The ecology of the New World fig-parasitizing wasps *Idarnes* and implications for the evolution of the fig–pollinator mutualism

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SUMMARY

Figs and their pollinating wasps are perhaps the classic example of an obligate mutualism. In addition, figs have a suite of non-pollinating parasitic wasps whose basic ecology is largely undescribed. Figs therefore present the interesting situation of a host that has two closely related taxa associated with it, one of which is mutualistic, the other parasitic. We show that the wasps belonging to the most abundant genus of New World parasites, the *Idarnes* wasps, develop at the expense of the pollinating wasps and not the viable seeds. However, the *Idarnes* wasps are not true parasitoids. We interpret these results to mean that the *Idarnes* wasps are in direct competition with the pollinator wasps for the same pool of flowers in which the larvae of either group can develop. Further, we infer that there is also a pool of flowers that cannot be exploited by either of these taxa. The observation that the pollinators and the parasites oviposit from different sides of the fruit strongly suggests that the basis for preserving some of the flowers to develop as viable seeds is not a direct result of spatial position of the ovaries or style length, as has been previously suggested. This idea is corroborated by detailed observations in many other fig systems. Taken together, these findings suggest an explanation for the stability of the fig–fig-pollinating wasp mutualism, as well as the structure of its parasite community.

1. INTRODUCTION

The factors that influence whether a pair of interacting species develop to mutualistic as opposed to parasitic relations have been the subject of considerable theoretical and empirical attention (Hamilton 1964; Futuyma & Slatkin 1982; Maynard Smith 1982; Thompson 1986; Bull *et al.* 1991; Leigh 1991; Nowak & May 1992; Taylor 1992; Herre 1993). For example, given the selfish interest of interactions even at the level of the genome (Eberhard 1980; Hurst 1992), several workers have found mutualisms and cooperation between unrelated organisms difficult to explain (Axelrod & Hamilton 1981). However, symbioses are ubiquitous throughout nature and probably provide the basis for eukaryotic life (Margulis 1981). But, given the assumption that parasites tend to evolve benign relations with their hosts over time, other workers have found the existence of coevolved parasites that obviously have a detrimental effect on their host difficult to explain (see Toft & Karter 1990). Yet there exist many parasites with ancient host associations that have not evolved to become harmless, and the usefulness of the idea that parasites become benign over time has been questioned (Ewald 1983; May & Anderson 1983; Thompson 1986; Toft & Carter 1990; Herre 1993).

Figs and their pollinating wasps provide a classical example of a highly coevolved mutualism (Corner 1940; Ramirez 1974; Galil 1977; Wiebes 1979; Berg 1989). Moreover, there are many associated non-pollinating wasps that are apparently parasitic and provide no obvious benefit to the fig. Figs therefore have two taxonomically closely related groups of wasps associated with them, one of which is comprised of mutualists and the other parasites.

The figs and their mutualistic pollinator wasps depend completely on each other for their long-term survival. However, the reproductive interests of the two partners are not identical (Kjellberg *et al.* 1987; Herre 1989). The fig needs female flowers, both for the production of viable seeds, and as a means for supporting the development of the pollinator wasps that will act as disperser agents for its pollen. However, the pollinating wasp only benefits directly from the fig's production of female flowers that are eaten by its own offspring. Pollinating wasps that could increase their own reproductive success, at the cost of the fig's viable seed production, would therefore be favoured by natural selection. None the less, the fig–pollinator interaction has existed for over 40 Ma (Collinson 1989) without the pollinators overexploiting the figs, begging the question of how this stability is maintained.

Figs also support a diverse community of parasitic non-pollinating wasps (Hamilton 1979; Janzen 1979; Godfray 1988; Murray 1989; Bronstein 1991; Compton & Hawkins 1992; Compton & van Noort 1992; Hawkins & Compton 1992; Boucek 1993; Compton 1993; Compton *et al.* 1994). Both morphological (Gordh 1975; Ulenberg 1985) and molecular data (Herre *et al.*, unpublished results) suggest

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an ancient association between these parasitic wasps and their hosts. Despite providing no pollinating services, and so having no apparent benefit to the fig, the parasitic wasps are very common, often out-numbering the pollinating wasps in an individual fruit (S. A. West & E. A. Herre, unpublished results; Janzen 1979; Bronstein 1991). However, very little is known about the ecology of any of the parasitic wasp species. Basic questions include: what are the natural histories of these non-pollinating wasps, and do such wasps have any detrimental effects on their host? Indeed, it has even been suggested (Bronstein 1991) that one reason these parasitic wasps may be so successful is that they have no fitness cost to the fig.

