

Seed Set and Wasp Predation in Dioecious *Ficus variegata* from an Australian Wet Tropical Forest¹

Key words: Agaonidae; Australia; *Ficus variegata*; fig wasps; mutualism; seed predation.

A RECENT REVIEW (Bronstein 1992) of the interaction between figs (*Ficus* species, Moraceae) and their pollinators (Agaonidae: Hymenoptera) evaluated some potential conflicts of interest that might constrain the evolution of the mutualism. One apparent conflict ensues when female wasps pollinate flowers while depositing their eggs in a fraction of fig ovaries. Some developing seeds are totally consumed by wasp larvae, and consequently, wasps are both pollinators and seed predators. Variable style lengths of fig flowers were thought to regulate the donation of ovaries to wasps in exchange for seeds in monoecious figs, since the ovaries of short-styled flowers are considered accessible to wasp ovipositors while the ovaries of long-styled flowers are generally not (Janzen 1979a). In monoecious species, however, most styles are of intermediate length, and there is insufficient evidence to conclude that the fate of fig ovaries is determined solely by style and ovipositor lengths (Compton & Nefdt 1990, Bronstein 1992).

Heterostyly in gynodioecious figs generates a different conflict of interest than for the monoecious figs and their pollinators. In gynodioecious fig populations, female trees produce figs containing only long-styled, seed-bearing flowers and hermaphroditic trees produce figs containing short-styled, wasp-bearing female flowers and pollen-producing male flowers (Verkerke 1989). Hermaphroditic figs are functionally male, producing few or no seeds due to intense predation by wasp larvae that become the pollen vectors as adults. Hundreds of *Ficus* species with gynodioecious morphology are thus functionally dioecious (Berg 1989).

The evolutionary conflict between gynodioecious figs and agaonid wasps arises from the separation of seed and wasp production between two sexes of trees. Wasps leave no offspring in female figs, but have access to every ovary in male figs. Thus, female trees are lethal to their pollinators, whereas the pollinators of male trees are reproductively successful (Valdeyron & Lloyd 1979). Kjellberg *et al.* (1987) supposed that intense selection against the pollinators of female figs could favor wasps capable of distinguishing the male figs from the females, but asynchronous flowering phenology between trees of different sexes could eliminate the opportunity for wasps to discriminate against females. Grafen & Godfray (1991) argued alternatively that male and female figs would be under strong selection to mimic each other to an extent that prevents wasps from discriminating between sexes.

Hypotheses that attempt to explain the evolutionary stability of the gynodioecious fig/pollinator interaction (Kjellberg *et al.* 1987, Grafen & Godfray 1991) cannot be fully evaluated until more empirical data are available, especially for gynodioecious species in tropical habitats. An initial step is to compare the reproductive output of a fig species and its pollinator, as did Janzen (1979b) when he asked what proportion of monoecious fig ovaries are forfeited to wasps in exchange for seeds. Corlett *et al.* (1990) compared seed set and wasp production between monoecious and dioecious figs in Singapore. Our study compares the reproductive output of female and male figs in *Ficus variegata* Blume in Queensland, Australia.

We measured levels of seed set and wasp predation in female and male trees in a population of *F. variegata* at Cape Tribulation, Australia (16°05'S, 145°27'E). *F. variegata* is gynodioecious and is pollinated by *Ceratosolen appendiculatus* Mayr (Condit 1969). Our study area is situated in a coastal lowland basin which receives over 4000 mm of rainfall annually. A humid and seasonally wet climate supports luxuriant vegetation classified as complex mesophyll vine forest (Tracey 1982). *F. variegata* is very common along watercourses in the basin, especially where natural regeneration has occurred following clearing of the vegetation for cattle pasture. We examined the fruit of 11 male and 9 female trees from a population of more than 200 marked individuals along the banks of Mason's Creek.

Figs were sampled during January and February of 1993, coincident with the annual peak period of

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TABLE 1. Results of fig dissections from 11 male and 9 female trees of *F. variegata*. Mean numbers of flowers per sample (SD), percentages of wasp-killed seeds (SD), of seed-producing flowers (SD), and of vacant ovaries (SD).

