Partial avoidance of female inflorescences of a dioecious fig by their mutualistic pollinating wasps

Marie Charlotte Anstett, Marc Gibernau and Martine Hossaert-McKey*

CNRS-CEFE, 1919 Route de Mende, 34293 Montpellier Cedex 5, France

Every dioecious species of fig is pollinated by a specific wasp that only reproduces within the inflorescences of male trees. Pollinators usually die within the closed urn-shaped inflorescence (fig or syconium) they visit. Thus pollinators that enter female syconia allow seed production but die without reproducing. In a previous study, pollinators of one dioecious fig where male and female trees flower synchronously, *Ficus hispida*, did not exhibit differential attraction or choice between inflorescences of the two sexes. Here we show that *Blastophaga psenes*, the pollinator of another dioecious species of different lineage, the common fig (*F. carica*), significantly avoided female syconia, when we experimentally induced a situation of choice. Paradoxically, choosiness can be demonstrated in *F. carica* where usually wasps do not face a choice because male and female trees do not flower synchronously. We discuss how the mutualism may be stable despite this discrimination and hypothesize why the two species of fig-pollinators exhibit different behaviour on dioecious figs.

Keywords: symbiosis, coevolution, *Ficus*, pollination by deceit, mutualism

1. INTRODUCTION

In plant–pollinator interactions, pollinators visit flowers to exploit rewards offered by plants (Pyke 1981; Simpson & Neff 1983; Waser 1983), and in doing so, may incidentally pollinate the flowers they visit. In nearly all plant–pollinator interactions, pollinators have no individual advantage in pollinating flowers. Thus the probability of pollen deposition after one visit greatly varies with pollinator species (e.g. see Herrera (1987) for insect pollinators). At one extreme, some flower visitors are cheaters and collect rewards without pollinating (Inouye 1980; Waser 1983). At the other extreme, some plants offer no reward to their insect pollinators (e.g. Dafni 1984; Alexandersson & Ågren 1996; Schemske *et al.* 1996), or even kill them (e.g. *Nymphaea* sp., Faegri & Van der Pijl 1971). Pollinators should thus be selected to avoid these plants or to learn how to avoid them. However, various systems of pollination by deceit are documented (Dafni 1984; Faegri & Van der Pijl 1971; Little 1983; Schemske *et al.* 1996). Pollinators of these plants often depend on many resources other than the deceitful plant. In these systems, the deceit may continue to work because the mimic is rare relative to resource-offering models (Lavery 1992). Deceptive pollination is frequent in dioecious species (one-third of tropical angiosperms: Renner & Feil 1993). Usually, in these dioecious species, pollinators only get rewards when visiting male flowers (e.g. Bawa 1980; Ågren *et al.* 1986; Renner & Feil 1993). Female flowers are thus selected to

mimic male flowers and dupe pollinators to ensure seed production. In these cases as well, deceitful plants constitute only a part of the spectrum of resources exploited by these generalist pollinators, and stability of the pollination system may be enforced by the low frequency of mimics relative to models. Encounters are not sufficiently frequent to lead to learning, or, over evolutionary time, to programmed avoidance of deceivers.

Pollination by deceit also characterizes the dioecious species of the genus *Ficus* (Moraceae), setting them apart from the monoecious species. In contrast to most other dioecious species with pollination by deceit, however, the pollination system of figs is quite unique in being species-specific for both partners. The sole pollinator of each species of figs is an agaonid fig wasp, each species of which uses only one fig species for reproduction. Within a dioecious fig species, male inflorescences offer the only breeding site for the wasps, while female inflorescences function as deadly traps (Valdeyron & Lloyd 1979; Gibernau *et al.* 1996). Even if some pollinators may exit the first inflorescence (fig or syconium) they visit and sometimes enter a second one (Gibernau *et al.* 1996), they cannot move among trees since the wasps lose their wings when entering the first syconium. The cost of a mistake for the individual pollinator is thus very high. Selection, then, should favour avoidance of female inflorescences by pollinators of dioecious figs, but this has not generally been found (Patel *et al.* 1995). Why, then, do pollinators of dioecious figs not avoid female inflorescences?