To understand fully the effect of these parasitic wasps on their host figs we have to determine their larval diets. More specifically, are the parasites developing directly at the cost of pollinator wasps, or viable seeds, or merely draining resources from the fruit? Theoretically, it is possible to answer this by looking for correlations between parasite presence, pollinator wasp and viable seed production. However, attempts to determine the larval diets of the parasitic wasps in this way have led to inconclusive results (Bronstein 1991). This is possibly due to the many other confounding factors that also influence the production of pollinator wasps and viable seeds. For example, the number of fig-pollinating wasps (found-resses) that enter a fruit to oviposit, and the resources available to that fruit, have a large effect on the number of pollinators and viable seeds produced in a fruit (Herre 1989; Bronstein 1992). These factors will cause large differences in viable seed and pollinator wasp production both between different trees and between different fruits on a tree, and should be statistically controlled for.

In this study we report on six species of monoecious New World figs (*Ficus*, subgenus *Urostigma*, section *Americana*), each with its own species of *Pegoscapus* pollinating wasp and *Idarnes* parasitic wasp. By controlling statistically for the effects of variable foundress number and between tree differences we show that the *Idarnes* parasites have a detrimental effect on the reproductive success of their hosts. Specifically, pollinator wasp production is negatively correlated with the number of *Idarnes* wasps emerging from a fruit. In contrast, there is no significant correlation between the number of *Idarnes* wasps emerging the viable seed production. Further, the *Idarnes* wasps are able to develop in the flowers of fruit that have not received pollinators. We interpret these observations to mean that the *Idarnes* wasps are not parasitoids of the pollinators but rather are in direct competition for flowers with the pollinator wasps. Therefore, the *Idarnes* and the pollinator wasps both use the same set of flowers to develop despite ovipositing in very different ways from different sides of the fruit wall. This observation strongly suggests that figs have come unexploitable flowers that cannot be used by either of these groups of wasps, and that the mechanism involved is not spatial position, as has been generally accepted (Moore 1994). This idea is corroborated by details from many other fig systems. The inability of the pollinator wasps to use all the flowers in a fruit to rear offspring helps explain the stability of the mutualism. In addition, these observations imply that the success of the parasitic *Idarnes* wasps is due to their exploiting the same resource as the pollinator wasps, which might make it difficult for the fig to exclude them.

2. BACKGROUND BIOLOGY

All studies were conducted in the vicinity of the Panama Canal with 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*. The host fig species studied were *Ficus bullenei*, *Ficus citrifolia*, *Ficus costaricana*, *Ficus obtusifolia*, *Ficus popenoei* and *Ficus trigonata*. The *Idarnes* wasps studied here are all in the *flavicollis* and *carme* species groups (Boucek 1993). Among these different species the fruit show a wide range in dry mass, number of flowers and average foundress number, as well as the size of both the pollinating and the *Idarnes* wasps (Herre 1989). Further, the size of the *Idarnes* and the pollinating wasps are correlated, and related to the mass of the seeds in the fruit in which they developed (Herre 1989).

Individuals of all the fig species may produce one to three fruit crops a year (Windsor *et al.* 1989). At the initiation of a fruit crop, the tree synchronously produces large numbers of receptive fruit. Mated, pollen-bearing female pollinating wasps (foundresses) arrive at the tree, enter these fruit, pollinate the receptive uniovulate flowers, probe the flowers with their ovipositors, and attempt to lay eggs in the ovaries. The foundress wasps die inside the fruit after pollinating and laying eggs. After being pollinated, a certain proportion of the total flowers begin to develop. Fruits that are not pollinated are usually aborted. In contrast to the pollinator wasps, the *Idarnes* females do not enter the fruit. Instead they penetrate the fruit wall with their characteristic long ovipositors and lay eggs from the outside. Importantly, individual larvae of both the *Idarnes* and the pollinators develop at the expense of one flower within the fruit. The abundance of the *Idarnes* species varies enormously between species, and between crops of the same species. The *Idarnes* species studied here occur on average in between 12 % (*F. bullenei*) and 79 % (*F. trigonata*) of all fruit sampled.

