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The ecology and evolution of the New World non-pollinating fig wasp communities

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Abstract. We present data on several previously undescribed species from six genera of New World non-pollinating fig wasps. We show that many of these species have a negative effect on the reproductive success of both the pollinator wasps and the host figs. Our results suggest that the two most abundant genera of non-pollinating wasps, the *Idarnes* and the *Critogaster*, compete for the same pool of female flowers as the pollinating wasps in the *Urostigma* and *Pharmacosycea* figs, respectively. Wasps from the genus *Aepocerus* induce and develop within large galls, in the *Urostigma* figs. By draining resources from the fruit these wasps may have a detrimental effect on the production

of pollinator wasps and viable seeds. Some of the species investigated are parasitoids of other non-pollinating species. We examine the importance of the various forms of spatial heterogeneity in the parasitism rate that can act to stabilise the host-parasitoid interaction. Finally, we discuss the factors underlying the large variation in the abundance and diversity of the non-pollinating wasps both among and within fruit crops.

Key words. *Ficus*, parasitoid, parasites, coevolution, density dependence, spatial heterogeneity, community structure.

I. INTRODUCTION

The wasp species that are only able to develop within the fruit of fig trees are collectively termed fig wasps. These species include both mutualistic pollinators and parasitic non-pollinators. While the fig trees are completely dependent upon the pollinators for the dispersal of pollen between fruit, the non-pollinators provide no apparent service. Each fig species usually has a single species specific pollinating wasp species (Ramirez, 1970; Wiebes, 1979; Herre *et al.*, 1996b). These pollinating wasps are all members of the chalcidoid family, Agaonidae, and have relatively similar life cycles. The non-pollinating wasps also generally appear to be species-specific to a single fig species (Gordh, 1975; Ulenberg, 1985; van Noort, 1991; Bouček, 1993; Machado, *et al.*, 1996). However, a single fig species may have several associated non-pollinating wasp species (e.g. Compton & Hawkins, 1992). These non-pollinating wasp species belong to several chalcidoid families and show a large range of life-cycles (Bouček, 1988, 1993).

Very little is known about the biology of any of the non-pollinating fig wasps. Basic questions include: what are the resources utilized for larval growth by these wasps, and does their presence have any detrimental cost to their host fig? These questions are closely linked because the effect that different species have on the reproductive success of their hosts will depend upon their larval diet. For example, species which are competitors or parasitoids of the pollinators will have a direct effect on the reproductive

success of the pollinating wasps and also the host figs, by reducing the figs' ability to disperse pollen (West & Herre, 1994). In contrast, species which merely gall the fruit wall or unoccupied ovaries may have less obvious costs to their hosts.

In this study we describe various aspects of the ecology of the non-pollinating wasps associated with two subgenera of monoecious New World figs (*Ficus*, subgenera *Urostigma* and *Pharmacosycea*). We found three common genera of non-pollinating wasps associated with the *Urostigma* figs in Panama: *Idarnes* Walker, *Aepocerus* Mayr and *Physothorax* Mayr. The *Idarnes* can be further split into two very different groups which we have referred to as *Idarnes* and *Idarnes (incerta)* (see section 2). The majority of the species that we have examined are undescribed. However, molecular work suggests that a distinct species of each of the four wasp groups is found in most of the *Urostigma* fig species (Machado *et al.*, 1996; Table 2). While the different species within each of these four groups appear to use the same resources for larval development, members of the different groups tend to use different resources (Table 1). All the *Idarnes* species develop within female flowers, which they appear to compete for with the pollinating wasps (West & Herre, 1994; section 3). The *Aepocerus* and *Idarnes (incerta)* wasps develop within much larger galls which protrude into the centre of the fruit and appear to arise from female flowers and possibly the fruit wall (section 2.2). The fourth and final group are the *Physothorax*, which are parasitoids of the *Aepocerus* wasps.

TABLE 1. The characteristics of the non-pollinating wasps collected in Panama. The host figs, taxonomic relationships, mode of oviposition, male morphology, resources utilized for larval growth and effect on pollinator wasp and viable seed production are given for the different fig genera that we have studied. *Idarnes* represents species from the *flavicollis* and *carne* species groups, while *Idarnes (i)* represents species from the *incerta* species group. Despite developing in different fig species the members of a single genus (or group in the case of the *Idarnes*) share many characteristics, such as the resources used for larval growth. However, there are large differences between the genera (see also section 2).

Figs Subgenera	Fig wasps				Resources utilized				Effect on	
	Family	Subfamily	Genus	Mode of oviposition	Males	Galled flowers	Galled fruit wall	Wasp larvae	Pollinator production	Seed production
<i>Urostigma</i>	Agaonidae	Agaoninae	<i>Pegoscapus</i>	Internal	Wingless	+				Pollinators
<i>Urostigma</i>	Agaonidae	Sycophaginae	<i>Idarnes</i>	External	Winged	+			-	None
<i>Urostigma</i>	Agaonidae	Sycophaginae	<i>Idarnes (i)</i>	External	Winged	?				
<i>Urostigma</i>	Agaonidae	Oritesellinae	<i>Aepocerus</i>	External	Winged	?	?			
<i>Urostigma</i>	Agaonidae	Oritesellinae	<i>Heterandrium</i>	External	Dimorphic	+			-?	
<i>Urostigma</i>	Torymidae	—	<i>Physothorax</i>	External	Winged			+	+	-?
<i>Urostigma</i>	Braconidae	Dorytinae	—	External	Winged			+		
<i>Pharmacosyceea</i>	Agaonidae	Agaoninae	<i>Tetrapus</i>	Internal	Wingless	+				Pollinators
<i>Pharmacosyceea</i>	Agaonidae	Sycorytinae	<i>Critogaster</i>	External	Dimorphic	+				None

In the *Pharmacosycea* figs that we have studied there are only two common types of non-pollinating wasps, both belonging to the genus *Critogaster* Mayr. The two types can easily be distinguished by the colour of the female's body and the morphology of the males (section 2). As with the *Urostigma* wasps, a distinct species from each of these groups is generally found in each of the *Pharmacosycea* fig species (Machado *et al.*, 1996). Both these types of *Critogaster* appear to compete for female flowers with the pollinating wasps in a similar way to the *Idarnes* wasps (section 3.2).

