

Vicarious selection explains some paradoxes in dioecious fig–pollinator systems

A. GRAFEN¹ AND H. C. J. GODFRAY²

¹ *Department of Plant Sciences, University of Oxford, South Parks Road, Oxford OX1 3RA, U.K.*

² *Department of Biology and NERC Centre for Population Biology, Imperial College at Silwood Park, Ascot, Berkshire SL5 7PY, U.K.*

SUMMARY

Fig trees (*Ficus* spp.) are pollinated by small hymenopteran wasps that develop within the fig. In dioecious species, female wasps enter and pollinate ‘female’ figs that produce only seeds and within which the wasp is unable to reproduce. A resolution for three paradoxes in the biology of dioecious fig–pollinator systems is suggested: (i) why wasps enter female flowers, (ii) why they maintain structures and behaviours needed to pollinate female figs, despite the absence of any direct selection on these phenotypes and (iii) why wasps entering male flowers go through the behaviours that would be required to pollinate female figs. Whereas it is obviously in a female fig’s interest to conceal her sex from the wasps, it is argued that it is also in a male fig’s interest to do so, because the male will benefit only from raising female wasps that, when they leave, successfully find, enter, and pollinate female figs (even though this will be fatal to the wasps).

The remarkable association between fig trees (*Ficus*: Moraceae) and their wasp pollinators (Agaonidae: Hymenoptera, Chalcidoidea) is well known, and has recently been the subject of much interest (Hamilton 1979; Janzen 1979; Frank 1984; Kjellberg & Valdeyron 1984; Herre 1985, 1987; Kjellberg *et al.* 1987; Murray 1987; Godfray 1988; Bronstein 1988*a, b*). Whereas most work has concentrated on monoecious fig trees, the subject of his paper is the subtle and surprising interactions of the conflicts of interest between fig trees and wasps in dioecious species. We argue that dioecious fig–pollinator systems show mutual mimicry between male and female figs and that male figs can be said to impose on wasps vicarious selection pressures appropriate to their behaviour in female figs. Before developing this argument, we briefly describe the natural history of fig pollination.

The fig, or syconium, is an inflorescence in which the flowers line the inside of a hollow cavity formed by a fleshy receptacle. There are three types of flowers: male flowers, female flowers that develop into seeds and female flowers that provide sustenance for pollinating fig wasps. In monoecious species, all three flower types are present in every fig. In dioecious species, the subject of this paper, ‘female’ trees bear figs containing only seed-producing female flowers whereas ‘male’ trees bear figs containing both male flowers and female flowers that support fig wasps (strictly these species are gynodioecious as ‘male’ trees contain female flowers although seeds are not normally produced). In dioecious species, female fig wasps carrying pollen enter male and female syconia through a small pore or ostium. In passing through the narrow pore, they lose their wings and never leave the fig. Inside a female

fig, the wasp pollinates seed-producing flowers but is unable to oviposit and dies without progeny (figure 1). Inside a male fig, the wasp both pollinates and oviposits into flowers that allow the development of larval wasps. When the progeny of the pollinating wasp emerge as adults, they mate among themselves and then the females, but not the males, leave the fig, either through the ostium or through a hole dug by the male wasps. Before leaving the fig, the female wasps collect pollen from a ring of male flowers around the ostium.

There are two apparent paradoxes in the dioecious fig–pollinator system (figure 1). The first is why wasps enter female figs. They pollinate the fig, and then die, unable to lay eggs. Why should they be selected to enter an evolutionary graveyard, and while there engage in complex behaviour designed to ensure the reproduction of the fig tree? Any mutations allowing wasps to avoid entering female figs would surely be favoured and genetic drift leading to the degeneration of the complex behaviour needed to ensure pollination would not be countered by selection.

