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0014-4754/89/070622-16\$1.50 + 0.20/0
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Coevolution of reproductive characteristics in 12 species of New World figs and their pollinator wasps

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Summary. 1) Figs (*Ficus*) and fig-pollination wasps (Agaonidae) are highly coevolved mutualists that depend completely on each other for continued reproduction. However, their reproductive interests are not identical.

2) The natural history of their interaction often permits the direct measurement of total lifetime reproductive success of the wasp and of major components of reproductive success for the fig.

3) Data from 12 monoecious species of New World figs (subgenus *Urostigma*) and their wasp pollinators (*Pegoscapus* spp.) indicate that fig fruit size (number of flowers per fruit), wasp size, and the number of foundresses that pollinate and lay eggs in any given fruit interact in complex but systematic ways to affect the reproductive success of both the wasps and the figs.

4) Different aspects of the interaction may work against the reproductive interests of either the wasp or the fig, or often, both. For example, in some species an 'average' foundress may only realize 25% of its reproductive potential due to the high average number of foundresses. However, that same crowding selects for more male-biased sex ratios in the wasps that reduce potential fitness gains through pollen dispersal for the fig. Nonetheless, the natural distributions of numbers of foundresses per fruit more clearly reflect the reproductive interests of the figs than of the wasps.

5) Generally, it appears that most of the fig species studied can be arranged along a continuum from those with physically small fruits that produce a relatively low proportion of viable seeds but are very efficient at the production of female wasps to physically large, relatively seed-rich fruits that are relatively inefficient at producing female wasps. The implications of these findings for the coevolution of figs and their wasps are discussed.

Key words. *Ficus*; figs; fig pollinating wasps; pollination mutualisms; coevolution; sex allocation; plant breeding systems.

Introduction

Like all naturally occurring figs (*Ficus*), the reproduction of the monoecious New World figs is inextricably linked to the reproduction of species-specific fig pollinating wasps^{24–26, 32}. However, in spite of the fact that the figs and their pollinating wasps depend completely on each other, for the continued sexual reproduction of the former and the completion of the life cycle of the latter, the reproductive interests of the two partners are not identical. The fig has an interest in producing its seeds both as a viable seed per se, and as a means for supporting the development of the female offspring of the wasps that pollinated the fruit to begin with. The female offspring are essential to the fig in order to disperse its pollen. On the other hand, the pollinating wasp only benefits directly from the fig's production of seeds that are eaten by its own offspring. Why the wasp species do not evolve ever higher fecundities to the ultimate ruin of the fig's production of viable seeds is a fascinating question to which the answer is not at all clear^{4, 18, 31}. However, the tension resulting from this incongruence of reproductive interests is inherent in the relationship of all figs and fig-pollinating wasps. Basic questions are what is the present resolution of that tension in different species pairs, and what are some of the factors that underly that resolution.

I will summarize preliminary results from ongoing studies describing various aspects of the reproductive biology of 12 species of wild figs (*Ficus*, subgenus *Urostigma*) and the wasps (*Pegoscapus* spp.) that pollinate them. After a brief discussion of the characteristics common to all of these species in their natural history, I will concentrate on several factors that affect the reproductive success of both the wasp and the fig. I will begin with a discussion of the consequences of variation in size of the fig and of the wasp, both among and within species. I will then discuss the effects of variation in the number of female wasps that pollinate and lay eggs in any individual fig fruit. As we shall see, the number of pollinators (foundresses) may have dramatic effects on the quality of the fruit and on the fitness of the individual foundress wasps. Finally, I will discuss the net effects of these interactions on both fig and wasp reproductive success. Throughout, I will emphasize the fact that although all 12 of these figs possess the same dependence on species-specific wasps for pollination, there are many variations on the basic theme and these variations have profound consequences for both members of this highly co-evolved mutualism.

Background natural history

The studies considered here were all conducted in the vicinity of the Panama Canal using fig species that naturally occur there. The fig species are all grouped in the subgenus *Urostigma*, section *Americana* and are pollinated by wasps belonging to the genus *Pegoscapus*^{24–26, 32}.

In all of the species considered here, individual fig trees may produce up to two or three fruit crops per year. Fruit crops of any species may be found at any time of the year. At the initiation of a fruit crop, the tree synchronously produces large numbers of receptive syconia (the enclosed fig inflorescence that ultimately develops into the ripe fruit). Mated, pollen-bearing foundress wasp(s) arrive at the tree, enter these syconia, pollinate the receptive uniovulate flowers, probe the flowers with their ovipositors and attempt to lay eggs in the ovaries. With few exceptions, the foundress wasps die inside the fruit after pollinating and laying eggs. After being pollinated, some portion of the total flowers begin to develop. Fruits that are not pollinated are usually aborted by the fig tree.

The female flowers within the fruit can be roughly characterized as ranging from those with ovaries close to the hollow center of the syconium, that is, close to the stigmatic surfaces (short-styled flowers) or as those with ovaries close to the wall of the fruit, far from the stigmatic surfaces (long-styled flowers)^{4, 30}. Therefore, the ovaries of the short-styled flowers are closer to the ovipositing foundress wasps. Generally, of those flowers that develop (total seeds), the long-styled flowers tend to develop as viable seeds (good seeds). On the other hand, the seeds developing from short-styled flowers tend to be eaten by the wasps' offspring. I will refer to seeds whose interiors are eaten by either pollinator or parasitic (see below) wasps as 'wasp seeds'. During its development, a single wasp larva consumes the contents of a single seed. The dry weight of a seed with an adult wasp about to emerge from it is roughly 2/3 to 3/4 that of an intact, good seed. As the fruit ripens, pollen-bearing male flowers grow inside the fruit. In most of the species considered, there are roughly 10–20 female flowers to each male flower (table 1).

Before final ripening takes place, wingless male wasps chew their way out of the seeds in which they have developed and crawl around the interior of the fruit searching for seeds with female wasps inside them. The males chew open these seeds and mate with the females. The females then emerge from their seeds, groom themselves, and collect pollen.

In the *Pegoscapus* species that I have studied, the emerging female wasps actively seek out the male flowers and collect pollen from them by prying the flowers open with the base of their antennae, removing pollen with their front legs, and placing it in specialized structures on their thorax (corbiculae)^{9, 23} (and pers. obs.). After actively gathering the pollen, the female wasps leave the syconium through a hole cut in the fruit wall by the males. The winged females then fly off to find a receptive fig tree and begin the cycle anew. After the female wasps leave, the fruit undergoes final ripening and becomes soft and sweet. The fruit is then often eaten and the seeds dispersed by any of a wide variety of animals (birds, bats, monkeys, etc.)^{2, 18, 22}.