The first aim of this paper is to answer fundamental questions about the biology of these non-pollinating wasps. Initially we describe in detail the natural history of the figs and wasps studied (section 2). Following this, we quantify the effects that the *Idarnes*, *Critogaster* and *Aepocerus* wasps have on viable seed and pollinator wasp production and, therefore, the reproductive success of their hosts (section 3). We then use these results to infer the larval diets of the wasps (section 3).

Our second aim is to show the ways in which non-pollinating fig wasps can be used to examine more general biological questions. For example, considerable theoretical and empirical attention has been paid to the factors that may explain the persistence of host-parasitoid interactions (reviewed in Hassell & Godfray, 1992; Jones, Hassell & May, 1994). Parasitoids such as *Physothorax* and their *Aepocerus* hosts may provide useful systems for the empirical study of potential stabilizing effects of various forms of parasitoid aggregation at many different spatial and temporal scales. In this study we examine the relationship between percentage parasitism and host density, and the factors that may contribute to the stability of their interaction, using data from the fruit of a single crop (section 4). As a second example we consider patterns at the community level. Specifically, we discuss factors that may influence the abundance and diversity of the various types of non-pollinating wasps across different fig species (section 5).

2. BACKGROUND BIOLOGY

2.1. The figs and their pollinators

We sampled naturally occurring fig species in the vicinity of the Panama Canal. The fig species are grouped in the subgenus *Urostigma*, section *Americana*, and the subgenus *Pharmacosycea*, section *Pharmacosycea*. The *Urostigma* figs are pollinated by wasps belonging to the genus *Pegoscapus* while the *Pharmacosycea* figs are pollinated by wasps belonging to the genus *Tetrapus*.

Individual trees of all the fig species may produce one to three fruit crops per year (Morrison, 1978; Milton *et al.*, 1982; 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 (Frank, 1984; Herre, 1989; van Noort, Ware & Compton,

1989; Ware *et al.*, 1993). These foundress wasps subsequently die inside the fruit. The proportion of the flowers in each fruit that begin to develop is dependent upon the number of foundresses that entered that fruit (Herre, 1989). Fruits that are not pollinated are usually aborted (e.g. Compton, Ross & Thornton, 1994).

The female flowers within the fruit show continuous variation in length of style 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 the 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 (Herre, 1989). It should, however, be noted that variation in style 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 (see also Verkerke, 1986, 1989; Bronstein, 1988a,b; Compton & Nefdt, 1990).

Just before final ripening of the fruit takes place, the wingless males of the pollinating wasps chew their way out of the flowers in which they have developed. They then crawl around the interior of the fruit searching for flowers which contain female wasps. The males chew open these flowers and mate with the females. The females then emerge from their flowers and gather pollen, before leaving through a hole in the fruit wall chewed by the male wasps.

2.2. The non-pollinating wasps

Before examining each genus in more detail we will first establish the features which are common to the biology of all the non-pollinating wasps that we have examined here. First, unlike the pollinator females, all the species considered in this study oviposit from outside the fruit wall (Table 1). Other studies have shown that some species of non-pollinating wasps do enter the fruit to oviposit (see Galil & Eiskikowitch, 1969; Murray, 1989; Compton, 1993b). Secondly, all the non-pollinating wasps emerge from their flowers at approximately the same time as the pollinators and exit the fruit through the hole chewed by the pollinator males. The non-pollinator wasps therefore depend upon the pollinating wasps to exit the fruit. However, we suspect that the *Aepocerus* males may be able to chew an exit hole in the absence of pollinator males, as some other species of non-pollinating wasps are able to do (e.g. Compton, Rasplus & Ware, 1994; Cook & Power, 1996).

The *Idarnes*, *Aepocerus* and *Physothorax* wasps are the most common non-pollinating genera found emerging from *Urostigma* figs in Panama. The *Idarnes* wasps can be split into two morphologically very different groups (Bouček, 1993; Machado *et al.*, 1996). Those belonging to the *flavicollis* and *carne* species-groups have wingless males and females with very long ovipositors. We refer to this group as *Idarnes*. In contrast, the *Idarnes* belonging to the *incerta* species-group have winged males and females with relatively short ovipositors. We refer to this group as *Idarnes (incerta)*.

TABLE 2. The non-pollinating fig wasps associated with various species of *Ficus* (subgenus *Urostigma*). *Idarnes* represents species from the *flavicollis* and *carne* species groups, while *Idarnes (i)* represents species from the *incerta* species group. A distinct species of wasp from each of the genera (or groups) is associated with each species of fig tree (Machado *et al.*, 1996).