The second paradox concerns the pollen-carrying behaviour of the female wasps. Before leaving the fig in which they emerged as adults, each female engages in the complex behaviour of filling special structures on her thorax or legs with pollen (Galil & Eisikowitch 1969; Ramírez 1969). The pollen is used to fertilize the modified female flowers in which the wasp larvae develop in the male fig. It appears that fertilization is a prerequisite for the successful production of the gall in most fig tree species (see, for example, Galil & Eisikowitch (1968*a*)) although some non-pollinating wasp species have evolved the ability to develop in unfertilized figs (Galil & Eisikowitch 1968*b*; Galil *et al.*

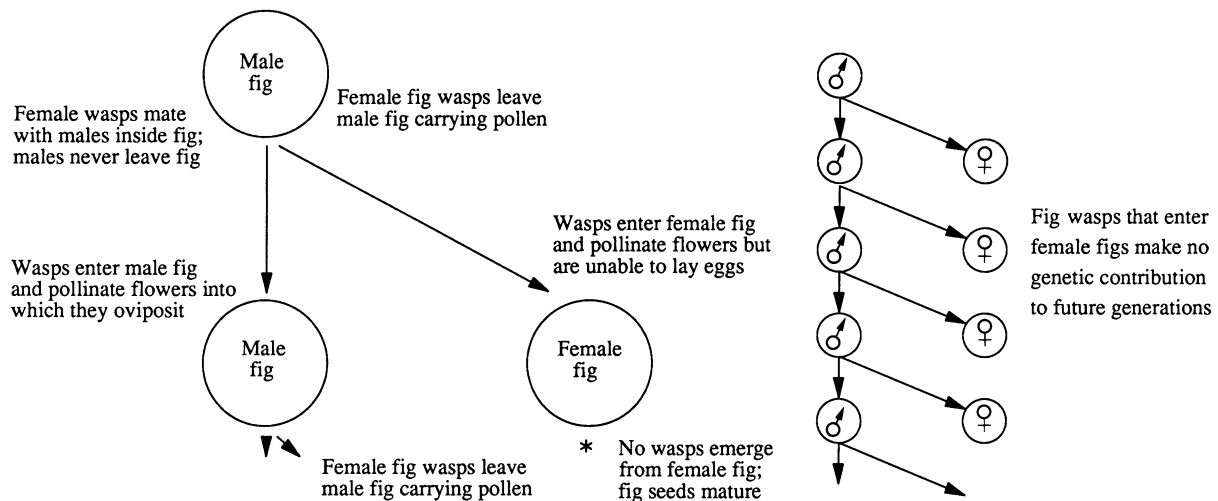


Figure 1. Schematic representation of the dioecious fig-pollinator interaction. The ancestors of a wasp have only experienced male figs yet the whole symbiosis depends on wasps possessing appropriate morphological and behavioural adaptations for being in female figs.

1970). The paradox appears when we consider the fate of a mutation expressed in the male fig tree that allows the growth, in the absence of pollination, of the plant tissue fed on by the wasp larvae. This mutation would be favoured, as it would increase the fig tree's production of pollinators: wasps that had failed to collect pollen, or had run out of pollen, would still be able to reproduce and their progeny would act as pollen vectors. Once reproduction by the male fig tree no longer required fertilization mediated by the wasp, selection would act on the wasp to omit the collection and transport of pollen, activities that probably carry some fitness costs, and the special pollen-bearing structures of the wasp would then be lost. Examples of the latter evolutionary sequence are known from agaonid wasps that parasitize the normal fig-wasp mutualism and which have identical life histories with the exception of pollen transfer (see, for example, Bouček *et al.* 1981). These examples show that there is a real paradox about why all the fig-wasp systems do not break down in this way.

A tempting explanation of both paradoxes is that if wasps and fig trees did do what it seems they should, then both would go extinct. So a species-selection argument would be that we see only those cases where relevant variation has not arisen. This is unlikely, as dioecy exists throughout high level taxa in the Old World. A more complex group-selection argument could no doubt be constructed that revolved around local extinctions and re-invasions. We now argue that these explanations are unnecessary, and that straightforward, though subtle, selection pressures exist that resolve both these paradoxes.

Beginning with why wasps enter female figs, we consider the evolutionary interests of male and female fig trees separately, and show that each sex is selected to mimic the other. A female fig must be entered by a wasp in order to be pollinated, and so is selected to mimic male figs, which wasps are selected to enter (Valdeyron & Lloyd 1979; Janzen 1979). More surprisingly, a male fig is selected to mimic a female fig.

At first sight, it might be expected that male and female figs would compete with each other for wasps, leading to male figs advertising their maleness. However, the interests of the male fig tree are served only by those of the wasps it produces that enter female figs, and so, on the principle that offspring wasps will resemble their parents, the male fig gains if it looks like a female fig and attracts only those wasps which would readily have entered a female fig. This selection for mutual mimicry will mean that male and female figs will become as similar as necessary to ensure that wasps do not reliably discriminate against female figs.