In a previous study of fig pollinator choice between male and female syconia, Patel *et al.* (1995) showed that pollinators of *Ficus hispida* L. do not discriminate between

*Author for correspondence

(hossaert@srvlinux.cefe.cnrs-mop.fr).

male and female syconia. In another lineage of dioecious figs (e.g. *Ficus carica* L., the common fig), because of the peculiar seasonal phenology of the trees, male and female syconia are almost never attractive to pollinators at the same time of year (Kjellberg *et al.* 1987). For these seasonal dioecious species (such as *F. carica*), flowering asynchrony between sexes has been considered to be sufficient to prevent the evolution of wasp discrimination between male and female syconia (Kjellberg *et al.* 1987; Patel *et al.* 1995).

In this paper, we present results of choice experiments where we induced, under field conditions, flowering synchrony of inflorescences of both sexes of *Ficus carica*. Since in natural conditions the number of foundresses greatly varies (Bronstein & Hossaert-McKey 1996), an experimental approach is essential. When male and female syconia are synchronous, pollinators of *F. carica* are in fact able to discriminate between inflorescence sexes. We will then discuss evolutionary scenarios to explain why the behaviour of the pollinator of *F. carica* (*Blastophaga psenes* L.) is different from that of *F. hispida* (*Ceratosolen marchali* Mayr).

2. MATERIALS AND METHODS

Ficus carica has a circum-mediterranean distribution where it is exclusively pollinated by *Blastophaga psenes* (Chalcidoidea: Agaonidae: Agaoninae). Fig flowers are enclosed within an urn-shaped inflorescence, the syconium (or fig; but to avoid any confusion we will use the term 'fig' only to designate the tree). Mutualistic wasps associated with fig trees have to make their way through the entrance hole of the syconium, the ostiole, losing their wings and parts of their antennae. Syconia of female trees bear only female flowers, but each syconium of 'male' trees contains both male and 'female' flowers. However, since female flowers of male figs almost never set seed (Valdeyron & Lloyd 1979; Weiblen *et al.* 1995), producing instead only pollen-carrying wasps, the reproductive system is functionally dioecious despite a gynodioecious morphology (Kjellberg *et al.* 1987; see Anstett *et al.* (1997) for a comparison with monoecious fig species).

During winter, wasp larvae develop within male syconia of *F. carica*. Each larva develops within a gall found in the ovary of a female flower. In early May, male wasps mate with female wasps just before they emerge from their gall. Male wasps are wingless and die within their natal syconium. Mated female wasps exit their natal syconium (without pollen since male syconia of the winter crop do not produce pollen). They are attracted to receptive syconia by volatile chemicals produced by the inflorescence (Van Noort *et al.* 1989; Hossaert-McKey *et al.* 1994). Female syconia are never receptive at this time of the year. Thus female wasps enter a new receptive male syconium (usually on the same male tree) where they lay eggs in the ovaries of 'female' flowers. The new generation of wasps emerge from their galls in July. Emerging female wasps get loaded with pollen when leaving their natal syconium. At this time, only syconia on female trees are receptive. Thus female wasps enter female syconia and deposit pollen, ensuring seed production. However, female flowers of female trees have a very long style and a different ovary structure (Verkerke 1987) and these traits prevent wasps from laying eggs within female syconia. A pollinator wasp which enters a female syconium loses its wings, cannot move to another host tree, and thus dies without reproducing. In August, new male syconia are receptive. The last

emerging wasps enter these syconia, where they lay eggs, ensuring the survival of the wasp population (Kjellberg *et al.* 1987).

We performed wasp choice experiments between male and female syconia at the Centre d'Ecologie Fonctionnelle et Evolutive (CEFE), Centre National de la Recherche Scientifique experimental garden in Montpellier (France). In France, only parthenocarpic varieties, which do not need pollination to set fruits, are cultivated, but there are very few orchards. Wild fig individuals are mainly used in private gardens in the area near Montpellier. Thus, artificial selection on figs or on wasps is negligible. All trees in our experimental garden are either wild ones or descendants of controlled crosses between wild individuals. As stated above, male and female syconia are not usually receptive at the same time of the year. To obtain receptive male syconia in July, when female syconia are receptive, we induced precocious development by cutting the terminal bud of branches on male trees in May. This treatment releases the apical dominance of the terminal bud and permits precocious development (and receptivity) of male syconia (normal male receptivity is in August). However, the response to this treatment is quite variable (e.g. in 1996 only 60% of the branches treated bore receptive male syconia suitable for use in our experiments). It is conceivable that the treatment used to obtain out-of-season male figs could have an effect on odour production. However the most likely effect would be a reduction in odour production. Such a situation would only make our test more conservative. In any case, the figs produced by manipulated branches of male trees appeared similar (in size and all other respects) to male figs produced naturally. All male syconia and branches on female trees were bagged prior to receptivity to avoid uncontrolled wasp visit.