Table 1. Characteristics of fruit of twelve species of figs collected in the vicinity of the Panama Canal. The sample size, mean, and standard deviations of dry weight of ripe fruit in grams, total number of uniovulate female flowers per fruit, and the total number of male flowers per fruit are followed by the mean size (head length in mm) of the pollinating wasp species. Where no data are available rough estimates taking into account the number of total seeds that develop are given (indicated by ~)

Species	Dry weight			Total flowers			Male flowers			Wasp size
	N	\bar{x}	SD	N	\bar{x}	SD	N	\bar{x}	SD	
<i>F. colubrinae</i> Standl.	10	0.05	0.01		~ 180		12	15	3	0.283
<i>F. perforata</i> L.	10	0.06	0.01		~ 200		132	19	5	0.275
<i>F. pertusa</i> L.f.	6	0.19	0.02		~ 300		20	26	6	0.350
<i>F. citrifolia</i> P. Miller	55	0.33	0.04	55	325	38	80	18	4	0.358
<i>F. bullenei</i> I. M. Johnston	59	0.21	0.04	31	340	35	66	35	8	0.308
<i>F. dugandii</i> Standl.	30	0.32	0.11		~ 400		3	15	5	0.370
<i>F. paraensis</i> (Miq.) Miq.	78	0.26	0.07	22	413	72	168	19	5	0.488
<i>F. nymphaeifolia</i> P. Mill.	74	1.4	0.26	65	675	113	144	71	29	0.438
<i>F. obtusifolia</i> H. B. K.	34	2.6	0.37	34	976	93	54	81	17	0.563
<i>F. popenoei</i> Standl.	78	0.90	0.13	77	1124	181	77	71	14	0.408
<i>F. near trigonata</i> L.	36	1.0	0.38	12	1582	316	48	128	44	0.368
<i>F. trigonata</i> L.	49	1.5	0.25	25	2051	303	47	92	20	0.423

There is also a large number of species of wasps that are parasitic either directly on the fig by consuming potentially viable seeds or indirectly through killing the fig-pollinating wasps. In contrast to the pollinator wasps, the mothers of the parasitic wasps do not enter the syconium. Instead, they penetrate the fruit wall from the outside with their long ovipositors and lay eggs in the interior seed layers of the fruit. The parasitic wasp offspring usually emerge from the same layer of seeds from which the pollinating wasps emerge. Therefore, they appear to be direct parasites on the pollinating wasps and thereby on the fig's male, pollen dispersal function. However, although the observations are suggestive, I have not yet found conclusive evidence on this point.

There are strikingly different rates of parasitism among fig species. For example, the parasites comprised roughly 8–10% of all wasps reared from fruits of *Ficus trigonata* and *F. dugandii*, whereas in other species (e.g., *F. perforata*, *F. nymphaeifolia*, *F. pertusa*), I have never found any parasites. This contrasts with Bronstein's⁴ report that parasites comprised 52% of all wasps reared from *F. pertusa* fruits from Monteverde, Costa Rica.

The bodies of the foundress wasps almost invariably remain, often intact, inside the developing figs. Therefore, the number of bodies of foundresses can be counted, and their physical dimensions measured. These characteris-

tics of the foundresses (size and number) may therefore be associated with characteristics of the individual fruits that they pollinated, such as number and proportion of flowers developed (total seeds) and of these, the proportion and number that develop into good seeds or wasp-eaten seeds. Of those wasp seeds the number eaten by pollinators and the number eaten by parasitic wasp species can be determined. Of the pollinating wasps reared from any given fruit, the number of male and female wasps can be counted. Therefore, the number of foundresses can also be associated with characteristics of the wasp broods, such as number and sex ratio of offspring^{10, 15, 16}. Also, the foundress distributions which are characteristic for the different fig species and the wasps that pollinate them can be determined (table 2). Therefore, the effects associated with changing numbers of foundresses on both fig and wasp reproduction can be related to the frequencies at which foundress numbers naturally occur in the different species¹⁶. I have followed techniques originally worked out by Dr Donald Windsor for studies of the reproductive biology of *Ficus insipida*, a member of the subgenus *Pharmacosycea* (Windsor, in prep., detailed methods are available on request).

An essential feature of this relationship is that figs are completely dependent on the foundress wasp(s) for the pollination of flowers and the production of viable seeds,

Table 2. Distributions of foundress numbers. For twelve species of *Ficus* occurring in the vicinity of the Panama Canal, the number of fruit crops with 20 fruits sampled followed by the proportion of fruits with between 1 and 6 + foundresses followed by the mean foundress number per fruit.

	n	Number of foundresses per fruit					Mean foundress number
		1	2	3	4	5	
<i>F. perforata</i>	12	1.0					1.00
<i>F. colubrinae</i>	11	0.99	0.01				1.01
<i>F. paraensis</i>	19	0.96	0.03	0.01			1.05
<i>F. pertusa</i>	8	0.95	0.05				1.05
<i>F. obtusifolia</i>	29	0.84	0.12	0.03	0.01		1.21
<i>F. citrifolia</i>	31	0.82	0.16	0.02			1.20
<i>F. bullenei</i>	12	0.74	0.17	0.05	0.02	0.02	1.41
<i>F. dugandii</i>	15	0.56	0.16	0.09	0.08	0.04	2.16
<i>F. nymphaeifolia</i>	16	0.48	0.18	0.10	0.06	0.05	2.64
<i>F. near trigonata</i>	16	0.32	0.27	0.18	0.10	0.06	2.57
<i>F. popenoei</i>	23	0.31	0.28	0.18	0.09	0.06	2.55
<i>F. trigonata</i>	18	0.09	0.14	0.15	0.18	0.15	4.53

i.e., 'female' function. Overall, the fig's investment in 'female' function largely consists of the production of seeds and the attractants to the potential seed dispersers (e.g. sugars, etc. in the fruit wall). It is true that, of the potential seeds that may develop, roughly 50% or more may be eaten by the offspring of the foundress wasp(s)¹⁹. However, the fig is also dependent on the female offspring of the foundress wasp(s) to carry its pollen off to pollinate other figs. Therefore, the seeds eaten by the wasps constitute a large part of the fig's investment in its own pollen dispersal. These seeds are not 'lost to seed predation', but rather, along with the production of pollen, contribute in an essential manner to the fig's 'male' function. The major inefficiency or 'cost' to the fig comes about through the loss of potential seeds or potential female wasps due to the production of male wasps or parasitic wasp species that provide no pollination services to the fig.