Fig species <i>Ficus</i>	Wasp genus					
	<i>Idarnes</i>	<i>Idarnes (i)</i>	<i>Aepocerus</i>	<i>Heterandrium</i>	<i>Physothorax</i>	Doryctinae
<i>bullenei</i>	+					
<i>citrifolia</i>	+	+	+	+	+	+
<i>colubrinae</i>	+			+		
<i>costaricana</i>	+		+	+		
<i>dugandi</i>	+	+	+	+	+	+
<i>obtusifolia</i>	+		+		+	
<i>perforata</i>	+					
<i>popenoei</i>	+	+	+			
<i>trigonata</i>	+	+	+		+	
<i>turbonata</i>	+	+		+		

Occasionally wasps from other genera are found in fruit, but due to the small numbers of such wasps that we have collected they will not be considered after this section (but see also Tables 1 and 2). Examples include wasps from the genera *Heterandrium* Mayr which gall the female flowers of several *Urostigma* species, and some *Braconidae*: *Doryctinae* which appear to be parasitoids of *Idarnes (incerta)* in *F. citrifolia* (pers. obs.; identified by S. van Noort) (Tables 1 and 2).

Female *Idarnes* wasps oviposit at the same stage of fruit development as the pollinator wasps (Herre, 1989; Bronstein, 1991; West & Herre, 1994), and appear to use the same attractant cues as the pollinators to find receptive trees (E.A. Herre, unpublished results; Bronstein, 1991). These wasps also appear to utilize and compete for the same pool of female flowers as the pollinating wasps across a range of fig species (section 3; West & Herre, 1994). The ecology of the *Idarnes* wasps therefore shares several basic features with that of the pollinating wasps (West & Herre, 1994). The females are approximately the same size as the pollinating wasps, and have ovipositors over twice their body length. The males are smaller and wingless, possessing mandibles with distinct teeth which they use in lethal mate competition with conspecific males (Hamilton, 1979; pers. obs.). The effect of *Idarnes* on the production of pollinator wasps and viable seeds are considered in more detail in section 3.1.

The *Idarnes (incerta)* females oviposit at an earlier stage of fruit development than the pollinating wasps. The larvae of these wasps develop within galls which protrude into the centre of the fruit, and arise from female flowers. The males are winged and so are able to mate with females inside their own fruit, and with females from other fruit who they encounter in the foliage of the natal tree (pers. obs.).

Female *Aepocerus* oviposit at a similar stage of fruit development as the pollinating wasps, and will often lay their eggs in a fruit before it has been pollinated. The galls within which the *Aepocerus* develop are the largest within any fruit. These distinctive galls protrude into the centre of the fruit, and appear to arise from either the fruit wall or female flowers (see also Bronstein, 1991). This large gall size is reflected in the size of the adult wasps. *Aepocerus* are

considerably larger than the pollinating or *Idarnes* wasps. The males are winged and so are able to mate with females both from their own and from other fruit, in a similar way to the *Idarnes (incerta)* males. In section 3.2 we consider the impact that the *Aepocerus* wasps may have on the production of pollinator wasps and viable seeds.

Although occurring in many *Urostigma* species (Table 2), *Physothorax* are only common in the fruit of *F. dugandi* (Table 3). We therefore only consider the *Physothorax* species associated with *F. dugandi*. Several observations suggest that *Physothorax* are parasitoids of *Aepocerus*. First, *Physothorax* is placed in the Torymidae, a family thought to consist mainly of parasitoids of gall-forming fig wasps (Bouček, 1993). Secondly, *Physothorax* and *Aepocerus* both emerge from the same type of large distinctive gall. Thirdly, a *G*-test shows that the presence of *Physothorax* and *Aepocerus* were significantly positively correlated between fruit of *F. dugandi* ($G=14.43$, $P<0.001$, $n=84$). We only found *Physothorax* once in a fruit that contained no *Aepocerus* (this fruit contained only two *Physothorax* individuals). Finally, *Physothorax* females have considerably longer ovipositors than *Aepocerus* females, suggesting that they lay their eggs in the fruit at a later stage of fruit development (see also Godfray, 1988; Compton, 1993a,b; Compton *et al.*, 1994). We will consider the effects of these parasitoids on their hosts in section 4.

Each species of *Pharmacosycea* fig has two common species of *Critogaster* wasp associated with it: one species with green females and small louse-like males (similar to *C. singularis* Mayr); and one species with yellow females and larger males (similar to *C. flavescens* Mayr). Occasionally green or yellow winged males are also found. The females of both groups have ovipositors several times their body length. Both morphological and molecular work has suggested that while the majority of *Critogaster* species are associated with only one fig species, at least one Panamanian *Critogaster* species is able to develop in the fruit of different fig species (Bouček, 1993; Machado *et al.*, 1996).

The various *Critogaster* species have very similar life histories. Females arrive at and start probing fruit several days before the pollinating wasps, and then continue to oviposit until a few days after pollination has occurred

TABLE 3. Examples of the prevalence of the different wasp genera in different crops (or trees) of various *Urostigma* figs. Different crops from the same species are displayed separately (e.g. *citrifolia* I and *citrifolia* II). The fig species is followed by the number of fruit sampled from that crop (*N*) and the number of those fruit that contained each wasp genera. The percentages of fruit containing each wasp genera are given in parentheses. *Idarnes* represent species from the *flavicollis* and *carne* species groups, while *Idarnes (i)* represents species from the *incerta* species group. The prevalence of the different non-pollinating wasp genera vary enormously both between different species of *Ficus*, and between different crops of the same species. However, the *Idarnes* are consistently the most common type of non-pollinating wasp.

