinators for getting through the ostiole.

Most of the non-pollinators, however, lay eggs by inserting their ovipositor through the fig wall from the outside of the fig. These wasps often have extremely long external ovipositor 'tails', the length of which has been evolutionarily determined by the thickness of the fruit wall of their host fig

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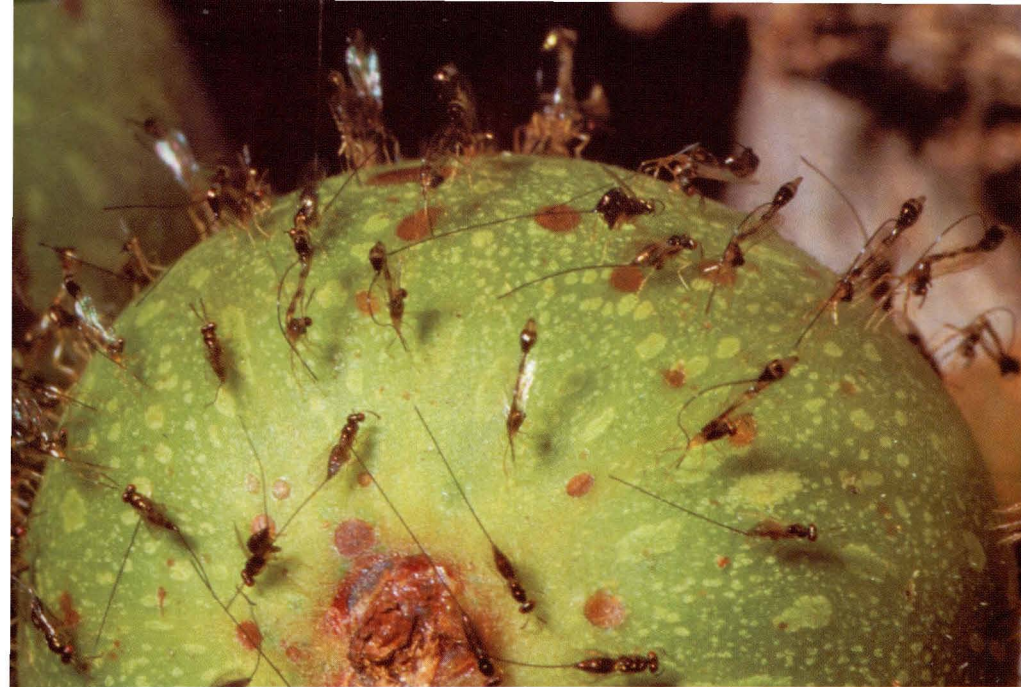
RIGHT: The fig wasp *Courtella wardi*, pollinator of *Ficus tremula*, the female at top and male below.

Illustration: Simon van Noort.

FAR RIGHT: A fig wasp, *Ceratosolen capensis*, female emerging from her natal gall within the cavity of *Ficus sur*.

Photo: Simon van Noort.





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TOP: Females of the non-pollinating fig wasp, *Apocrypta guineensis*, laying eggs through the fig wall of *Ficus sur*. ABOVE LEFT: Three non-pollinating fig wasps. *Philocaenus* (top) enters the fig to lay eggs, *Sycoryctes* (centre) has a long ovipositor for laying eggs through the fig wall, and *Otitesella* (below) also lays eggs through the fig wall, but the ovipositor is concealed within the body. ABOVE RIGHT: *Philocaenus rotundus* (a non-pollinating fig wasp that enters the fig) laying eggs inside a receptive *Ficus abutilifolia* fig that has been split open. Photos and illustrations: Simon van Noort.

species. Fig size varies tremendously across species, from smaller than a marble to as large as a tennis ball.

Given the short life span of the adult pollinating fig wasps and the lack of synchrony of fig production, how then is the relationship maintained? Usually on emergence the female wasps have to leave the tree they bred on, because the figs in a particular crop are normally all at the same stage of development. Some species, however, have figs at different stages of development within the same crop and in these cases the

female wasp has only to fly a short distance to locate a receptive fig.

The cycling of the mutualism can, therefore, continue on the same tree. More commonly the cycling phenomenon relies on the presence of a suitably sized population of trees of a particular species in a given area, so that somewhere within the population there will be a tree with figs that are receptive for pollination. The lack of synchrony in fig crop production between trees is an essential trait to ensure this. If all the trees in a population produced figs at

the same time, the fig wasp population would die out.

Local extinctions of wasps do occur, when they are not able to locate a tree with figs in the receptive phase, and there will also be abortions of fig crops that pollinators have not managed to locate.

Nevertheless, in the larger picture this is a very successful interaction, which is borne out by the high diversity of both fig trees and fig wasps.

For more about figs and fig wasps, visit the website at www.figweb.org.

Further reading

Burrows, J. & Burrows, S. (2003). *The figs of southern & south-central Africa*. Umdaus, Pretoria. Includes a chapter on the interaction of fig wasps and figs by the author of this article. For more further reading material, contact the Editor at voget@kinglsey.co.za.