The fig pollinating wasps, in turn, depend completely on the fig to provide it with sites to lay eggs and complete its life cycle. In order to produce offspring, female fig wasps must carry pollen to a receptive fruit, pollinate the flowers, and lay eggs in some of them¹¹. Otherwise the flowers will not develop into either viable seeds or seeds that

are eaten by the wasps' developing offspring, and the fruit will be aborted^{3,11}.

An important point to note is that lifetime reproductive success for the foundress wasps (number of offspring) can often be unambiguously determined. This is certainly true in fruits that were pollinated by single foundresses (fig. 1 a). Similarly, the number of developed flowers (total seeds) per fruit associated with pollination by a single foundress may be clearly determined (fig. 1 b). In multiple-foundress fruit, the parentage of the wasp offspring as well as the number of flowers pollinated by each foundress may be uncertain. However, mean numbers of offspring as well as mean numbers of flowers pollinated per foundress may be determined.

On the other hand, determining lifetime reproductive success in the figs is nearly impossible. Most fig trees will produce thousands of fruit per fruiting episode and individual trees may live scores of years and fruit hundreds of times. The level of analysis of fig reproductive success that I present will be the seed and female wasp production per individual fruit because the fruit is the level at which the interaction between individual wasps and the tree is effected. Further, the production of viable seeds and female wasps are clearly the basic currency by which the fig's reproductive success can be measured and will be reflected by the summed productivity of individual fruits. However, a complete analysis of whole tree productivity must include considerations of total fruit production as well as analyses of the factors affecting the productivity of the individual fruits^{4,12} (Herre, in prep.). Later, I will address the question of the relative worth of good seeds and female wasps to the fig.

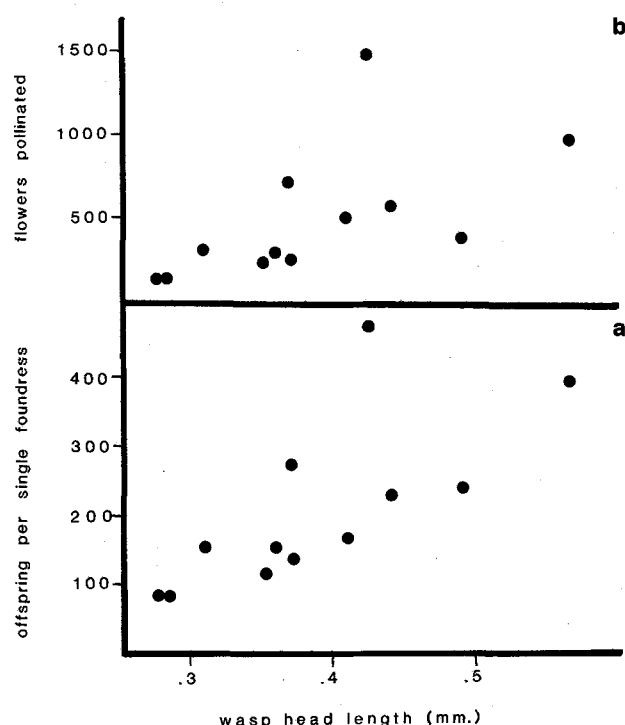


Figure 1. a The relationship between the average head length of the species of fig-pollinating wasp and average number of offspring in fruit with single foundresses (fecundity of one female wasp) for twelve species of *Pegoscapus* wasps that pollinate figs of the *Urostigmata* (strangler) group of New World figs. Physically larger species of fig wasps generally have more offspring. b The relationship between the average head length of the fig-pollinating wasp species and the number of pollinated flowers that develop either into viable seeds or into seeds that are eaten by developing wasps in fruit with single foundresses. Physically larger wasp species generally result in the development of larger numbers of seeds, implying greater ability to pollinate. See text.

Basic characteristics of the species

Table 1 presents the basic characteristics of the fruit of the 12 *Ficus* species. The mean dry weight of the ripe fruit of the different species ranges from 0.05 (*F. colubrinae*) to 2.6 g (*F. obtusifolia*). The mean number of female flowers per fruit in the different species ranges from (approximately) 200 to over 2000. The mean head length of the pollinating wasp species (a good indicator of body size) ranges from 0.275 to 0.563 mm. The mean number of foundress wasps per fruit ranges from 1.0 in *F. perforata* (I have never found fruits with more than one foundress) to 4.53 in *F. trigonata*. The essential point is that among the different species there is a wide range in the dry weights, flower numbers, average foundress numbers, and size of the pollinating wasps. Generally, the species with the highest dry weights also have the largest number of flowers per fruit. However, there are notable exceptions. For example, *F. trigonata* fruits have by far the most flowers, yet are not the heaviest. Their flowers (and seeds) are considerably smaller than those of *F. obtusifolia*. Generally, fig species that have larger numbers of flowers per fruit also have, on average, higher numbers of foundresses per fruit. Here, as well, there are notable

exceptions. For example, *F. obtusifolia* has one of the highest numbers of flowers per fruit and yet has one of the lowest numbers of foundresses, and *F. dugandii*, with a relatively small fruit, has an intermediate number of foundresses. Generally, smaller species of wasp pollinate fig species with fewer flowers per fruit²⁵. A striking exception here is given by *F. paraensis* in which the second largest wasp pollinates one of the smaller fruits. Here, the essential point is that although there are general trends in the relationships among these characters, there are exceptions to all of them. I will now illustrate some consequences of among-species and within-species variation of these characteristics for both wasp and fig reproductive success.

The relationship between wasp size and wasp and fig reproductive success

Between species

There is an over two-fold difference in head length (roughly an eight-fold difference in body size) among the pollinating fig wasp species within the *Pegoscapus* group studied. There is a very close relationship between the body size of the fig pollinating wasp species and the number of offspring that a single foundress mother normally produces (fig. 1 a). However, compared to the other species, the wasp species that pollinate *F. trigonata* and *F. near trigonata* produce many more offspring than would be expected given their body size. These are wasps that pollinate figs that possess very large numbers of flowers per syconium (the largest and the next largest number, see table 1). Interestingly, the wasp species that pollinates *F. popenoei* is also a relatively small wasp in a relatively large fig, yet its fecundity does not tend in the same direction.