Fig species	<i>N</i>	Wasp genera				
		<i>Pegoscapus</i> (pollinators)	<i>Idarnes</i>	<i>Idarnes (i)</i>	<i>Aepocerus</i>	<i>Physothorax</i>
<i>bullenei</i>	34	34 (100%)	4 (12%)	0	0	0
<i>citrifolia</i> I	20	20 (100%)	0	0	0	0
<i>citrifolia</i> II	51	51 (100%)	37 (73%)	34 (67%)	0	0
<i>columbrinae</i>	28	28 (100%)	5 (18%)	0	0	0
<i>costaricana</i> I	10	10 (100%)	1 (10%)	0	0	0
<i>costaricana</i> II	8	8 (100%)	8 (100%)	0	3 (38%)	0
<i>dugandi</i> I	55	55 (100%)	26 (47%)	12 (22%)	35 (64%)	4 (7%)
<i>dugandi</i> II	150	138 (92%)	68 (45%)	0	124 (83%)	60 (40%)
<i>obtusifolia</i>	40	40 (100%)	40 (100%)	0	10 (25%)	1 (3%)
<i>perforata</i>	56	56 (100%)	1 (2%)	0	0	0
<i>popenoei</i> I	28	26 (93%)	20 (71%)	0	0	0
<i>popenoei</i> II	44	44 (100%)	20 (45%)	0	0	0

(D.M. Windsor, unpublished observations). The *Critogaster* appear to compete with the pollinators for female flowers in a similar way to the *Idarnes* (section 3.3). As the two types of *Critogaster* have very similar biologies we have grouped them together when examining their effect on the production of pollinator wasps and viable seeds.

3. THE EFFECT OF NON-POLLINATING WASPS ON POLLINATOR WASP AND VIABLE SEED PRODUCTION

To understand fully the effect of the non-pollinating wasps on viable seed and pollinator wasp production we have to determine their larval diets. More specifically, we need to know if the non-pollinating wasps are developing directly at the cost of pollinator wasps, or viable seeds, or merely draining resources from the fig? Theoretically, it is possible to answer this by looking for correlations between non-pollinator presence, pollinator wasp and viable seed production. However, attempts to determine the larval diets of the non-pollinating wasps in this way have led to inconclusive results (Bronstein, 1991). This may be due to the many confounding factors that influence the production of pollinator wasps and viable seeds. For example, the number of foundresses (pollen-bearing female pollinating wasps) 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 fig (Herre, 1989, 1996; Bronstein, 1992; West & Herre, 1994). 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 therefore be controlled for statistically.

We collected data from several fig species in order to examine the effect of *Idarnes* and *Aepocerus* wasps on

pollinator wasp and viable seed production in *Urostigma* figs, and *Critogaster* wasps on pollinator wasp and viable seed production in *Pharmacosycea* figs. Fruit from which only the male wasps had already emerged from their seeds were collected late in the ripening cycle. The fruit were then cut open and the number of foundresses within each fruit recorded. Each fruit was subsequently 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 the species of each wasp within each fruit (including the wasps that emerged from it) were recorded. This technique allowed the number of pollinator wasps and seeds that developed within each fruit to be related to both the number of foundresses that entered the fruit and the number of non-pollinating wasps that also developed within the same fruit. As we mentioned earlier, this is important because the number of foundresses that enter a fruit to oviposit has a large effect on the number of pollinators and viable seeds produced in a fig (Herre, 1989). Exceptions were *F. costaricana* and *F. yoponensis*, in which only pollinating and non-pollinating wasps were counted.

We analysed the data from each fig species separately using the GLIM statistical program (GLIM 3.77, Numerical Algorithms Group, Oxford, 1985; Crawley, 1993). To determine the effect of the non-pollinating wasps we compared the viable seed and pollinator wasp production across fruits with variable parasitism rates. In order to control for the confounding factors that influence viable seed and pollinator production we carried out an ANCOVA with crop and foundress number as factors.

3.1. The effect of *Idarnes* wasps in *Urostigma* figs

After controlling for the effects of variable foundress numbers and between-crop differences there was a significant

TABLE 4. ANCOVA on number of pollinators and viable seeds produced in individual fig fruits for five species of *Ficus* (subgenus *Urostigma*). 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 or viable seeds explained by each of the covariates. *, $P < 0.05$; ***, $P < 0.01$. Also given are the slopes of the relationships between *Idarnes* presence and the number of pollinators or viable seeds when the effects of crop and foundress number are controlled for. In all cases there was a significant negative correlation between the number of *Idarnes* reared from a fig fruit and the number of pollinating wasps. Further, in all cases there was no significant relationship between the number of *Idarnes* reared from a fig fruit and the number of viable seeds.

Fig species	<i>n</i>	<i>N</i>	Crop	Number of foundresses	<i>Idarnes</i>	<i>Idarnes</i> slopes
% Total variance in pollinator production explained						
<i>F. bullenei</i>	3	31	12	37***	12*	-2.47
<i>F. citrifolia</i>	3	73	1	24***	14***	-1.24
<i>F. costaricana</i>	4	27	14	19	21*	-1.09
<i>F. obtusifolia</i>	3	63	27***	1	12***	-1.61
<i>F. trigonata</i>	4	74	3	59***	7***	-0.75
% Total variance in viable seed production explained						
<i>F. bullenei</i>	3	31	26*	1	2	0.84
<i>F. citrifolia</i>	3	70	18***	2	2	-0.22
<i>F. obtusifolia</i>	3	39	59***	2	3	-0.85
<i>F. trigonata</i>	2	47	8	16	1	0.20

TABLE 5. ANCOVA on number of pollinator wasps and viable seeds produced in individual fig fruits of *Ficus popenoei* (subgenus *Urostigma*). Fruit with one and more than one foundress were analysed separately. 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. The number of foundresses 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. *, $P < 0.05$; ***, $P < 0.01$. Also given are the slopes of the relationships between *Idarnes* presence and the number of pollinators or viable seeds when the effects of crop and foundress number are controlled for. In fruit which contained only one foundress the *Idarnes* were negatively correlated with viable seeds, and showed no correlation with pollinator wasps. However, in fruit which contained more than one foundress the *Idarnes* were negatively correlated with pollinator wasps, and showed no relationship with viable seeds. Therefore, in these fruit the *Idarnes* had a similar effect to other fig species.

