

The 900 or so species of figs each have their own uniquely coevolved pollinator species, all from a single family of wasps¹. Figs are inflorescences containing hundreds of separate staminate (male) and pistillate (female) florets, which line a hollow, nearly sealed cavity. A few tiny pollinator wasps push their way into the fig through a narrow passage. They dust pollen carried from their birthplace onto some florets, lay a single egg in each ovary of other florets, and then die. The pollinators destroy many florets in each fig, but in return, they carry pollen to and from the closed fig inflorescence. Meanwhile, wasps of several parasite species lay eggs in the florets by drilling through the outside wall of the fig with their long ovipositors (Fig. 1). The parasite species in each fig also destroy florets, but do not carry pollen. Each floret ovary will produce either a single wasp or a single seed.

About one month after eggs are laid, adult pollinator and parasite males crowd into the dark floret-garden within the fig. A male finds floret ovaries containing females of his own species; occasionally he has to fight off aggressive rivals. He then chews a hole into the floret, and mates by inserting his genitalia through the hole and to the female. Males often mate with sisters, since only one or a few females lay eggs in each fig. After a period of mating, the pollinator males chew an exit tunnel through the wall of the fig; in some fig species, the narrow passage used for entry swells open. Bearing pollen, the pollinator females depart from the ripening fig, and begin the cycle again.

Extraordinary diversity has evolved over the long history of this intricate mutualism^{1,2}. For example, an unusual form of dioecy has appeared at least once, and the pollinator wasps of these dioecious figs have appropriately different behaviour and morphology from those of other figs. The relationship between wasps and figs is an excellent system for studying aspects of coevolution, although their remarkable pollination system makes many of figs' evolutionary puzzles unique.

Several parasitic wasp genera from different families also have a long evolutionary relationship with figs. These groups show many convergent characters undoubtedly shaped by the peculiar life style within the closed environment of the fig. Three traits, each one itself rare among insects, have evolved together a number of times³: many

of these parasites produce wingless males; some use deadly mandibles (Fig. 1) and heavily shielded bodies in lethal combat over females; several species produce both the pug-nacious wingless type and a delicate winged male – a male dimorphism so profound that, on several occasions, two morphs from the same species were placed in separate genera.

The causes of male dimorphism have received little attention. Hamilton³ noted that flying males sometimes mate outside the fig: this lessens competition among brothers for access to the few females inside, and increases the level of outbreeding. A wingless male either mates within his natal fig, or fails to reproduce. When the greatest challenge to being a successful sire is other males rather than the search for a female, one might imagine that deadly weapons could be a useful, perhaps even essential, adjunct to reproduction. Wingless parasitic males commonly use their dangerous mandibles in fights. Yet the pollinator males, which are invariably wingless, have harmless mandibles and never seem to fight. Why is there such diversity in male morphology? Do those with weapons always fight, or do they behave according to local densities and conditions, as in most other animals^{4,7}? In spite of the widespread occurrence of figs, and spectacular aspects of the wasps' morphology and behaviour, no theoretical framework or set of observations has been brought to bear on these questions, except for Hamilton's introduction to the subject³. A recent pair of papers^{5,6}, however, reports some general ideas about fighting, some specific predictions for fig wasps and some tests of these predictions.

Murray and Gerrard's⁵ general model of fighting assumes that four sets of parameters determine behaviour: the maximum possible gain from a particular resource locality, the rates at which the value of a locality diminishes and remaining resources can be extracted, the search time for finding a resource, and the time between challenges for ownership of a particular locality. Murray⁶ then makes explicit assumptions about how to estimate these parameters for fig wasps, or what a reasonable range of values might be. Each 'locality' is presumed to be a floret with a single female; the resources to be extracted from that locality are successful sirings of the female's offspring. The number

of offspring remaining to be sired from each female is assumed to decline steadily with time, at a rate described by a particular parameter value. Search time is assumed to be proportional to the spacing of suitable females among the florets. The interval between challenges is similarly assumed to be proportional to the spacing of male rivals among all wasps encountered. Specific hypotheses about fighting in fig wasps follow from these assumptions.

The length of fights and the severity of injury per fight are predicted to increase as male spacing or the ratio of females to male competitors increases, since the frequency of challenges declines, and the benefit for winning a fight therefore rises. Both