Larger wasp species are also generally associated with more flowers pollinated and developing into either good or wasp seeds (fig. 1 b). The striking exception to the general pattern here are the wasps that pollinate *F. paraensis*. Here, a large wasp is the pollinator of a rela-

tively small fig. Interestingly, *F. paraensis* is characterized by a far lower proportion of good seeds than any of the other species (table 3).

Therefore, the relationships among wasp size, fig size, and the reproductive properties of the fig and of the wasp are complex. Generally, as would be expected, larger wasp species can pollinate more flowers and lay more eggs than the smaller species. However, the size of the fig, in particular the number of flowers, may limit (as is apparently the case with *F. paraensis*) or open greater pollination and oviposition opportunities (as is apparently the case with *F. trigonata* and *F. near trigonata*) for wasp species of a given size. Why some species (e.g., *F. popenoei*) have not taken the apparent opportunity to evolve higher fecundities is not clear (figs 1 and 3).

Within-species variation in wasp body size

There is also considerable within-species variation in wasp body size. In a sample of twenty-two pollinator wasp families from one fruit crop of *F. obtusifolia*, there was a significant positive correlation between the head length of the foundress mother (a good indicator of general body size) and her number of offspring ($r = 0.564$, $p < 0.05$, $n = 22$). Moreover, a regression analysis of head length of six female offspring per family against both mother's head length and the average dry weight of the seeds in the fruit in which the wasp families developed was significant ($p = 0.032$). The significance levels for seed dry weight and mother's body size were, respectively, 0.034 and 0.051. This admittedly small sample suggests that there are both environmental (fruit, via seed weight) and genetic (maternal) effects on the body size of offspring wasps. Further, the mean size of offspring was smaller than the size of the foundress mothers. The mean head length of the 22 foundresses was 0.664 mm (s.d. = 0.069). The mean of the 22 family mean head lengths was 0.635 mm (s.d. = 0.030).

If this pattern is representative, these data suggest that of the wasps that are born, the larger ones have a greater chance to reach a receptive fig fruit. Of those foundresses

Table 3. Twelve species of figs listed in ascending order of number of flowers per fruit (see table 1) followed by the number of trees sampled (N), the number of fruit sampled (F), the proportion of the potential number of offspring realized by an average foundress wasp of the species that pollinates that fig species, the proportion of good seeds in an average fruit of that species, the number of good seed in an average fruit of that species, the number of female wasps in an average fruit of that species, and the expected number of good seeds that an average female wasp pollinates in that species ('seed equivalency' of a female wasp). See text.

	N	F	Proportion pot. offspring	Prop. good seeds	Number good seeds	Number female wasps	Ratio good seed/female wasp
<i>F. colubrinae</i>	2	20	0.99	0.42	61	76	0.80
<i>F. perforata</i>	5	100	1.00	0.47	73	79	0.93
<i>F. pertusa</i>	3	49	0.96	0.42	89	108	0.83
<i>F. citrifolia</i>	2	80	0.83	0.46	126	148	0.85
<i>F. bullenii</i>	4	98	0.76	0.48	138	151	0.92
<i>F. dugandii</i>	4	81	0.50	0.44	123	126	0.98
<i>F. paraensis</i>	1	51	0.95	0.32	118	240	0.49
<i>F. nymphaeifolia</i>	3	145	0.46	0.48	278	217	1.28
<i>F. obtusifolia</i>	1	34	0.83	0.55	511	374	1.37
<i>F. popenoei</i>	2	78	0.71	0.54	389	233	1.67
<i>F. near trigonata</i>	4	48	0.75	0.52	572	399	1.43
<i>F. trigonata</i>	3	84	0.25	0.46	845	564	1.49

reaching a receptive fig fruit, the larger ones have more offspring and their offspring tend to be larger. However, the mean size of the wasps leaving fig fruits is smaller than the mean size of the foundresses that enter. The fig fruit appear to act as a 'step down valve' for wasp size. In so far as the number of female offspring represent an essential component of the fig's pollen dispersal, the foundress size appears to be positively associated with the fig's 'male' function. These results from *F. obtusifolia* suggest that heritable phenotypic variation for morphological characters among individuals within one species of a pollination mutualism affects components of fitness in the other. Such a condition would document a prerequisite for coevolution to occur. Nonetheless, there would have to be genetically based variation not only in the wasp's morphological characters but also in the figs' ability to attract or admit into their fruit different sized pollinator wasps^{28, 29} (C. Horvitz, pers. comm.).

On the other hand, the correlations between foundress size and number of offspring were not significantly different from zero in families sampled independently from *F. nymphifolia* ($n = 26$, $r = 0.28$, n.s.), *F. popenoei* ($n = 37$, $r = 0.21$, n.s.), and *F. citrifolia* ($n = 29$, $r = 0.22$, n.s.). If there is an advantage in larger wasp size within these species, then it generally appears to be rather small, and very large sample sizes would be needed to detect it with confidence. Work is underway to replicate and expand these studies both within the same species and across different species. At any rate, both the among-species comparisons and at least one of the within-species comparisons indicate that there may be consequences of foundress size for the reproductive success of both members of this mutualism.

The effects of variation in the number of foundresses on fig and wasp reproduction

The number of female pollinator wasps (foundresses) that enter any given fruit may vary greatly, both among individual fruits within a fig species and among species (table 2). Some of the fig species may be characterized as having very low average numbers of foundresses with low variation among fruit and others as having relatively high average numbers of foundresses with high variation among fruit. This variation often has dramatic consequences for the reproductive success of both the wasp and the fig.

Consequences for the wasps

The fitness of the foundress wasps is affected by the number of co-foundresses in at least two ways. The first is the most obvious; as the number of foundresses rises, the average number of offspring per foundress falls in all of the species studied (figs 3f and 4a). Female wasps always realize the greatest mean reproductive success in terms of number of offspring when they are the sole foundresses. Using the number of offspring that are associated with single foundresses as an indication of the wasp's potential fecundity (fig. 1a), the average female

wasp that successfully reaches and enters a fig fruit may be limited to roughly 25% of its reproductive potential (table 3, *F. trigonata*). While there may be advantages in producing offspring in situations in which they are likely to outbreed, these advantages would have to be large and immediate to compensate for the direct numerical reduction of offspring encountered by most species. The observations that potential foundresses prefer to penetrate non-occupied receptive fruits (Ramirez, pers. comm.) and that potential foundresses appear to push others off receptive fruits in some species (Geber, pers. comm.) suggest that the observed decrease in offspring per capita represents a reduction in fitness.