On the morning of a sunny day with no wind, receptive syconia (haphazardly chosen) were placed, still attached to their branch, in water-filled vases. We then placed the vases on the ground, around a tree which wasps were leaving. When receptive, there is no apparent visual external difference between male and female syconia. Vases were placed every metre, on one curved line, at 1.5 m from the tree foliage, alternating vases with male and vases with female syconia. At the end of the day (always before 1930 h) we counted the number of female wasps present in the water, on the branches, on each syconium, and within each syconium. When possible, the duration of the experiment was chosen to be short enough to avoid any exit of pollinators (it was found, for *F. aurea*, that exit of pollinators never occurred in the first 10 h after experimental wasp introduction (Anstett 1994)). Moreover, no wingless females were observed outside the syconia, showing that, in fact, they did not have time to re-exit in the experiments presented here.

Since female wasps present on a receptive syconium almost always enter it, and since this number was always small, we calculated the number of foundresses per syconium as the number of wasps within and on each syconium. We also calculated the number of wasps in each vase (in water + on branches) and the total number of wasps per vase (foundresses + in water + on branches). This experiment was performed four times, with slight differences owing to the restrictive conditions for conducting such choice experiments e.g. the need to obtain precocious receptive male syconia exactly synchronous with receptive female syconia and to have good weather conditions (no rain and no directional wind).

Experiments were performed on July 6–7, 1992 (experiment 1, $n_1=23$ female syconia in eight vases and $n_2=21$ male syconia in

seven vases); on July 10, 1992 (experiment 2, $n_1=21$ female syconia in seven vases and $n_2=25$ male syconia in eight vases); on July 19, 1993 (experiment 3, $n_1=26$ female syconia and $n_2=24$ male syconia; for this experiment receptive syconia were placed in individual vases); and on July 17, 1996 (experiment 4, $n_1=36$ female syconia in 12 vases and $n_2=39$ male syconia in 13 vases). Experiment 1 lasted two days because of heavy rain in the afternoon of July 6th that prevented wasp visitations. Thus re-exiting of pollinators was possible but because most vases overflowed with water, it was impossible to check for wingless, re-exited females. Thus we did the analysis of the results of this experiment on the number of visited syconia based on the brownish colour of probed styles. For experiments 2 and 3, all pollinators were found inside the syconium cavity and none in the water nor on the syconium surface.

3. RESULTS

If an individual syconium is not visited, it can remain receptive for two to three weeks (Khadari *et al.* 1995). During this period it continues to grow rapidly. Thus syconium diameter is a rough indicator of the phase of receptivity (Anstett *et al.* 1996) and of the quantity of chemical attractants produced (M. Hossaert-McKey, unpublished data). Syconium attraction increases, then decreases, during receptivity (Patel *et al.* 1995), a feature probably linked to the quantity of chemical attractant produced by individual syconia. It is thus important to determine whether we used in our experiments the whole range of syconium receptivity or at least a comparable range for each sex. In all experiments, there was no difference in the mean diameter of male and female syconia (table 1; figure 1 for the shape of size distribution in experiment 4). Figure 1 shows the mean number of foundresses per syconium for the different diameter classes and for both sexes for experiment 4. Both curves have an overall bell-like shape, showing that we effectively used the whole range of diameter and receptivity for each sex. The same pattern was observed in all the experiments.

In all experiments, a higher total number of foundresses was found in male syconia (table 1), pollinators being more abundant in the fourth experiment, where we captured a total of 234 pollinators, 187 (80%) in male syconia (mean number of foundresses $\pm$ s.e., 4.8 ± 1.3), and 47 (20%) in female syconia (mean number of foundresses $\pm$ s.e., 1.3 ± 0.4). Male syconia tended to have a higher mean number of foundresses in all experiments. However, because of a position effect of the number of foundresses, leading to many vases with zero foundresses, direct tests of comparisons of means cannot be performed. To control for this position effect around the experimental tree, for experiments 2 and 4, we compared the number of foundresses for each female vase to the mean of the two adjacent male vases, using a one-tailed Wilcoxon signed-rank test (Statistix 1994, table 1). For experiment 1, we compared the number of visited syconia for each male vase with the mean number of visited syconia of the two adjacent female vases by a one-tailed Wilcoxon signed-rank test (table 1). In experiment 3, only seven syconia (all male) out of 50 were visited. It was thus impossible to perform a Wilcoxon signed-rank test. We instead calculated the binomial probability of such an event under a 'no choice' hypothesis. The number of female syconia

visited in a sample of seven visited syconia follows a binomial law of probability 0.52 (correcting for unequal sample size; table 1).