| Sex | Tree | N | Flowers | % Wasps | % Seeds | % Vacant |
|--------|---------|-----|----------|---------|-----------|----------|
| Male | 22 | 10 | 206 (28) | 62 (14) | 0.1 (0.3) | 38 (14) |
| Male | 28 | 10 | 218 (41) | 46 (15) | 0 (—) | 54 (15) |
| Male | 37 | 10 | 167 (32) | 56 (21) | 0.4 (0.5) | 43 (21) |
| Male | 110 | 10 | 198 (30) | 44 (23) | 0 (—) | 56 (23) |
| Male | 114 | 10 | 165 (30) | 76 (9) | 0.5 (1) | 23 (9) |
| Male | 115 | 10 | 144 (21) | 66 (13) | 1 (1) | 33 (13) |
| Male | 117 | 10 | 135 (32) | 62 (25) | 0.2 (0.4) | 38 (25) |
| Male | 145 | 10 | 177 (23) | 50 (11) | 0.1 (0.2) | 50 (11) |
| Male | 196 | 10 | 143 (20) | 62 (20) | 1.6 (3) | 36 (20) |
| Male | 221 | 10 | 174 (26) | 90 (6) | 0 (—) | 10 (6) |
| Male | 225 | 6 | 131 (16) | 67 (9) | 0 (—) | 33 (9) |
| Male | Grouped | 106 | 167 (37) | 63 (20) | 0.4 (1) | 37 (20) |
| Female | 43 | 10 | 180 (55) | 0 (—) | 79 (13) | 21 (14) |
| Female | 62 | 10 | 282 (30) | 0 (—) | 56 (19) | 44 (19) |
| Female | 102 | 10 | 172 (14) | 0 (—) | 88 (5) | 12 (5) |
| Female | 103 | 10 | 208 (29) | 0 (—) | 83 (9) | 17 (9) |
| Female | 108 | 10 | 235 (28) | 0 (—) | 53 (14) | 47 (14) |
| Female | 187 | 10 | 255 (49) | 0 (—) | 54 (13) | 46 (13) |
| Female | 201 | 10 | 217 (21) | 0 (—) | 83 (10) | 17 (10) |
| Female | 218 | 10 | 203 (20) | 0 (—) | 56 (14) | 44 (14) |
| Female | 219 | 10 | 194 (26) | 0 (—) | 72 (18) | 28 (18) |
| Female | Grouped | 90 | 216 (46) | 0 (—) | 69 (19) | 31 (19) |

fruit production for *F. variegata* at Cape Tribulation (H. Spencer, pers. obs.). We collected ripe figs which had freshly fallen to the ground beneath their parent trees. These were preserved in 70 percent ethanol. From a sample of approximately 20 figs per tree, ten were selected at random for dissection under $15\times$ magnification. Due to the abundance of flowers per fig, we examined a subsample representing approximately five percent of the estimated 4000 flowers per fig. In an effort to minimize position effects, we dissected flowers within a 2 mm wide longitudinal section of each fig. We observed three distinctive classes of flowers: mature seeds with hard seed coats, seeds killed by wasps with conspicuous exit holes, and vacant ovaries which were much smaller than the first two classes. We counted totals for each class and calculated percentages based on the total number of ovaries in the sample.

We found that 63 percent of the ovaries in male figs were preyed on by wasps and 69 percent of the ovaries in female figs set seed (Table 1). Occasionally, we counted mature seeds in male figs, but this occurred so infrequently that we choose to refer to functional gender in describing the wasp-producing figs. The term "gall" fig employed by Hill (1967) and Lambert (1992) may be misleading in the case of *F. variegata* because short-styled flowers will produce seeds if wasps pollinate them but fail to oviposit. At the population level, we observed a bimodal distribution of style lengths in mature figs of *F. variegata*, as did Hill (1967). The mean difference between style lengths in figs from female trees (1.7 ± 0.2 mm, $N = 10$) and figs from male trees (0.3 ± 0.1 mm, $N = 10$) was large (1.3 mm). Although style lengths of ripe figs do not reflect absolute differences at the time of pollination, the relative style length difference between male and female figs is suggestive of heterostyly.

A direct, between-sex comparison of seed set and wasp production is statistically uninformative, due to the nearly complete separation of seed and wasp occupancy between male and female trees. Instead, we compared the distribution of vacant ovaries between the sexes. Data conformed to a near-normal distribution within figs and varied substantially among trees of each sex (Table 1). We found that despite significant variation among individual trees, the percentage of vacant ovaries in female figs was significantly lower than in male figs (Table 2). Subsamples from female figs had more flowers on average (216 ± 46) than male figs (167 ± 37 ; one-way ANOVA; $F = 67.7$, $P < 0.001$). However, male fig diameters (35.9 ± 4.1 mm) were on average significantly larger than for female figs (34.4 ± 4.1 mm; one-way ANOVA; $F = 6.9$, $P < 0.01$). Due to the between-sex size difference, we did not attempt to extrapolate

TABLE 2. Results of one-way analyses of variance in percentages of vacant ovaries for male and female trees in *F. variegata*. While there was substantial variation in ovary vacancies among individual trees, we found a significantly higher percentage of ovary vacancies in samples from male trees.

| Source | df | Sum of squares | Mean square | F-test |
|---------------|-----|----------------|-------------|-------------|
| Between trees | 19 | 35,728.8 | 1880.5 | 8.5 |
| Within trees | 176 | 39,096.3 | 222.1 | $P < 0.001$ |
| Total | 195 | 74,825.1 | | |
| Between sexes | 1 | 1924.2 | 1924.2 | 5.12 |
| Within sexes | 194 | 72,900.9 | 375.8 | $P = 0.025$ |
| Total | 195 | 74,825.1 | | |

the absolute number of female flowers per fig. Flowers in male figs could be less tightly packed, but still more numerous than flowers in female figs. The lack of a correlation between the number of flowers per sample and fig diameter ($N = 196$, corr. coeff. = -0.028 , r -squared = 0.001) might also be influenced by variation in the thickness of the syconium wall.