Within wasp species, as the number of foundresses increases the brood sex-ratios shift, becoming less female biased (fig. 2). This shift is selected for by a form of frequency-dependent selection known as local mate competition^{8, 10, 13-16}, which actually reduces the mean fitness of the wasps. This feature of the shift in wasp sex ratio can be most clearly understood by considering that for a given total number of offspring, the more females there are in the group, the more potential sets of grandchildren there are^{7, 8, 17}. Among species, those that normally have lower foundress numbers tend to exhibit more female-biased sex ratios for broods with any given number of foundresses, apparently owing to the effects of increased mother-daughter relatedness associated with increased inbreeding (fig. 2)^{15, 16}.

An important point to note is that fig fitness is also reduced by this shift in sex ratio because the male wasps that are being produced in increasing proportions as the number of foundresses increases provide no pollination services for the fig. The male pollinators' only direct value to the fig lies in cutting the exit hole for the females, and very few are needed for this. Therefore, those sex

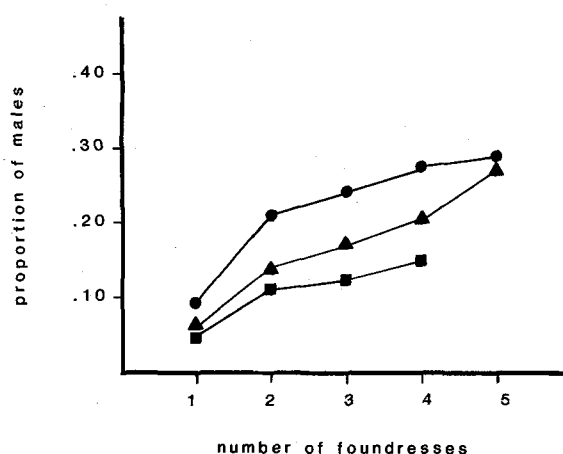


Figure 2. The relationship between the brood sex ratio (proportion of males) and the number of foundress mothers contributing to broods for three species of fig-pollinating wasps (the wasps that pollinate *F. obtusifolia* ■, *F. bullenae* ▲, and *F. popenoei* ●). Notice that as the number of foundresses increases the brood sex ratios become less female-biased. Fig fitness is reduced by this shift in sex ratio because the male wasps that are being produced in increasing proportions as the foundress number increases provide no pollination services for the fig. See text.

ratio shifts that are selected for within the populations of fig wasps by local mate competition are embedded in the reproductive biology of the fig and act to reduce the fig's fitness. The sex ratio shift provides one of the clearest examples of a response to selective pressures in one of the members of this mutualism that is absolutely contrary to the interest of the other.

Consequences for the fig

As should be apparent by now, the interactions underlying effects of varying numbers of foundresses on the fig fruit's production of viable seeds and female wasps are complex. The proportion and number of flowers that are pollinated and develop (fig. 3a), and of these, the number that develop as good (fig. 3c) or wasp seeds (fig. 3b); of the wasp seeds, the number and proportion that produce female wasps (fig. 3d) generally all change with increases in foundress number. These changes may benefit the fig or they may be clearly detrimental. However, across the species the consequences of changing foundress number are comprehensible in terms of the mechanisms that generate them.

As the number of foundress wasps per fruit increases, the number and proportion of flowers that develop into seeds tend to rise in all of the species examined. In most of the fig species with relatively few flowers, a single foundress wasp is usually associated with high pollination and flower development rates (see pollination curve for *F. bullenei*, fig. 3a). In fact, even in the larger fig species, single foundresses may pollinate a substantial

proportion of the flowers. This fact is most strikingly demonstrated in *F. obtusifolia* (fig. 3a), the fig species pollinated by the physically largest wasp. However, in several species (e.g., *F. popenoei*, fig. 3a), one foundress does not seem to be able to pollinate even half of the flowers and flower development rises dramatically with foundress number. Interestingly, this rise is generally less than would be expected on the basis of the demonstrated pollination abilities of single foundresses and assuming random pollination by all co-foundresses (Herre, in prep.).

Of the flowers that develop into seeds, the number and, often, the proportion of those seeds that are eaten by developing wasps generally rises with foundress number (fig. 3b). Of the wasp seeds, the proportion that are eaten by male wasps rises with increasing foundress number (fig. 2). Therefore, the per fruit production of viable seeds and female wasps (which are necessary to the fig for dispersal of its pollen) may rise or fall with increasing numbers of foundresses (fig. 4b). The form of this relationship's rise or fall is apparently determined in part by the relative sizes of the wasp and the fig fruit (number of flowers) and reflects the average number of foundresses that the fig species normally encounters. Fig species with large numbers of flowers in their fruits and medium to small sized wasps (e.g., *F. popenoei*, *F. trigonata*, *F. near trigonata*, and *F. nymphaeifolia*) normally have higher numbers of foundresses per fruit. These species show increased per fruit productivity of viable seeds and female wasps at higher foundress numbers (fig. 4b). Fig