In experiment 4, where sufficient pollinators were available, female syconia had a smaller mean number of foundresses ($n=12$, $p=0.006$), and vases with female syconia attracted fewer insects (for both wasps in vases and total wasps, $n=12$, $p=0.02$). The difference in attraction was also significant in the third experiment and close to significant for the first two experiments (table 1). Thus *B. psenes* does significantly discriminate between male and female syconia, being attracted to and entering preferentially into male syconia (combined probability from independent tests of significance, for the four experiments d.f.=8, $p=7.10^{-5}$; Sokal & Rohlf 1981, p. 780).

4. DISCUSSION

These experiments clearly show that differences exist between male and female syconia of *F. carica* which can be perceived by wasps. Wasps are attracted to receptive syconia by volatile chemical substances (Hossaert-McKey *et al.* 1994). Wasp choice could be due to differences in the chemical attractant produced by the two kinds of syconia. Such differences may be qualitative (different molecules) and/or quantitative. Chemical analysis of volatile compounds emitted by receptive syconia of *F. carica* has shown that qualitative differences do exist between the sexes (Gibernau *et al.* 1997). Because the production of volatile attractant may vary in quantity with the phase of receptivity (Hossaert-McKey *et al.* 1994) and because determining the precise phase of receptivity requires bioassay with wasps (Khadari *et al.* 1995), quantitative differences due solely to the sex of the syconia will be difficult to demonstrate. Further studies are needed to assess whether pollinators are differentially attracted by these chemicals, and if quantitative differences are important.

In their study of *F. hispida*, Patel *et al.* (1995) found that *Ceratosolen marchali* do not significantly choose between male and female syconia. Our choice experiment shows that male syconia of *F. carica* are more visited by *B. psenes* than are female syconia. However, *B. psenes* still visits female syconia by mistake, even when given a choice. This raises two different questions. What are the consequences of wasp behaviour for the stability of the mutualism? Second, why does the pollinator of *F. carica* choose, while that of *F. hispida* does not?

These two dioecious fig species belong to different sections that at least appear to have resulted from two independent instances of the evolution of dioecy (Berg 1989). Moreover they differ strongly in their phenology (Patel *et al.* 1995; Patel 1996) and this could have evolutionary links to wasp behaviour. *F. carica* (section *Ficus*) has a highly seasonal flowering period, male trees being receptive synchronously in spring (April), followed by female trees in summer (July) (Kjellberg *et al.* 1987). In contrast, *F. hispida* (section *Sycocarpus*), has female and male trees that produce receptive syconia all year round (with all syconia on one tree being receptive simultaneously). These differences in fig phenology lead to differences in the fig-wasp cycle.

Table 1. *Results of wasp (Blastophaga psenes) choice experiments between male and female figs of Ficus carica*

experiment	number of syconia		difference in diameter between male and syconia ¹	total number of foundresses in syconia		choice for male figs (one-tailed Wilcoxon signed rank test)
	male	female		male	female	
1 (6–7 July 1992)	21	23	$t = -0.87$ d.f. = 45 $p = 0.38$	11	4	d.f. = 7 $p = 0.11^2$
2 (10 July 1992)	25	21	$t = -0.96$ d.f. = 44 $p = 0.34$	54	23	d.f. = 7 $p = 0.11^3$
3 (19 July 1993)	24	26	$t = 0.43$ d.f. = 48 $p = 0.67$	11	0	binomial probability (7; 0.52) = 0.006
4 (17 July 1996)	39	36	$t = -0.53$ d.f. = 73 $p = 0.60$	187	43	d.f. = 12, $p = 0.001^3$

¹Two-sample *t*-test for equal variance.²Test on the number of visited syconia.³Test on the number of foundresses.