As the fruit ripens, pollen-bearing male flowers grow inside the fruit. Just before final ripening takes place, the 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 pollinating wasp males chew open these seeds and mate with the females. In contrast, the *Idarnes* males possess powerful mandibles and, as in many other parasitic fig wasps, indulge in combat with each other over females (Hamilton 1979; Murray 1989; Herre *et al.* 1995). The females of the pollinating wasps then emerge from their seeds, groom themselves, collect pollen and leave through a hole cut in the fig wall by their males. It is important to note

Table 1. *General linear model* ANCOVA *on number of pollinators reared out of individual fig fruits for six species of* Ficus

(The crop sampled from, number of foundresses of each fruit sampled, and the number of *Idarnes* wasps reared out of each fruit sampled were used as covariates. *Ficus* species is followed by number of crops sampled per species (n), total number of fruit sampled (N), followed by the proportion of total variance in the number of pollinators explained by each of the covariates. In all cases there was a significant negative relation between the number of *Idarnes* wasps reared from a fig fruit and the number of pollinating wasps.)

| | | | total variance explained (%) | | | |
| | | | | number of | | Effect of |
fig species	n	N	Crop	foundresses	*Idarnes*	*Idarnes*
F. bullenei	3	31	12	37***	12*	negative
F. citrifolia	3	73	1	24***	14***	negative
F. costaricana	4	27	14	19	21*	negative
F. obtusifolia	3	63	27***	1	12***	negative
F. popenoei	4	113	1	55***	12***	negative
F. trigonata	4	74	3	59***	7***	negative

* $P < 0.05$.
*** $P < 0.01$.

that, because the female pollinating wasps are the fig's only pollen dispersal agent, they represent the fig's allocation to male functions. The *Idarnes* females emerge and leave without collecting pollen.

The female flowers within the fruit vary continuously, ranging from those with ovaries close to the hollow centre of the fruit, that is, close to the stigmatic surfaces (short-styled flowers) to those with ovaries close to the wall of the fruit, far from the stigmatic surfaces (long-styled flowers). The ovaries of the short-styled flowers are closer to the ovipositing foundress wasps. Of these flowers that develop, the long-styled flowers tend, in general, to develop as viable seeds, whereas the seeds developing from short-styled flowers tend to be eaten by the wasps' offspring. It should be noted, however, that variation in seed length is gradual and by no means bimodal, and that the characterization of flowers as 'short' and 'long' styled is an oversimplification made purely for convenience. Style length has been proposed as the mechanism that prevents some flowers being oviposited in by pollinator wasps (see Discussion).

3. METHODS

Fruit was collected late in the ripening cycle when only the male wasps had already emerged from their seeds, and the number of foundresses within each fruit was recorded. The fruit were opened and sealed between two Petri dishes, and all the wasps were allowed to emerge into the Petri dishes before being frozen. Later, the number of viable seeds and each species of wasp within each fruit (including the wasps that emerged from it) were recorded. Importantly, this technique allows the number of pollinator wasps and seeds that developed within each fruit to be associated with both the number of foundresses that entered the fruit and the number of *Idarnes* wasps that also developed within the same fruit. An exception was *F. costaricana*, in which only pollinator wasps and *Idarnes* were counted.

4. ANALYSIS

Statistical analysis was done with GLIM (Crawley 1993), with data from each species being analysed separately. To determine the effect of the *Idarnes* wasps, the viable

seed and pollinator wasp production was compared across fruits with variable parasitism rates. We distinguished between fruit with different numbers of foundresses to allow for the large difference that foundress number can have on wasp and seed production among fruit of a single crop (Herre 1989). Further, we also distinguish between crops to allow for the fact that differences may occur between trees is viable seed and pollinator wasp production for many reasons unconnected to the presence of parasitic wasps. An example of such a difference comes from the study of *F. pertusa* (Bronstein 1989 *a*, *b*, 1992) in which there was enormous variation between crops in the average number of pollinator wasps and viable seeds produced. Specifically, crops in which a higher proportion of fruit were pollinated and not, therefore, aborted, produce fewer viable seeds and pollinator wasps per fruit than did crops with relatively low pollination rates and the subsequent high abortion rates (Bronstein 1988 *a*, *b*; M. C. Anstett & F. Kjellberg, personal communication). This pattern strongly suggests that the Costa Rican population of *F. pertusa* is largely resource limited and that the trees that support the fewest fruit are able to allocate the most resources to each (Herre 1989). We statistically controlled for these effects by doing an ANCOVA analysis with crop and foundress number as factors.

5. RESULTS

The results from all species are summarized in tables 1 and 2. There was large variation in pollinator wasp and viable seed production associated with the number of foundresses entering a fig (see Herre 1989) and between-tree differences. The presence of *Idarnes* wasps had a significant negative correlation with pollinator wasp production in all six species of fig studied. In contrast, there was no significant correlation between the number of *Idarnes* wasps and seed production in the five species in which seeds were counted.