Number of foundresses	<i>n</i>	<i>N</i>	Crop	Number of foundresses	<i>Idarnes</i>	<i>Idarnes</i> slopes
% Total variance in pollinator production explained						
1	4	37	8	—	1	0.03
>1	4	78	3	36***	14***	-2.24
% Total variance in viable seed production explained						
1	4	37	35***	—	8*	-0.54
>1	4	78	42***	8	0	-0.12

negative correlation between the presence of *Idarnes* and pollinator wasp production in five species of fig studied (Table 4). In contrast, there was no significant correlation between the number of *Idarnes* and seed production in the four of the five species in which seeds were counted (Table 4).

The importance of controlling for confounding variables in these analyses was well demonstrated by the data from *F. popenoei*. In *F. popenoei* the relationship between *Idarnes* and both pollinator wasp and viable seed production was dependent upon the number of foundresses that entered a fruit (Table 5). This result can be explained by considering the effect that the resources (eggs and pollen) provided by variable numbers of foundresses had on fruit development. If only one foundress entered a fruit then the *Idarnes* were negatively correlated with viable seeds and showed no relationship with pollinator wasps (Table 5). A single foundress in *F. popenoei* is not capable of saturating all of

the flowers that are available for the development of wasp offspring with her own eggs (Herre, 1989). These pollinated flowers that do not receive a pollinator or *Idarnes* egg are therefore able to develop as viable seeds. The number of wasps that a fruit is capable of producing does not plateau until at least three or four foundresses have entered (Herre, 1989). *Idarnes* only have a negative effect on the production of pollinator wasps in these fruit in which pollinator production has saturated (Table 5). The majority of *F. popenoei* fruit receive more than one foundress (Herre, 1993) and so the general effect of *Idarnes* presence was reduction of the pollinators, as in the other fig species.

The importance of controlling for confounding variables was further demonstrated by the data from *F. trigonata*. An analysis of this data without the inclusion of crop and foundress number as factors showed no correlation between *Idarnes* presence and pollinator wasp production ($F_{1,73} = 2.33$, $P > 0.05$). However, as shown in Table 4, when the

number of foundresses entering a fruit and between crop differences were controlled for there was a significant negative correlation between the number of *Idarnes* and the number of pollinators in a fruit. The most important factor confounding the effects of *Idarnes* in this case was likely to be that the production of pollinator wasps in *F. Trigonata* varies enormously with the number of foundresses that enter a fruit (Herre, 1989; Table 4). This confounding effect of foundress number was so great because the fruit of *F. trigonata* are very large and require several foundresses before pollinator wasp production plateaus (Herre, 1989).

We have shown that *Idarnes* wasps have a negative correlation with the number of pollinator wasps developing in a fruit (except for *F. popenoei* fruit which contained only one foundress). This suggests that the *Idarnes* are either competitors, parasites or parasitoids of the pollinating wasps.

Additional observations strongly suggest that *Idarnes* are not directly parasites or parasitoids of the pollinators (West & Herre, 1994). *Aepocerus* can prevent fruit which received no pollinator wasps from being aborted (section 3.3). We observed *Idarnes* develop in these unpollinated fruit 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). *Aepocerus* occur in much lower numbers per fruit and in very different galls than the *Idarnes* (Table 3; section 2.2). Therefore, the *Idarnes* are not parasitoids of these other non-pollinating wasps.

These results, coupled with the fact that the *Idarnes* wasps usually emerge from the same layer of flowers as the pollinating wasps (Herre, 1989), suggest that the *Idarnes* utilize and compete for the same pool of flowers as the pollinating wasps. This idea is further supported by two observations suggesting that *Idarnes* reproduction may actually be greater in the absence of the pollinating wasps. First, the *Idarnes* wasps occur in significantly greater numbers in unpollinated fruit that were not aborted (Bronstein, 1991; West & Herre, 1994). Secondly, the *Idarnes* wasps of *F. popenoei* appear to develop preferentially in flowers that do not contain pollinators in fruit where pollinator production has not saturated (Table 5 and above).

3.2. The effect of *Critogaster* wasps in *Pharmacosycea* figs

We examined the effect of *Critogaster* wasps on pollinator wasp and viable seed production for three species of *Pharmacosycea* figs. *Critogaster* exhibit similar patterns to the *Idarnes*. After controlling for the number of foundresses that entered a fruit, and between crop differences the presence of *Critogaster* and pollinator wasp production were negatively correlated in all three species of fig studied (Table 6). In contrast, there was no significant correlation between the number of *Critogaster* wasps and seed production in the two species in which seeds were counted (Table 6).

As with the *Idarnes* this negative effect of the *Critogaster* on the production of pollinator wasps suggests that the *Critogaster* are either competitors, parasites or parasitoids of the pollinating wasps. Two observations suggest that

the *Critogaster* are also likely to be competitors of the pollinators, rather than their parasitoids. First, Muller (1887; see Bouček, 1993) has already listed the *Critogaster* species as gall producers in the *Ficus* subgenus *Pharmacosycea*. Secondly, it has been noticed that females will arrive at and probe fruit with their ovipositors several days before the pollinating wasps (section 2.2). If these females are ovipositing before the arrival of the pollinators then they are unlikely to be their parasitoids.

3.3. The effect of *Aepocerus* wasps in an *Urostigma* fig (*F. dugandi*)

Finally, we consider the effect of *Aepocerus* wasps on viable seed and pollinator wasp production in *F. dugandi*. *Aepocerus* develop in 60% of fruit and are commonly parasitised by *Physothorax* (sections 2.2 and 4). To calculate the number of *Aepocerus* that were laid in each fruit we summed the number of both *Aepocerus* and *Physothorax* wasps that emerged.