In *F. carica*, tree phenology imposes constraints on the pollinator: when the majority of wasps emerge from male syconia, there are only receptive female syconia. Because we managed to manipulate male tree phenology by cutting branches, natural damage to the branches might produce the same result. However, field observations suggest this must be a very infrequent event. Due to their short lifespan (about two days; Kjellberg *et al.* 1988), wasps cannot wait for receptive male syconia and they have the choice between dying or entering a female syconium. This mechanism would be similar to that operating in other systems of pollination by deceit, where pollination occurs mainly (or is more efficient) when the model of the mimicry is absent (Dafni 1984). Pollination of dioecious fig species however differs from these other systems of pollination by deceit since fig wasps enter a single type of inflorescence in their life and do not have the possibility to learn the differences between male and female syconia.

In *F. hispida*, chemical similarity between sexes may impose constraints on pollinators which cannot respond to selective pressure to discriminate because of other antagonistic selective pressures. When wasps are faced with limited discriminability between the sexes of syconia, there is a trade-off between the risk of never entering a male syconium and the risk of entering a female syconium (Patel *et al.* 1995). With the combination of a short lifespan, limited egg-laying sites and high probability of mortality in flight (Bronstein 1992), the best strategy for a wasp could be to enter the first receptive syconium (i.e. selection to rush; Patel *et al.* 1995).

In dioecious figs, trees of each sex are selected to mimic the other: female trees to dupe the pollinators and male trees to produce pollen carriers that will be attracted by female trees (Grafen & Godfray 1991). On the other hand, selection on wasps should act to enhance their discriminatory ability. Selection on each partner depends on the character state of the other, a true coevolutionary process. The outcome of these conflicting selective forces should depend on the strength of selection on each partner, and on the ability of each partner to constrain the possible responses of the other. The observed differences in wasp behaviour could be due to different selective pressures, acting either on the wasp (to discriminate) or on the tree (mimicry of syconia of both sexes to make discrimination difficult), or to different history of the interaction.

Figure 1. Results of the fourth experiment. Histograms indicate the size (diameter) distribution of syconia of each sex (and sample size for each class). Lines indicate the mean number of foundresses per syconium for different size classes (dashed line for female syconia, solid line for male syconia).

Concerning wasp behaviour, pollinators of deceptive flowers are expected to show decreasing choosiness as the abundance of good types (here male syconia) increases (Bawa 1980; Ågren *et al.* 1986). Thus, selective pressure for choice should be less strong for *B. psenes* than for *C. marchali*. For *B. psenes* there are never female syconia receptive at the time when male syconia of *F. carica* are receptive (the period without male syconia is irrelevant for selection, since wasps emerging at that time always die without reproducing). But for *F. hispida*, female syconia (bad type) are on average as abundant as male syconia when wasps emerge. Thus the observed difference in wasp discriminatory ability between the two pollinator species is in the opposite direction to expectations.

On the other hand, differences in the strength of selection for mimicry between male and female trees could better explain the observed differences in wasp behaviour. In *F. hispida*, even a slight ability of the wasp to choose would strongly reinforce the selection for mimicry between male and female syconia. This in turn would lead to a lower ability of wasps to discriminate between the two sexes of syconia. However, in *F. carica*, since male and female syconia are not receptive at the same time, a perfect mimicry between the two sexes seems less

important: when only female syconia are available, wasps will still enter them because there is no alternative resource and because they do globally resemble male syconia. Not to enter these female syconia in such a no-choice situation would confer no selective advantage on the wasps, and would thus be an example of spiteful behaviour, the existence of which in animals is controversial (Gadagkar 1993). If mimicry is costly in figs, or if mutations leading to a more perfect mimicry are rare, we can expect that selection on intersexual mimicry will be relaxed in seasonal dioecious figs, making it easier for wasps to discriminate. Moreover, since there are few syconia per male tree for the winter crop, and since long distance attraction of wasps must be linked to the total production of attractant of the tree, male trees could be selected to produce more attractant per syconium. This would explain possible quantitative differences in the production of the chemical attractant in addition to known qualitative differences (Gibernau *et al.* 1997). Distinct patterns of selection linked to seasonality of flowering could explain the observed patterns.