An additional argument is that wasps are unlikely to be selected to use discrimination abilities that are less than perfect. Only a very small proportion of wasps find a fig and reproduce (Janzen 1979), and so a wasp would prefer to enter a fig, even if it is probably a female, as the chances of finding a male fig are so small. In an important study of the European fig *Ficus carica*, Kjellberg *et al.* (1987) showed that male and female figs were receptive at different times of the year and that there was thus no selection on wasps to discriminate between male and female figs. In at least some tropical species, male and female figs are present simultaneously (Godfray 1988) although further work is needed on the phenology of dioecious figs to assess the importance of the temporal staggering of male and female figs (Kjellberg & Valdeyron 1984).

The second paradox has a parallel resolution. The reproductive interests of male fig trees are served only by those wasps it produces that subsequently enter a female fig, and there behave appropriately. By demanding from the wasps that enter it all the behaviour that would have been required in a female fig, the male fig ensures that the mothers of the wasps it produces behave appropriately. This is especially important for the behaviour that potentially has no function in the male fig, such as the complex behaviour required of the wasp to ensure efficient pollination. The male fig can be said to be imposing vicarious selection on the wasps.

Developing fig wasp larvae feed on the endosperm of pollinated flowers within male figs. The female origin of flowers supporting pollinators can be demonstrated by their experimental fertilization in the absence of fig wasps which leads to the formation of seeds (Galil & Neeman 1977). Our explanation of the maintenance of pollination would be redundant if it is impossible for mutations expressed in male figs to liberate the tree from the necessity of pollination. We suspect that this hard constraint does not exist as endosperm tissue can be reproduced without fertilization by autonomous apomixis in many Compositae (Johri 1984; Richards 1986). There are also parthenogenetic varieties of the European fig. Of course, the contemporary necessity of pollination is not evidence for such a constraint as it is also predicted by our arguments. In some species, seeds are sometimes found in male figs that are entered by pollinators (Valdeyron 1967; Muenchow & Grebus 1989). Our arguments would also need to be modified if it were shown that reproduction through seeds made a significant contribution to the fitness of male fig trees.

These arguments also explain how evolution can occur in circumstances where selection would seem to be irrelevant. Suppose the morphology of the female fig changed for some reason and that this required a modification in the behaviour or the structure of the wasp for the continued efficient pollination of the seeds. This change in fig morphology could be the result of many different selection pressures, for example selection imposed by the mammalian or bird seed dispersers. Let us suppose that the wasp needs a longer ovipositor, with appropriate behavioural modifications, to improve its reproductive potential. How can selection change wasp morphology or behaviour in female figs when no wasp or its progeny ever emerge from female figs? Among the male figs, those that required longer ovipositors would be more successful in transferring pollen to female figs. Male figs would thus evolve to resemble female figs, or, at least, to require the same behavioural and structural modifications in the wasps that are needed to exploit female figs. Selection on female figs is therefore transferred to male figs, and vicarious selection on wasps in male figs brings about adaptation to the female fig.

In the millions of years for which dioecious figs have existed, the behaviour and morphology of wasps in female figs must have changed many times, just as details of most biological systems are forced to adapt to changing circumstances. If the behaviour and morphology pertaining to the wasp's role in female figs really could not be selected in wasps, then the survival of fig and wasp species would be seriously compromised. We thus disagree with Kjellberg *et al.* (1987) that the behaviour of wasps in female figs remains adapted only through the absence of selection. If this were the case, neutral drift would cause a slow but inevitable deterioration in all the behaviours and structures that were peculiar to the wasp's role in the female fig.

It is not difficult for male figs to be similar to female figs, and to apply the necessary vicarious selection. The male and female trees are, at the least, genetically very similar. The selective force on male figs ensures that

while some differences are necessary if the two types of fig are to function differently, males retain the ability to detect whether they would have been successfully fertilized, had they been female.