It is interesting to note that if the confounding effects of foundress number and between-crop effects are not accounted for in the analysis then, in some cases, the correlation between the *Idarnes* and the pollinator

Table 2. *General linear model* ANCOVA *on number of viable seeds contained in individual fig fruits for five species of Ficus*

(The crop sampled from, number of foundresses of each fruit sampled, and the number of Idarnes wasps reared out of each fruit sampled were used as covariates. *Ficus* species is followed by number of crops sampled per species (n), total number of fruit sampled (N), followed by the proportion of total variance in the number of viable seeds explained by each of the covariates. In all cases there was no significant relation between the number of *Idarnes* wasps reared from a fig fruit and the number of viable seeds.)

| | | | total variance explained (%) | | | |
fig species	n	N	Crop	number of foundresses	Idarnes	Effect of Idarnes
F. bullenei	3	31	26*	1	2	positive
F. citrifolia	3	70	18***	2	2	negative
F. obtusifolia	3	39	59***	2	3	negative
F. popenoei	4	113	27***	8	1	negative
F. trigonata	2	47	8	16	1	negative

* $P < 0.05$.
*** $P < 0.01$.

wasps is not detected. For example, in *F. trigonata*, an analysis of the data without foundress number and crop as factors showed no effect of *Idarnes* presence on pollinator production ($F_{1,73} = 2.33, p > 0.05$).

6. DISCUSSION

In all six fig species studied the *Idarnes* wasps had a detrimental effect on the reproductive success of their host fig. Specifically, the *Idarnes* wasps had a negative effect on pollinator wasp production, which directly effects the fig's ability to disperse pollen. However, there was no significant effect on viable seed production. Interestingly, additional observations showed that the *Idarnes* wasps are not direct parasitoids of the pollinators. Some parasitic galling wasps can prevent unpollinated fruit being aborted (Galil & Eisikowitch 1968; Compton 1993), and we observed *Idarnes* wasps develop in these figs that had received no pollinators, in *F. popenoei*, *F. dugandi* and *F. trigonata* in Panama. This has also been observed to occur in *F. pertusa* in Costa Rica (Bronstein 1991). These parasitic galling wasps occur at much lower densities and in very different galls from the *Idarnes* wasps. Therefore, the *Idarnes* wasps are not parasitoids of these galling wasps. These observations provide strong evidence that the *Idarnes* wasps are not direct parasitoids of the pollinators. Instead, these results (coupled with the observation that the *Idarnes* wasps usually emerge from the layer of short-styled flowers (S. A. West & E. A. Herre, unpublished observations; Herre 1989)) suggest that the *Idarnes* utilize and compete for the same pool of flowers as in the pollinating wasps across a range of fig species. In addition, the *Idarnes* wasps occur in significantly greater numbers in the fruit that have not received pollinators (Bronstein 1991), suggesting that parasitic reproduction is greater in the absence of the pollinating wasps.

The *Idarnes* parasites appear to be the most common type of non-pollinating fig wasp parasite in figs of the subgenus *Urostigma* studied in Mexico (Gordh 1975), Costa Rica (Bronstein 1991; E. A. Herre, unpublished results), Brazil (Hamilton 1979), Peru (E. A. Herre,

unpublished results) and in Panama (this study). This success of the *Idarnes* wasps in exploiting the fig–pollinator mutualism may be explained by the fact that these parasites are apparently utilizing the same pool of flowers as the pollinators. The parasitic wasps exploit flowers in which the pollinators grow and in which the fig apparently cannot differentiate between a parasite and a pollinator. In addition, the *Idarnes* parasites arrive at a receptive tree at the same time as the pollinators (S. A. West and E. A. Herre, unpublished results: Bronstein 1991), and appear to use the same attractant cues as the pollinators to find receptive trees (E. A. Herre, unpublished results; Bronstein 1991). Therefore, a fig tree cannot attract its pollinator wasps without also attracting its *Idarnes* parasites.

Molecular studies suggests that different *Idarnes* species are associated with each fig species, and that the phylogeny of these *Idarnes* parasites is congruent with that of the pollinating wasps (Herre *et al.*, unpublished results). It also appears that the pollinator wasps are a sister taxa to the *Idarnes* and other parasitic wasps such as *Critogaster* and *Philotrypesis* (Boucek 1993). Therefore, although both the pollinating and the Idarnes wasps currently exploit the same resource, and apparently have always done so, they have evolved very different life-history strategies to do this. The pollinator wasps are usually constrained to enter only one fig fruit and then reproduce in a short burst of time. By comparison, the parasitic wasps are able to ovoposit in different fruits on individual trees, and so are not constrained to 'put all their eggs in one basket'. The resulting differences in population structure of the pollinators and the parasites are reflected in differences in sex ratios and male mating strategies (Hamilton 1979; Murray 1989; Herre *et al.*, 1995).