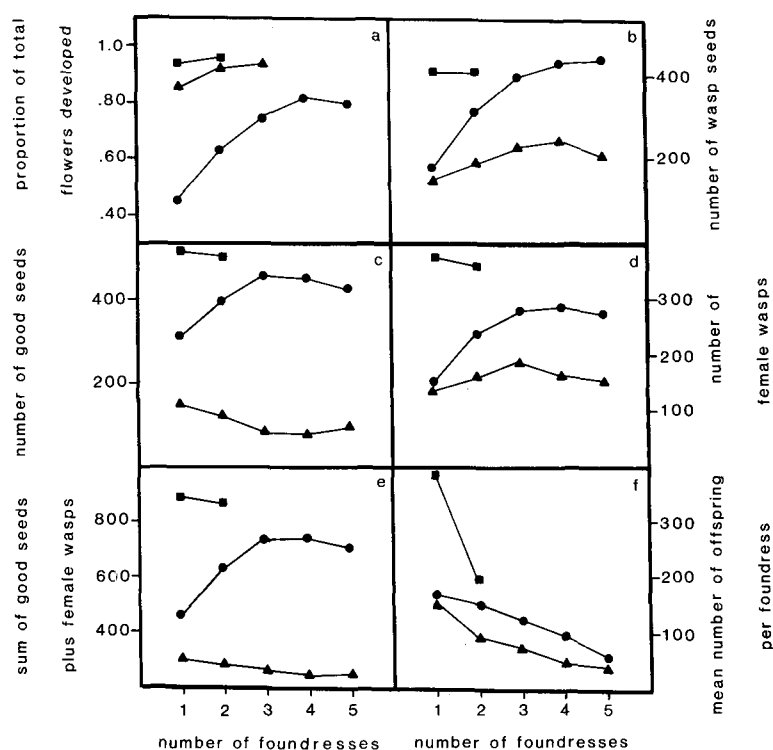


Figure 3. The relationships between the number of foundress wasps per fruit and various aspects of the fig's and the wasp's reproduction for three species of figs, *F. obtusifolia* ■, a large fig with many flowers (~976) pollinated by a large wasp, *F. popenoei* ●, a large fig with many flowers (~1100) pollinated by a relatively small wasp, and *F. bullenei* ▲, a small fig with relatively few flowers pollinated by a relatively small wasp. *a* The proportion of total flowers that develop as a function of the number of foundresses. Generally flower development increases with more foundresses. Notice that single foundress wasps are able to bring about high levels of flower development in *F. obtusifolia* and *F. bullenei* but not in *F. popenoei*, the large fig with physically small wasps. *b* The relationship between the number of seeds eaten by developing wasps and the number of foundresses. *c* The number of viable seeds that develop as a function of the number of foundresses. Notice that only in *F. popenoei* does this number at first rise with foundress number. *d* The number of female wasps as a function of the number of foundresses (see text, fig. 4). *e* The relationship between the sum of good seeds and female wasps (an indicator of fig reproductive success) and the number of foundresses. Notice that only in *F. popenoei* does this rise with the number of foundresses (see text, fig. 4). *f* The relationship between the average number of offspring per foundress wasp (wasp fitness) and the number of foundresses. Notice that in all cases there are fewer offspring per foundress in figs with multiple foundresses (fig. 4a).

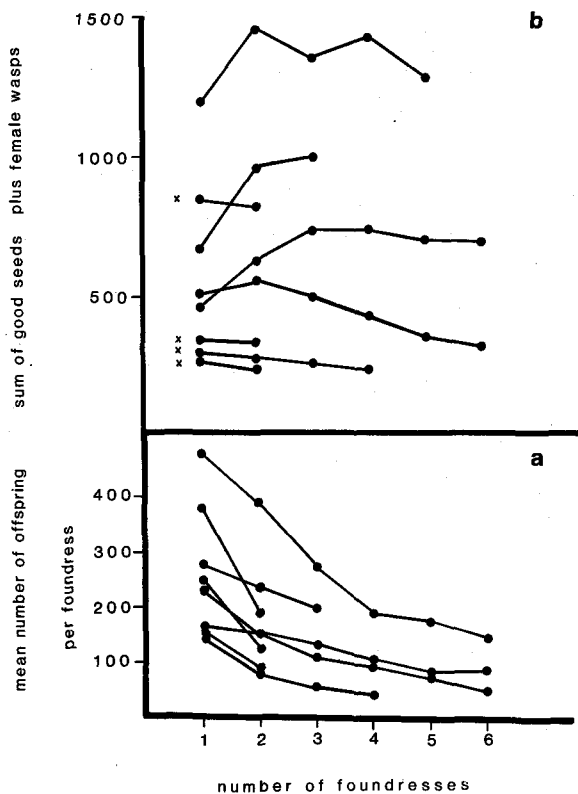


Figure 4. The relationship between the average number of offspring per foundress and the number of foundresses in eight species of fig pollinating wasp. Notice that the fitness of foundresses (as judged by their number of offspring) always drops with increasing foundress number. *b* The relationship between the sum of the number of viable seeds and of the number of foundress wasps (an indicator of fig reproductive success) with the number of foundress wasps. Fig species in which over 80% of the fruits are pollinated by single foundresses are indicated by *. Notice that only in the species that normally have higher numbers of foundresses does the sum of viable seeds and female wasps rise with the number of foundresses (see text).

species with smaller numbers of flowers per fruit (e.g., *F. bullenei*, *F. paraensis*, and *F. citrifolia*) or large fruit with large wasps (*F. obtusifolia*) normally have lower numbers of foundresses. These species show no change or a decline in productivity with increased foundress numbers (fig. 4b). For reasons that are not entirely clear, overall, the natural distribution of foundress numbers appear to more closely reflect the reproductive interests of the figs than of the wasps. This appears to be especially true for the fig species with higher average foundress numbers.

Net effects on fig and wasp reproductive success

We have considered how the interactions among number of flowers per fruit, body size of the wasp, and changes in foundress number may affect both fig and wasp reproductive success. Moreover, for each fig species, it is possible to estimate net per fruit production of good seeds, wasp seeds, total pollinator offspring, female wasps, and offspring per foundress produced by the 'average' fig fruit. These estimates illustrate numerous aspects of the relationship between the fig and the wasp. For example,

in most species the average proportion of good seeds is between 0.45 and 0.55 (table 3). This figure is in broad agreement with estimates published for other species^{4, 19}. It is interesting to note that there is a weak but significant positive relationship between the fruit size of the fig species and the proportion of good seeds.

In addition, we can estimate the likelihood in each species that any given female wasp will successfully reach a receptive fig tree and enter a fruit. This estimate is made by assuming roughly constant numbers of fruit produced during the course of the study and dividing the average female wasp production (table 3) by the average foundress number per fruit (table 2). As a rough average across all the species, 1 out of 120 female wasps successfully enters a receptive fruit on another tree.

We know that each female wasp consumes the contents of one seed as it matures. How many good seeds will it generate? Given the likelihood of a female wasp reaching a receptive fig fruit, the average number of foundresses per fruit, and the average good seed content per fruit (tables 2 and 3), we can estimate the number of viable seeds that a female wasp, on average, brings into being using the pollen of the tree in which it was reared. That is, for each species we can calculate the rough 'seed equivalency' of female wasps (table 3). The 'seed equivalency' of female wasps will be positively associated with the proportion of good seeds in the average fruit, the average proportion of male wasps, (and, therefore, negatively associated with average foundress number), and the average levels of parasitism per fruit.

Fig species with smaller fruit tend to have lower proportions of good seeds. Also, the smaller species of figs generally have the fewest foundresses and, therefore, the wasp broods exhibit the most female-biased sex ratios. These two factors underlie the observation that in smaller fig species the average female wasp does not replace the potentially good seed that it eats in order to mature. On the other hand, in the larger species, an average female wasp more than replaces the potentially good seed that it eats (fig. 5).