We examined the fruit crop of a single tree and found that fruit which did not contain *Aepocerus* produced more viable seeds ($F_{1,30} = 1.53$, $P > 0.05$) and significantly more pollinator wasps ($F_{1,31} = 12.65$, $P < 0.01$) than fruit which did contain *Aepocerus* (Table 7). A larger sample size would be likely to show that the presence of *Aepocerus* has a significant negative effect on the production of viable seeds. There was no significant effect of increased numbers of *Aepocerus* in a fruit on pollinator wasp ($F_{1,31} = 1.97$, $P > 0.05$) or viable seed ($F_{1,30} = 0.002$, $P > 0.05$) production.

Aepocerus drain resources from the fig tree in at least two ways. First, *Aepocerus* can prevent abortion of both unpollinated fruit, and fruit which were developing a few pollinators (pers. obs.) (see also Galil & Eisikowitch, 1968; Bronstein, 1991; Compton, 1993b; Cook & Power, 1995). These fruit would normally be aborted so that the tree could divert the resources to other fruit, where they could possibly be used more profitably (Herre, 1989, 1996; West & Herre, 1994). This is likely to be why fruit which did not contain *Aepocerus* contained more pollinator wasps than fruit which did contain *Aepocerus*. Secondly, the *Aepocerus* wasps will drain resources from the fig for their own development.

4. POPULATION DYNAMICS, PHYSOTHORAX PARASITOIDS AND THEIR AEOCERUS HOSTS

A major question in the dynamics of any host–parasitoid system is what factors promote the stability of the interacting populations (Pacala, Hassell & May, 1990)? A host–parasitoid interaction is termed stable if the host and populations densities remain roughly steady, and both species are able to co-exist over ecological time. Parasitoid aggregation at certain patches has been suggested as an important factor in stabilizing host–parasitoid interactions (Pacala *et al.*, 1990).

Parasitoid aggregation may occur for two reasons. First, parasitoids may aggregate in patches of high host density; and secondly, parasitoids may aggregate in certain patches

TABLE 6. ANCOVA on number of pollinators and viable seeds produced in individual fig fruits for three species of *Ficus* (subgenus *Pharmacosycea*). The crop sampled from, number of foundresses of each fruit sampled, and the number of *Critogaster* 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 or viable seeds explained by each of the covariates. *, $P < 0.05$; ***, $P < 0.01$. Also given are the slopes of the relationships between *Critogaster* presence and the number of pollinators or viable seeds when the effects of crop and foundress number are controlled for. In all cases there was a significant negative correlation between the number of *Critogaster* reared from a fig fruit and the number of pollinating wasps. Further, in all cases there was no significant relationship between the number of *Critogaster* reared from a fig fruit and the number of viable seeds.

Fig species	<i>n</i>	<i>N</i>	Crop	Number of foundresses	<i>Critogaster</i>	<i>Critogaster</i> slopes
% Total variance in pollinator wasp production explained						
<i>F. glabrata</i>	1	20	—	63***	11*	−3.31
<i>F. insipida</i>	21	580	36***	6***	1*	−0.35
<i>F. yoponensis</i>	1	22	—	70***	13***	−1.01
% Total variance in viable seed production explained						
<i>F. glabrata</i>	1	20	—	9	5	−0.19
<i>F. insipida</i>	21	580	63***	1	0	−0.12

TABLE 7. The average number of pollinator wasps and viable seeds in thirty-three fruit from a single crop of *F. dugandi*. Fruit are divided between those in which *Aepocerus* were absent or present. Standard errors are given in parenthesis. Fruit in which *Aepocerus* were present contained fewer pollinator wasps and viable seeds (see section 3.3).

	Pollinator wasps	Viable seeds
<i>Aepocerus</i> absent	154.7 (24.0)	74.0 (20.0)
<i>Aepocerus</i> present	58.5 (12.5)	46.5 (7.6)

irrespective of host density. These two types of parasitoid aggregation have been termed host density dependent (HDD) and host density independent (HDI) (Pacala *et al.*, 1990).

Parasitoid aggregation is stabilizing because it leads to competition between individual parasitoids for hosts and a reduction in the average parasitoid searching efficiency. The reduction in the average parasitoid searching efficiency caused by aggregation increases as the average parasitoid density increases. This reduction in searching efficiency at high parasitoid densities introduces temporal density dependence into the system which can potentially stabilise the host-parasitoid interaction (Free, Beddington & Lawton, 1977; Hassell & Pacala, 1990).

Pacala *et al.* (1990; Hassell & Pacala, 1990; Pacala & Hassell, 1991; Hassell *et al.*, 1991) have recently developed a useful framework within which the relative importance of HDD and HDI can be determined from the spatial heterogeneity in the parasitism rate of field samples. This involves the calculation of the coefficient of variation squared ($CV^2 = \text{variance}/\text{mean}^2$) of the distribution of searching parasitoids weighted for hosts within any particular patch. This variation can then be partitioned into the HDD and the HDI components. The relationship between these different components is given by: $CV^2 = \text{HDD} \times \text{HDI} - 1$. Pacala *et al.* (1990) developed a simple rule that if $CV^2 > 1$ then the host-parasitoid interaction will be stable (but see below).

We examined the spatial variation in the parasitism rate

of the *Physothorax* parasitoid on its *Aepocerus* host in *F. dugandi*. Data from the fruit crop of a single tree was analysed in two ways. First, we examined if the parasitism rate was significantly correlated to the density of hosts in a fruit (i.e. is there HDD?). Secondly, we determined the relative possible importance of HDD and HDI in stabilizing the host-parasitoid interaction. The values of HDD and HDI were obtained using a Turbo Pascal program written by Pacala.