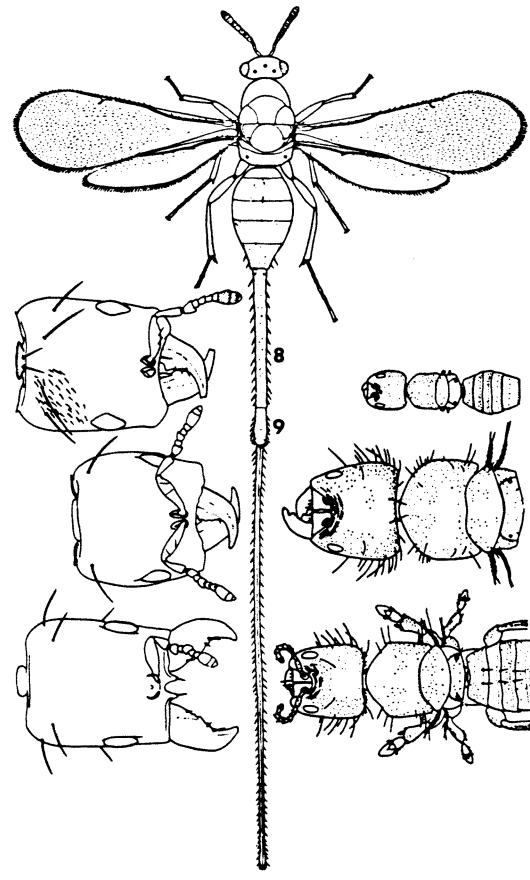


Fig. 1. Parasitic fig wasps. Center: The female of *Philotrypesis caricae*, a species in the same genus as the wasp studied by Murray; the numerals 8 and 9 show the elongated eighth and ninth abdominal segments, followed posteriorly by the long sheaths that hold the ovipositor, which is used to drill through the outside wall of the fig into the ovaries of the pistillate florets inside. Right: According to Joseph⁹, these are three forms taken by males of *P. caricae*; as expected from the different shapes of the mandibles, the one in the center is much more aggressive, and has been observed using its mandibles in deadly fights over florets containing females. Left: The heads of males from three species of the parasitic wasps, with mandibles suggesting the ability to kill opponents. Top to bottom: *Sycoryctes hirtus*, *Sycoryctes remus* and *Sycosapter cornutus*. Drawings of *P. caricae* reproduced from Ref. 7 with permission; drawings of *Sycoryctes* and *Sycosapter* spp. reproduced from Ref. 8 with permission.

the frequency of fights and the frequency of injuries are expected to decline as male or female spacing increases, or as the ratio of females to male competitors rises, since the frequency at which males actually meet would decline. The percentage of time spent fighting and the lifetime extent of injury are predicted to increase steeply to a peak and then to decline gradually when plotted against male or female spacing, or the ratio of females to males, since these measures are the products of length or severity per bout multiplied by the frequency of bouts, which were described in the first two predictions.

Murray⁶ tested these predictions by observing the wingless and armed males of the parasite *Philotrypesis pilosa*, which inhabit figs of *Ficus hispida*. The observed patterns of fighting and mating are complex, and often do not fit the simple assumptions and predictions of the model. For example, the proportion of lengthy fights did not decline as predicted when the numbers of

rivals present increased. Murray notes that when a male had only one or two rivals, 19% of the fights were associated with mating opportunities, whereas with higher numbers of competitors, 52% of the fights were near females. Among mating fights, the proportion of long fights was indeed higher with lower numbers of males.

The mating fights tended to be costly in terms of length and severity of injury. Murray interprets these and other data by suggesting that when there are few males, serious fights are rare but costly; when there are many males, brief interactions are frequent and serious fights are rare. The lifetime cost of fighting per male was highest in the middle range of male densities, as predicted by the model.

Males did not adjust their behaviour with changes in search time (female spacing) or the ratio of females to males in the ways predicted by the model. Murray points out that the model assumes a steady decline in the value of a mating,

whereas males frequently returned to a previous mate to copulate again, suggesting that later matings produce a larger number of fertilizations. Also, this 'checking-back' differs from the model's assumptions concerning the searching behaviour and encounter frequency of the males. New models based on more accurate assumptions about male movement and sperm competition, with tests on independent data sets, are therefore needed to determine if the adaptive significance of fighting can be explained by this general approach. The behavioural details provided by Murray are a good starting point for further work.

The striking differences between the pollinator and parasite males stand out as an unsolved challenge. The pollinator males are usually abundant in each fig, and must be present for the fig to develop. By contrast, parasite densities vary widely. Can Murray's model, based on densities of competitors and potential mates, explain the contrast in weapons and fighting between pollinators and parasites? Or, according to the current rage of 'non-adaptive' explanations, is the lack of large mandibles and special head morphology for fighting simply a constraint imposed by selection on the pollinator female's head shape, since the female's head must fit the particular design of the entrance to the fig, which differs among species? With thousands of wasp species distributed on figs throughout the tropics, opportunities abound for developing and testing these sorts of questions, while accumulating a rich store of comparative natural history and morphology for evolutionary analyses.

References

- 1 Wiebes, J.T. (1979) *Annu. Rev. Ecol. Syst.* 10, 1–12
- 2 Janzen, D.H. (1979) *Annu. Rev. Ecol. Syst.* 10, 13–51
- 3 Hamilton, W.D. (1979) in *Sexual Selection and Reproductive Competition in Insects* (Blum, M.S. and Blum, N.A., eds), pp. 167–220, Academic Press
- 4 Thornhill, R. and Alcock, J. (1983) *The Evolution of Insect Mating Systems*, Cambridge University Press
- 5 Murray, M.G. and Gerrard, R.J. (1985) *J. Theor. Biol.* 115, 367–389
- 6 Murray, M.G. (1987) *Anim. Behav.* 35, 488–506
- 7 Joseph, K.J. (1958) *Ann. Sci. Nat. Zool. Biol. Anim., Series 11* 20, 197–260
- 8 Bouček, Z., Watsham, A. and Wiebes, J.T. (1981) *Tijdschr. Entomol.* 124, 149–222