We have used the term 'vicarious selection' to mean selection relevant to one situation being 'artificially' imposed in a second situation through the action of another organism, and there are many potential examples. The dioecious fig-pollinator system, however, has two features that to our knowledge are without parallel in nature. Vicarious selection maintains in the wasps complex adaptations that make sense only in terms of their role in female figs, a role never experienced by any of the wasp's ancestors. The very existence of both fig and wasp species depends on the continued existence of those adaptations and therefore of the vicarious selection underlying them.

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REFERENCES

- Bouček, Z., Watsham, A. & Wiebes, J. T. 1981 The fig wasp fauna of the receptacles of *Ficus thonningii* (Hymenoptera, Chalcidoidea). *Tijdschr. Entomol.* **124**, 149–233.
- Bronstein, J. L. 1988a Limits to fruit production in a monoecious fig: consequences of an obligate mutualism. *Ecology* **69**, 207–214.
- Bronstein, J. L. 1988b Mutualism, antagonism and the fig-pollinator interaction. *Ecology* **69**, 1298–1302.
- Frank, S. A. 1984 The behaviour and morphology of the fig wasps *Pegoscapus assuetus* and *P. jimenezae*. Descriptions and suggested behavioural characters for phylogenetic studies. *Psyche* **91**, 289–308.
- Galil, J. & Eisikowitch, D. 1968a On the pollination ecology of *Ficus religiosa* in Israel. *Phytomorphology* **18**, 356–363.
- Galil, J. & Eisikowitch, D. 1968b On the pollination ecology of *Ficus religiosa* in East Africa. *Ecology* **49**, 259–269.
- Galil, J. & Eisikowitch, D. 1969 Further studies on the pollination ecology of *Ficus sycomorus* L. *Tijdschr. Entomol.* **112**, 1–13.
- Galil, J. & Neeman, G. 1977 Pollen transfer and pollination in the common fig (*Ficus carica* L.). *New Phytol.* **79**, 163–171.
- Galil, J., Dulberger, R. & Rosen, D. 1970 The effects of *Sycophaga sycomori* L. on the structure and development of the syconia in *Ficus sycomorus* L. *New Phytol.* **69**, 103–111.
- Godfray, H. C. J. 1988 Virginité in haplodiploid populations: a study on fig wasps. *Ecol. Entomol.* **13**, 283–291.
- Hamilton, W. D. 1979 Wingless and fighting males in fig wasps and other insects. In *Sexual Selection and Reproductive Competition in Insects*. (ed. M. S. Blum & N. A. Blum), pp. 167–220. London: Academic Press.
- Herre, E. A. 1985 Sex ratio adjustment in fig wasps. *Science, Wash.* **228**, 896–898.
- Herre, E. A. 1987 Optimality, plasticity and selective regime in fig wasp sex ratios. *Nature, Lond.* **329**, 627–629.
- Janzen, D. H. 1979 How to be a fig. *A. Rev. Ecol. Syst.* **10**, 13–51.
- Johri, B. M. 1984 *Embryology of angiosperms*. Berlin: Springer Verlag.

- Kjellberg, F. & Valdeyron, G. (ed.) 1984 *Minisymposium: figs and fig insects*. Montpellier, France: CNRS.
- Kjellberg, F., Gouyon, P.-H., Ibrahim, M., Raymond, M. & Valdeyron, G. 1987 The stability of the symbiosis between dioecious figs and their pollinators: a study of *Ficus carica* L. and *Blastophaga psenes* L. *Evolution* **41**, 693–704.
- Muenchow, G. E. & Grebus, M. 1989 The evolution of dioecy from distyly: reevaluation of the hypothesis of the loss of long-tongued pollinators. *Am. Nat.* **133**, 149–156.
- Murray, M. G. 1987 The closed environment of the fig receptacle and its influence on male conflict in the old world fig wasp *Philotrypes pilosa*. *Anim. Behav.* **35**, 488–506.
- Ramírez, W. 1969 Fig wasps: mechanism of pollen transfer. *Science, Wash.* **163**, 580–581.
- Richards, A. J. 1986 *Plant breeding systems*. London: George Allen & Unwin.
- Valdeyron, G. 1967 Sur le système génétique du figuier, *Ficus carica* L. Essai d'interprétation évolutive. *Annls Inst. natn. agron., Paris* **5**, 1–167.
- Valdeyron, G. & Lloyd, D. G. 1979 Sex differences and flowering phenology in the Common Fig, *Ficus carica* L. *Evolution* **33**, 673–685.

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