Analysis of proportion data, such as the parasitism rate, results in non-normal error distribution, non-constancy of the variance and loss of information of the size of the sample from which each proportion was calculated (Crawley, 1993). To avoid these problems we analysed the data with a general linear model analysis of deviance, assuming binomial errors, in the GLIM statistical package (GLIM 3.77, Numerical Algorithms Group, Oxford, 1985). The number of *Physothorax* in a fruit was used as the response variable and the total number of *Aepocerus* and *Physothorax* in a fruit as the binomial denominator. The data were found to be overdispersed, which may result in overestimation of significance levels (Crawley, 1993). To account for this we rescaled the deviance by an appropriate heterogeneity factor (the ratio of Pearson's χ^2 to the degrees of freedom). The heterogeneity factor (HF) is given in the text. Hypothesis testing was carried out using χ^2 approximations.

Physothorax parasitized 21.0% of *Aepocerus*. There was a positive correlation between the proportion of galls parasitized by *Physothorax* and the number of galls in a fruit ($\chi^2 = 13.98$, $P < 0.001$, HF = 2.66, $n = 41$). Such a relationship is termed positive density dependence. A possible explanation for this pattern is that parasitoids aggregated at fruit containing high densities of hosts. Alternatively the parasitoids and their hosts may respond to the same fig cues.

Host density dependent variation in the parasitism rate/aggregation (HDD = 2.55) was greater than host density independent variation in the parasitism rate/aggregation (HDI = 1.41). The total CV^2 for this data set ($CV^2 = 2.59$) exceeded unity, so the heterogeneity in parasitism has the potential to stabilize the interacting populations. In fact

with $HDD > 2$, there is sufficient host density dependent heterogeneity for this to potentially stabilize the interaction on its own (Pacala & Hassell, 1991).

Care should, however, be taken in making conclusions from this analysis. First, we have examined data from only a single fruit crop. Second, the CV^2 framework makes fundamental assumptions about the biology of the interactions between host and parasitoid (Hassell & Pacala, 1990; Taylor, 1993). The assumptions were summarized by Hassell & Pacala (1990) as: (1) the parasitoid species in question are specialists on one host species; (2) the host and parasitoids have discrete generations; (3) parasitoids encounter their hosts at random; (4) the host–parasitoid interaction is of predominant importance to the overall dynamics; factors such as competition between hosts and parasitoid interference are neglected. In addition, the underlying model assumes no parasitoid redistribution within the season, something that has more recently been shown to be important in modulating the stabilizing power of HDD aggregation (Rohani, Godfray & Hassell, 1994).

It would be extremely useful to explore how the level and form of heterogeneity in the parasitism rate changes with spatial scale and over time. Variation at different spatial scales and over time may have important consequences for the population dynamics of a host–parasitoid system (Hassell & Pacala, 1990; Taylor, 1993). However, long-term field data documenting such patterns are scarce (but see Hails & Crawley, 1992; Redfern, Jones & Hassell, 1992; Jones, Hassell & Pacala, 1993). Fig wasps may provide a useful system for detailed field studies designed to examine such questions because they can easily be sampled at several natural spatial scales (e.g. fruit, branch, tree).

The observed pattern of parasitism may also have important implications for the behaviour of the host wasps. An individual female may be selected to change the distribution of her progeny across patches (in this case fruit) as a response to parasitoid attack (Thompson, 1986a; Godfray, 1987, 1994). For example, positive density dependent rates of parasitism may favour hosts that lay smaller numbers of eggs in each patch. This individual behaviour would then be reflected in the distribution and structure of the population. Population structure has been shown to be the major determinant of the sex ratios and male mating strategies for both pollinating and non-pollinating fig wasps (Hamilton, 1979; Frank, 1985; Herre, 1985, 1987, 1993; Herre *et al.*, 1996a; Murray, 1987, 1989). Consequently, by influencing their host's distribution, parasitoids such as *Physothorax* may have played a part in determining their host's reproductive strategies.

5. COMMUNITY STRUCTURE

The abundance and diversity of non-pollinating wasps varies enormously at many different levels: between different fig species (Herre, 1989; Compton & Hawkins, 1992; Tables 2 and 3), between samples of the same fig species at a single location (Table 3) and between different fruit on the same tree. In this section we will first discuss some of the factors that are likely to be controlling the relative abundances of the different types of wasps. Then we will go on to discuss

variation in wasp species diversity across the different fig species.

The *Idarnes* are consistently the most abundant type of non-pollinating fig wasp in figs of the subgenus *Urostigma* throughout the Central and South America (E.A. Herre, unpublished results; Gordh, 1975; Bronstein, 1991; West & Herre, 1994). In Panama, the *Idarnes* occur in a higher proportion of fruit (Table 3) and in higher numbers per fruit than any other group of non-pollinating wasps. This success of *Idarnes* wasps in exploiting the fig pollinator mutualism may be explained by the fact that these wasps appear to be utilizing the same pool of flowers that the pollinators use (section 3). The *Idarnes* wasps exploit flowers in which the pollinators grow and in which the fig apparently cannot differentiate between a non-pollinator and a pollinator. In addition, *Idarnes* wasps arrive at a receptive tree at the same time as the pollinators (Bronstein, 1991; West & Herre, 1994), and appear to use the same attractant cues as the pollinators to find receptive trees (Bronstein, 1991; E.A. Herre, unpublished results). Therefore, a fig tree cannot attract its pollinator wasps without also attracting its *Idarnes* non-pollinating wasps. It would be extremely instructive to know if the abundance of other genera of non-pollinating wasps, such as *Critogaster* and *Philotrypesis*, can be similarly explained. Our results (section 3) suggest that at least with *Critogaster* this may be the case.