However, wasp choice could have evolved before tree seasonality of flowering. In this case, only female trees flowering when no male trees are receptive would have been pollinated, and the only efficient pollen donors would have been male trees releasing wasps when no other male trees are receptive. Thus, there should be disruptive selection on the date of flowering on male and female trees (following the same general process as exposed by Kjellberg & Maurice 1989). It will be difficult to distinguish between these two evolutionary pathways (seasonality of flowering, then choice, or choice, then seasonality) since they have the same consequences for fig phenology and wasp behaviour, and since both traits could have evolved at the same time in a true coevolutionary process.

Mutualisms are reciprocal exploitations with an overall benefit for each species. Sustainability of mutualisms depends on endogenous and exogenous factors regulating the costs and benefits of the interactions. Because of that, conflicts are omnipresent in mutualisms. They are particularly obvious when the trait/behaviour that leads to a benefit to the other species is costly for the individual that expresses this trait/behaviour (e.g. entering female syconia for a pollinating wasp). In this case, there is an apparent paradox between predicted selection (wasps should avoid female syconia) and observed patterns (wasps still visit female syconia). This study illustrates that such a paradox can be understood when one incorporates knowledge of the complexities of the pollinator–host interactions. In *F. carica* and *F. hispida*, resolution of this paradox is different. In *F. carica*, the stability of the system seems to be assured by a constraint imposed by the long-lived tree (seasonal phenology) to which the short-lived pollinator cannot respond. In *F. hispida*, the system seems to be stabilized by intersexual mimicry. Thus even within a restricted taxonomic sphere (here the genus *Ficus*) there may be great variation in the functioning of species interactions. Comparative studies of such variation could lead to new generalizations about the evolutionary mechanisms involved in species interactions.

This study was partly supported by a post doctoral fellowship to M.C.A. (EC Institutional Fellowship ERBCHBGCT940526). We

thank Doyle McKey, John Thompson, Camille Parmesan and Carine Brouat for their helpful comments on various versions of our manuscript.

REFERENCES

- Ågren, J., Elmqvist, T. & Tunlid, A. 1986 Pollination by deceit, floral sex ratios and seed set in dioecious *Rubus chamaemorus* L. *Oecologia* **70**, 332–338.
- Alexandersson, R. & Ågren, J. 1996 Population size, pollinator visitation and fruit production in the deceptive orchid *Calypso bulbosa*. *Oecologia* **107**, 533–540.
- Anstett, M. C. 1994 Contraintes et libertés dans l'évolution des mutualismes figuier/pollinisateurs. PhD. Université Montpellier II, France.
- Anstett, M. C., Kjellberg, F. & Bronstein, J. L. 1996 Waiting for wasps: consequences for the pollination dynamics of *Ficus pertusa* L. *J. Biogeogr.* **23**, 459–466.
- Anstett, M. C., Hossaert-McKey, M. & Kjellberg, F. 1997 Figs and fig pollinators: evolutionary conflicts in a coevolved mutualism. *Trends Ecol. Evol.* **27**, 97–99.
- Bawa, K. S. 1980 Mimicry of male by female flowers and intra-sexual competition for pollinators in *Jacaratia dolichaula* (D. Smith) Woodson (Caricaceae). *Evolution* **34**, 467–474.
- Berg, C. C. 1989 Classification and distribution of *Ficus*. *Experientia* **45**, 605–611.
- Bronstein, J. L. 1992 Seed predators as mutualists: ecology and evolution of the fig/pollinator interaction. In *Insect–plant interactions*, vol IV (ed E. A. Bernays), pp. 2–44. Boca Raton, FL: CRC Press.
- Bronstein, J. L. & Hossaert-McKey, M. 1996 Variation in reproductive success within a subtropical fig/pollinator mutualism. *J. Biogeogr.* **23**, 433–446.
- Dafni, A. 1984 Mimicry and deception in pollination. *A. Rev. Ecol. Syst.* **15**, 259–278.
- Faegri, K. & Van der Pijl, L. 1971 *The principles of pollination biology*, 2nd edn. 291 pp. Oxford: Pergamon.
- Gadagkar, R. 1993 Can animals be spiteful? *Trends Ecol. Evol.* **8**, 232–234.
- Gibernau, M., Buser, H. R., Frey, J. E. & Hossaert-McKey, M. 1997 Volatile compounds from extracts of figs of *Ficus carica* (Moraceae). *Phytochem.* **46**, 241–244.
- Gibernau, M., Hossaert-McKey, M., Anstett, M. C. & Kjellberg, F. 1996 Consequences of protecting flowers in a fig: a one way trip for pollinators? *J. Biogeogr.* **23**, 425–432.
- Grafen, A. & Godfray, H. J. C. 1991 Vicarious selection explains some paradoxes in dioecious fig–pollinator systems. *Proc. R. Soc. Lond. B* **245**, 73–76.
- Herrera, C. M. 1987 Components of pollinator 'quality': comparative analysis of a diverse insect assemblage. *Oikos* **50**, 79–90.
- Hossaert-McKey, M., Gibernau, M. & Frey, J. E. 1994 Chemosensory attraction of fig wasps to substances produced by receptive figs. *Entomol. Exp. Appl.* **70**, 185–191.
- Inouye, D. W. 1980 The terminology of floral larceny. *Ecology* **61**, 1251–1253.
- Khadari, B., Gibernau, M., Anstett, M. C., Kjellberg, F. & Hossaert-McKey, M. 1995 When figs wait for pollinators: the length of fig receptivity. *Am. J. Bot.* **82**, 992–999.
- Kjellberg, F. & Maurice, S. 1989 Seasonality in the reproductive phenology of *Ficus*: its evolution and consequences. *Experientia* **45**, 653–660.
- Kjellberg, F., Doumesche, B. & Bronstein, J. L. 1988 Longevity of a fig wasp (*Blastophaga psenes*). *Proc. K. Ned. Akad. W. C.* **91**, 117–122.
- 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**, 693–703.