We predicted from style and ovipositor lengths that all available ovaries in male figs could be occupied by wasps, but 37 percent of the ovaries in samples of male figs were vacant. Corlett *et al.* (1990) also found high percentages of vacancies in dioecious figs, suggesting that limited wasp production and seed set may result from failed oviposition and pollination. Bronstein (1992) cautioned against interpreting apparent constraints on wasp fecundity as an adaptive strategy by figs to limit exploitation by wasps. Pollinator limitation, selective ovule abortion, or extrinsic constraints on plant resource availability are factors that could account for the high percentage of vacant ovaries in our samples. We cannot conclude which of these factors accounts for limited seed set and wasp occupancy in *F. variegata*, since our method did not distinguish between nonpollinated ovules and aborted ovules.

Explanations for the apparent evolutionary stability of gynodioecious fig pollination (Kjellberg *et al.* 1987, Grafen & Godfray 1991) have assumed that pollinators of male figs achieve higher reproductive success than pollinators of female figs. This appears to be the case in *F. variegata*, since we did not detect the presence of wasp offspring in our samples of female figs. Interestingly, we observed that male figs had on average a higher percentage of vacant ovaries than female figs. A similar pattern has been reported for dioecious figs in Indonesia, where female figs were more likely to be pollinated than male figs (Compton *et al.* 1994), and in Singapore, where ovary occupancy was also higher in female figs than in male figs (Corlett *et al.* 1990). However, more data are needed to describe patterns of seed set and wasp predation, since numbers of flowers per fig can be highly variable among trees and among seasons in gynodioecious *Ficus* (J. Bronstein, pers. comm.).

We observed a major seasonal difference in the abundance of male and female figs in *F. variegata*, and we might expect ovary occupancy to vary between the sexes according to season. Fruiting phenology in *F. variegata* follows a pattern similar to that of gynodioecious *F. carica* (Kjellberg *et al.* 1987). At the population level, female trees produce seed primarily during the wet season. Seed is fathered by male trees that produce figs continuously and maintain the pollinator population throughout the year (H. Spencer, pers. obs.). In contrast to *F. carica*, there is within-sex asynchrony in the receptivity of figs to pollinators in *F. variegata* during the wet season. It has been supposed that female figs could be selected to mimic male figs during the pollination phase to an extent that prevents wasps from distinguishing between the two sexes (Valdeyron & Lloyd 1979; Grafen & Godfray 1991). During the seed dispersal phase, however, female figs may be under selection to appear different from male figs in order to attract frugivorous animals to the seed-bearing figs (Lambert 1992). In *F. variegata*, the mature female figs tend to be sweeter and more odorous than male figs, which are not usually dispersed. We also noted that female figs outnumber the male figs available to pollinators prior to the peak period of fruit production in *F. variegata*. Male trees that are pollinated during this predominant female phase could play a vital role in maintaining the wasp population through the dry season.

We also observed parasitic wasps (*Apocrypta caudata* (Girault)) of the subfamily Sycophaginae ovipositing through the syconium wall of male figs. No sycophaginines were found in female figs, suggesting that they are indeed parasitoids of *C. appendiculatus*. An unknown number of ovaries in male figs were

occupied by other nonpollinating wasp species, further reducing the occupancy of the pollinators. A few of our samples contained mostly nonpollinating, long-ovipositor wasps trapped in the fig cavity, which suggests that they cannot escape their host fig without an exit hole made by departing pollinators. If the sycophagines depend on agaonids in this way, then parasitoid reproduction could be limited by negative feedback.

Our preliminary results confirm that seed and wasp production in *F. variegata* and its pollinator, *C. appendiculatus*, is segregated between the male and female trees. Based on the strong seasonality of *F. variegata* reproductive phenology at Cape Tribulation (H. Spencer, pers. obs.), we might expect wasp populations to be sharply reduced during dry periods. A logical step toward understanding why dioecious fig pollination is evolutionarily stable in the tropics may require examining seasonal variability in seed set and wasp predation. We anticipate that such studies may have implications for the broader issues of seed dispersal and the role of dioecious figs as keystone species in tropical communities.

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