The data presented in this study also shed light on the interaction between figs and their pollinators. A major unanswered question is why do the fig-pollinating wasps not evolve the ability to exploit more flowers at the expense of the figs' viable seed production (Ramirez 1974; Janzen 1979; Murray 1985; Kjellberg *et al.* 1987; Bronstein 1988*b*, 1992; Herre 1989; Addicott *et al.* 1990)? It has been shown that, as the

number of pollinating foundress wasps per fruit increases, the total number of developing wasps plateaus, while the average brood size per foundress declines (Herre 1989). Viable seeds are still produced in the fruit in which pollinator wasp production has reached its maximum (Herre 1989). This suggests that the number of flowers in which the wasps can lay their young is limited. It had been generally assumed that style length variation was the mechanism by which figs prevented some flowers developing as wasps (Galil & Eisikowitch 1968; Ramirez 1974; Galil 1977; Janzen 1979; Kiester *et al.* 1984; Murray 1985; Kjellberg *et al.* 1987; Bronstein 1992; Moore 1994). Under this scenario the ovules of long-styled flowers are thought to mature as good seeds because they are safely out of the reach of pollinating wasps, but the ovules of short-styled flowers are close enough to the pollinating wasps to have eggs laid in them. However, accumulating empirical evidence is inconsistent with this idea, and instead demonstrates that the pollinating wasps can reach a much larger proportion of flowers than they actually use (Kjellberg *et al.* 1987; Bronstein 1988*b*; Compton & Nefdt 1990).

Although the *Idarnes* wasps are closer to the long-styled flowers when ovipositing, these are not the flowers they exploit. Instead they appear to reach past them with their ovipositors to the short-styled flowers. The idea that ovary position is the only determinant of whether or not flowers can be used by ovipositing wasps is inconsistent with this observation. These results suggest that, despite being able to reach all the seeds in a fig fruit, both the pollinating and the parasitic wasps only use the shorter-styled flowers. This in turn suggests that a certain proportion of flowers cannot be used by any pollinator or parasite wasps, and which result in unbeatable seeds. This idea is corroborated by details in many other fig systems. For example, there is no evidence that any non-pollinating fig wasps are seed predators (Compton *et al.* 1991; Compton & van Noort 1992). Further, it has been noted in *Ficus sur* (subgenus *Sycomorus*) (J. Rasplus, personal communication) and *F. pertusa* (Bronstein 1991) that all the parasitic wasp species exploit the same layer of flowers as the pollinator, despite having different ovipositor lengths. Moreover, there is a distinct absence of parasitic wasps on the fruit of female dioecious fig trees (Compton *et al.* 1994; J. Rasplus & F. Kjellberg, personal communication) which produce only viable seeds and no pollinator wasps.

These observations strongly suggest that some portion of the flowers can only develop as viable seeds, while others can develop as viable seeds (if no egg is laid in them) or support the development of wasps (if an egg is laid in them). One possible mechanism might be that the surface of the ovaries of certain flowers cannot be penetrated by the ovipositors of either the pollinators or the parasites. Consistent with this suggestion is the observation by Verkerke (1986) that the pedicals of longer-styled flowers are also wider and firmer. Another possible explanation is that only some flowers are physiologically capable of nurturing a wasp egg. That is, some flowers respond to the gall-inducing chemical secreted by pollinator wasps (Grandi 1961),

while others do not. It is interesting to note that the pollinators of *F. carica* (F. Kjellberg, personal communication) and *F. burtt-davyi* (Compton 1993), and the *Idarnes* (this study) and other parasitic wasps (Bronstein 1991), do not require a flower to be pollinated for development to occur.

We conclude that the portion of the figs' flowers that the wasps are able to utilize is determined primarily by the fig. The fig appears to be the controlling partner in the mutualism, as it also appears to do in most other cases where there is an identifiable conflict of interest with the pollinators (Herre 1989). Interestingly, these results are contrary to the general notion that when two species coevolve the species with faster generation times and therefore faster mutation rates will be able to exploit the other species (Ladle 1992; Nowak & May 1994). Indeed, differences in generation time much smaller than that between figs and their pollinators have been used to argue that coevolution is unlikely to occur (Herrera 1985). It would be extremely instructive to know if more mutualisms are characterized by the dominance of the partner that provides resources and has a direct self interest in the reproduction of both partners. This appears to be the case with yuccas and their pollinating moths, another widely cited example of a complex pollination mutualism (O. Pellmyr, personal communication).

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