We might expect that a mutant fig of one of the smaller species that could sacrifice a female wasp in order to produce a good seed would be favored. By the same token, we might expect that a mutant in one of the larger species that could sacrifice a good seed in order to produce a female wasp would be favored. It is probably also clear that given the complex relationships that exist between wasp size, fig size, foundress number, wasp sex ratio, and reproductive output of both the fig and the wasp that it would not be at all straightforward to produce such changes.

However, the seeds of fig species with larger fruits tend to be dispersed primarily by larger species of bats² (Handley, Stockwell, pers. comm. and pers. obs.). Generally, the larger species of bats have larger home ranges. Therefore, one consequence of larger fruit size may be larger average dispersal distances for the seeds. If the relative

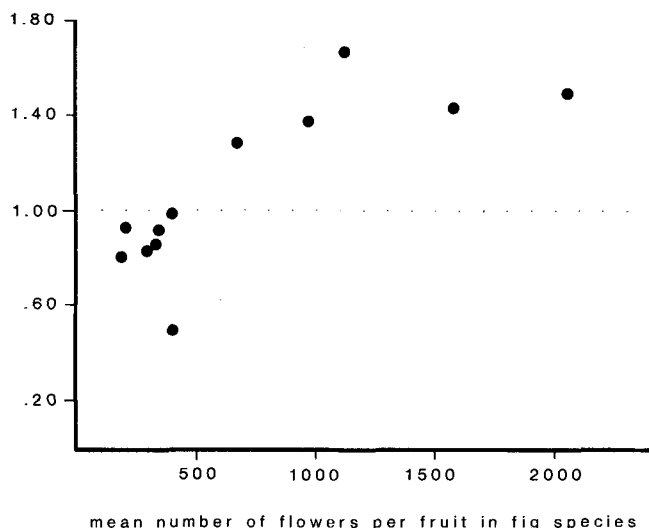


Figure 5. The relationship between the number of viable seeds that a newborn female fig wasp may be expected to pollinate (the wasp's expected 'seed equivalency') and the fruit size (number of flowers per fruit) in twelve species of figs.

seed to pollen dispersal distances are in fact larger for larger fruited species than we might expect selection to favor relatively greater 'female' investment in these species⁵.

These observations suggest that some characteristics (e.g., low foundress number, small fruit size) may favor efficiency of the fig's 'male' (pollen dispersal) function while others (e.g., high foundress numbers, large fruit size) may favor the 'female' (seed production and dispersal) function. If these observations are generally true, then the patterns in the tradeoffs between fig 'male' and 'female' functions that are illustrated across these monoecious species may give insight into the character combinations and the selective forces that could promote specialization of individual trees for male or female function, i.e., the evolution of dioecy in figs. Further, we may begin to quantify the selective forces that may be underlying the relative stability of monoecy and dioecy in figs^{21, 27} (and Herre, in prep.).

Dioecy has apparently evolved at least twice in the genus *Ficus*^{1, 21, 27}. In general, we should expect that in dioecious species male fruits should be small compared to the female fruits (male fruits do not need to be an attractive food for seed dispersers). We should expect that the number of foundresses per fruit should be low or foundresses should be highly related in order to promote highly female biased sex ratios and efficient pollen dispersal. Female fruits should exhibit large numbers of foundresses, if possible from many different 'paternal' trees, so as to increase the efficiency of pollination and the genetic variability of the pollen. Female fruits should be relatively large and attractive to seed dispersers and produce their fruit during times of the year that promote seed germination and establishment. These predictions seem to be

generally supported by what is known of the morphology and ecology of dioecious species^{18, 21, 27}.

Discussion

Within the species of the *Urostigma* group, there is still no completely satisfactory understanding of the factors that prevent the wasps from evolving the ability to use all of the fig's seeds as sites for rearing its offspring. The observation that even with large numbers of foundresses individual fruits may still produce high proportions of good seeds rules out an insufficient egg supply as an explanation. On the other hand, the distribution of style lengths has frequently been identified as the mechanism by which the fig keeps some of the ovaries out of reach of the wasp's ovipositor so that they can develop as good seeds. It is interesting to note that the species with by far the lowest proportion of good seeds, *F. paraensis*, has an extraordinarily large wasp in relation to the size of the fruit. It may be that the comparatively larger foundress wasps have or can force access to more ovules than can the smaller wasps in the small, medium, or large figs.

However, Bronstein⁴ found that a large proportion of the flowers of *F. pertusa* that were within reach of the wasp's ovipositor did not develop into seeds eaten by the wasp's offspring, casting doubt on the generality of the proposition. Further, based on detailed dissections of flowers in *Ficus ottoniifolia*, an African species in the *Urostigma* group, Verkerke³¹ has suggested that style width and the resulting style firmness rather than style length is the critical factor that controls wasp access to the fig's ovaries. This promising suggestion lends itself to further testing.

Also, although clearly an important factor affecting the reproduction of both the wasp and the fig, the mechanisms underlying the observed foundress distributions are also not understood. Although it is logical to suppose that tree density must have an influence at some spatial level (if there are no trees, then there can be no wasps), there is no obvious relationship between the commonness of these species in the study area and their average foundress number. A first approximation towards an answer may lie in the observation that when the fruits are smaller, generally more of them may be produced, diluting the potential foundresses that arrive at a tree. On the other hand, we do not even know if these same species exhibit similar foundress distributions over different parts of their range.

Do the figs limit the wasps? Yes. First, fig wasp population size is directly limited by the total number of individuals of the host fig. Generally, wasp populations will be constrained by the total number of wasp-containing seeds in what at any one time is a fraction of the total number of fig trees. Moreover, if the female wasps do not encounter a receptive tree, they will leave no offspring. Of the female wasps born, only 1 in 120 (roughly) successfully enters a receptive fruit in the average species

studied. Even if an individual female wasp does enter a receptive fruit, the 'average' foundress, across all of the species, only realizes roughly 75% of its reproductive potential, as judged by the number of offspring associated with single foundresses of that species (table 3). Both the population size and the reproductive success of individual wasps are clearly limited by their interaction with the fig.