- Laverty, T. M. 1992 Plant interactions for pollinator visits: a test of the magnet species effect. *Oecologia* **89**, 502–508.
- Little, R. J. 1983 A review of floral food deception mimics with comments on floral mutualism. In *Handbook of experimental pollination biology* (ed. C. E. Jones & R. J. Little), pp. 294–308. New York: Van Nostrand Reinhold Company Inc.
- Patel, A., Anstett, M. C., Hossaert-McKey, M. & Kjellberg, F. 1995 Pollinators entering female dioecious figs: why commit suicide? *J. Evol. Biol.* **8**, 301–313.
- Patel, A. 1996 Variation in a mutualism: phenology and the maintenance of gynodioecy in two Indian fig species. *J. Ecol.* **84**, 667–680.
- Pyke, G. H. 1981 Optimal foraging in nectar-feeding animals and coevolution with their plants. In *Foraging behaviour, ecological, ethological and psychological approaches* (ed. A. Kamil & T. Sargeant), pp. 19–48. New York: Garland STPM.
- Renner, S. S. & Feil, J. P. 1993 Pollinators of tropical dioecious angiosperms. *Am. J. Bot.* **80**, 1100–1107.
- Schemske, D. W., Ågren, J. & Le Corff, J. 1996 Deceit pollination in the monoecious, neotropical herb *Begonia oaxacana* (Begoniaceae). In *Floral biology: studies on floral evolution in animal pollinated plants* (ed. D. G. Lloyd & S. C. H. Barrett), pp. 292–318. London: Chapman & Hall.
- Simpson, B. B. & Neff, J. L. 1983 Evolution and diversity of floral rewards. In *Handbook of experimental pollination biology* (ed. C. E. Jones & R. J. Little), pp. 142–158. New York: Van Nostrand Reinhold Company Inc.
- Sokal, R. R. & Rohlf, F. J. 1981 *Biometry*, 2nd edn, 859 pp. New York: Freeman & Co.
- Statistix 1994 Version 4.1. Analytical software. Tallahassee FL.
- Valdeyron, G. & Lloyd, D. G. 1979 Sex differences and flowering phenology in the common fig, *Ficus carica* L. *Evolution* **33**, 673–685.
- Van Noort, S., Ware, A. B. & Compton, S. G. 1989 Pollinator specific volatile attractants released from the figs of *Ficus burtt-davyi*. *S. African J. Sci.* **85**, 323–324.
- Verkerke, W. 1987 Syconial anatomy of *Ficus asperifolia* (Moraceae), a gynodioecious tropical fig. *Proc. K. Ned. Akad. Wet. C.* **90**, 91–124.
- Waser, N. M. 1983 The adaptive nature of floral traits: ideas and evidence. In *Pollination biology* (ed. L. Real), pp. 242–285. Orlando, FL: Academic Press.
- Weiblen, G., Flick, B. & Spencer, H. 1995 Seed set and wasp predation in dioecious *Ficus variegata* from an Australian wet tropical forest. *Biotropica* **27**, 391–394.