Do the wasps also limit the figs? The population size of fig trees ultimately depends on successful recruitment of seedlings. This depends not only on the successful production and germination of seeds, but on their dispersal to appropriate habitats. Many species of figs only recruit in riverine environments or large light gaps. There is evidence that different species of strangler figs are preferentially associated with certain host tree species³⁰ (and pers. obs.). Appropriate habitat types are likely to be determined by fig physiology, and access to those habitats is likely to be determined by the behavior and availability of appropriate seed dispersers.

Also, the photosynthetically active tissues in fig leaves and fruits are the source of all the fixed carbon used to produce fruits, seeds, wasps, pollen, etc. In that sense, the entire system is ultimately resource-limited. Further, I have found clear indications of resource-limitation in some fruit crops (unpublished data).

However, the limiting factor for an individual fig's production of seeds and/or female wasps in any given fruiting episode a given fig tree may be pollinator-limited, in the sense that some fruit that could have been supported remained entirely without pollinators and were therefore aborted. It may also be that all fruits were pollinated but with an insufficient number of pollinators to develop all the flowers into seeds and produce all the wasps that could have been developed. In this case, absence of aborted fruit would be misleading as an indication of a lack of pollinator limitation. However, it may also be that fruits without pollinators are aborted but those that remain on the tree do not have sufficient resources to develop the flowers that have been pollinated. In this case, the presence of unpollinated, aborted fruit would be misleading with respect to the absence of resource limitation. Instead, the much more difficult question of whether it is better for the tree to have fewer, more fully developed fruits or more, less fully developed fruits is raised^{4,5}. Finally, the possibility of too many pollinators is raised; pollinator limitation of both 'female function' (seed set) and 'male function' (production of female wasps) caused by an over-abundance of foundresses seems to be a real possibility (figs 3e and 4b).

It appears that fruit and seed production in individual crops may at times be limited by the availability of wasps⁴ (Ramirez, pers. comm., and pers. obs.). Also, the decreasing female bias in the sex ratio of wasp broods associated with increasing foundress number works against the reproductive interests of the fig. On the other hand, the observations that the wasp populations are

directly limited by host fig abundance, that individual wasp reproductive success is generally limited by their interaction with the fig, that the wasps have not evolved the ability to exploit all of the seeds in fig fruits for the rearing of their offspring, and that the natural foundress distributions more clearly reflect the reproductive interests of the fig seem to indicate that the figs are generally the 'controlling partner' in this mutualism.

The results and the interpretations presented here should properly be considered preliminary and tentative, requiring further substantiation both within these species and across others. The patterns presented here may not necessarily be expected to apply to other groups of figs. For example, it appears that many of the details of the biology of fig species in the monoecious New World sub-genus *Pharmacosycea* are different and some of the findings here do not apply (Windsor and Herre, in prep.). However, it is clear that the coevolution of the relationships of figs and wasps involves the interaction of a large number of complex and often antagonistically related characters. Specifically, both among and within the species studied here, wasp size, fig fruit size, and the foundress number may all interact to raise or lower different components of the reproductive success of the fig and overall success of the wasp. Further, these characters interact in complex yet systematic ways that, in part, underlie the many different variations observed on the basic theme of fig and wasp biology.

Acknowledgments. I principally thank Donald Windsor. He introduced me to the figs studied here, helped support the work with both institutional and personal funds, and provided a wealth of techniques, ideas, and encouragement. This work would never have happened without his help. I thank Esther Jaen, Rob Mihalik, Lisa Papernik, and Elena Rodriguez for field assistance. I thank Barbara Taylor and Diane Mahoney of the Savannah River Ecology Laboratory for allowing me use of their *Bio-Quant* system for measuring body parts of the wasps. I thank Egbert Leigh, Henry Howe, Lisa Papernik, Eric Fischer, Martin Burd, Jess Zimmerman, Finn Kjellberg, William Ramirez, and Jonathan Losos for comments on earlier drafts of this manuscript. I thank Donald Windsor, Egbert Leigh, Joseph Wright, Alan Smith, Carol Horvitz, Douglas Schemske, Janis Antonovics, Gene Schupp, Jess Zimmerman, Monica Geber, Jan Sevenster, Eldridge Adams, Bob Srygley, Jill Gregg, Charles Handley, Elizabeth Stockwell, Truman Young, and William Hamilton for stimulating discussions during the course of the work. This work was primarily supported by the Smithsonian Tropical Research Institute through its Environmental Sciences, Pre- and Post-Doctoral Fellowships Programs and the Department of Biology of the University of Iowa through its Teaching and Research Fellowships Programs. Finally, I thank Daniel Janzen for first introducing me to the fascinating biology of the New World figs and their wasps.

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0014-4754/89/070637-11\$1.50 + 0.20/0

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Phenology of fruit and leaf production by 'strangler' figs on Barro Colorado Island, Panamá

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Summary. Fruit and leaf initiation by 26 trees representing five 'strangler' *Ficus* species in the subgenus *Urostigma* were monitored for 5–8 years in a seasonal lowland forest of central Panamá. Individual trees of each species initiated fruit in synchronized 'crops'. High variation in the number of crops, intervals between crops and dates of crop initiation indicate that these species, like species in the subgenus *Pharmacosycea*, initiate fruit crops the year around. Nevertheless, mean crop initiation dates for four of five species fell within the four-month dry season. Similarly, all species produced new leaf flushes throughout the year, however, mean leaf flush dates of all species fell within the first three months of the dry season.

Key words. Fig; *Ficus*; phenology; neotropical; Panamá.

Setting *Ficus* apart from most other dicotyledonous plant genera is an obligatory association with agaonid wasp pollinators^{10,15,24,30}. Most *Ficus* species have only a single reliable wasp pollinator species^{23,25} and pollinator species normally associate with only a single fig species³. Female agaonid wasps arrive, enter the fig ostiole, pollinate many of the stigmatic surfaces within the fig while laying eggs of the next generation of wasps in the ovules, and then die. Wasp larvae prey on roughly one-third to one-half of developing seeds^{5,11,16}, eclose, mate, gather pollen and then disperse to other figs to start the cycle again.

The development of flowers within syconia (the compound reproductive structure or 'fig') is highly synchronized²⁸, and the development of syconia within crowns of individual trees is normally synchronized into recognizable 'crops'^{4,25}. Both Janzen¹⁵ and Bronstein^{3,4} argue that crop synchronization allows individual trees to send a stronger chemical signal and thus be better competitors for pollinating wasps in the neighborhood. Field observations suggest that unlike a great many tropical trees which have tightly synchronized anthesis and fruit production cued by environmental changes such as dry season rainfall^{1,9,13,14,21,22}, the reproduc-