Wasps such as *Aepocerus* are able to short-circuit the fig's ability to abort unpollinated fruit, and are therefore able to exist independent of the pollinator (see also Compton, 1993b). We might therefore expect these wasps to be far more prolific than they are (Table 3). However, a possible factor limiting the abundance of these wasps is their parasitoids. Theoretical studies, laboratory experiments and biological control programmes have demonstrated that parasitoids may play an important role in the regulation of their hosts (Hassell & Godfray, 1992). In addition, modern methods of analysing detailed field data have made it possible to estimate the degree to which a particular parasitoid depresses its host population level (e.g. Jones *et al.*, 1993). Although a more detailed field study is required, the data presented in section 4 are suggestive that *Physothorax* may play an important part in depressing the populations of their *Aepocerus* hosts.

More generally, the abundance of any of the non-pollinating wasp species could also be influenced by the fruiting phenology of their host trees (see also Cook & Power, 1996). For example, if a tree is sufficiently asynchronous in its fruiting phenology then non-pollinating wasps would be able to find fruit suitable for oviposition on the tree from which they have emerged. In this case we might expect these wasps to become more common as they go through several generations on a single tree. This may explain why a sample from an asynchronous crop of a *F. costaricana* tree (Table 3: *costaricana* I) had a much lower prevalence of *Idarnes* and *Aepocerus* wasps than a sample taken several weeks later from the same crop (Table 3: *costaricana* II). It would be relatively easy to test this idea further by exploiting the fact that there exists geographical variation in the fruiting phenology of certain fig species (C. Smith, this issue).

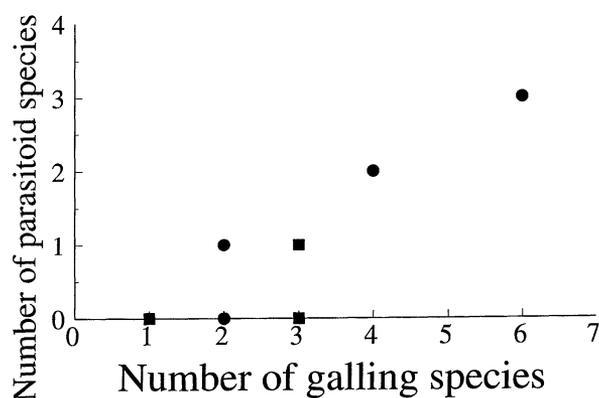


FIG. 1. The relationship between galling wasp and parasitoid species diversity for the non-pollinating fig wasps of ten species of *Urostigma* figs. The square points represent two species. Data from only two samples (forty fruit in each sample) of each fig species were included in this analysis to control for the large effect that sample size has on species diversity (Compton & Hawkins, 1992; Memmot, Godfray & Gauld, 1994). The diversity of parasitoid species is positively correlated with the diversity of galling species ($\chi^2 = 7.70$, $p < 0.01$, $n = 10$).

We now turn to the variation in the diversity of non-pollinating fig wasps across the different fig species. This topic has recently been addressed using the South African fig species (Compton & Hawkins, 1992; Compton & van Noort, 1992; Hawkins & Compton, 1992; Compton *et al.*, 1994). Compton & Hawkins (1992) considered the factors that influence the diversity of the gall-forming wasps (e.g. *Idarnes* or *Aepocerus*) and their parasitoids (e.g. *Physothorax*). They have shown that, across fig species, the diversity of Southern African galling wasps is positively correlated with tree height and wasp taxon size (Compton & Hawkins, 1992). They suggest that these results demonstrate the importance of both phylogenetic constraints and ecological factors in determining species diversity of the galling wasps. Phylogenetic constraints are likely to play a part in the evolution of non-pollinating wasp communities because the high host-specificity and probable cospeciation between figs and their wasps (Thompson, 1986b; Herre *et al.*, 1996b; Machado *et al.*, 1996) is likely to limit the number of galling species associated with any fig species (Compton & Hawkins, 1992; Hawkins & Compton, 1992). Tree height may be important because larger trees will produce more fruit and may be easier for non-pollinating wasps to find (Compton & Hawkins, 1992). Compton & Hawkins (1992) also showed that the diversity of parasitoid species was strongly correlated with galling wasp diversity across the African fig species. We have found the same relationship between parasitoid and galler diversity across the *Urostigma* figs from Panama (Fig. 1). These results suggest that the variability of available hosts is the most important factor determining parasitoid diversity (Compton & Hawkins, 1992).

6. CONCLUSIONS

In this study we have described various aspects of the ecology of several non-pollinating fig wasp species. First,

we demonstrated that non-pollinating fig wasps may have a large detrimental effect on the reproductive success of both the figs and their pollinating wasps. Specifically, we have shown that both *Idarnes* and *Critogaster* have a direct negative effect on pollinator wasp production, which in turn effects the figs' ability to disperse pollen (sections 3.1 and 3.3). In contrast, *Aepocerus* are likely to have only an indirect effect on pollinator wasp and viable seed production, by draining resources from their host tree (section 3.2). Nonetheless, these results emphasize the importance of considering non-pollinating wasps in studies that investigate pollinator wasp and viable seed production (see also Pellmyr, 1995).

Given that non-pollinating wasps have a large detrimental effect on the reproductive success of their host figs, they are likely to have been an important selective pressure shaping many aspects of fig biology. Indeed, it has been demonstrated that the ants tending homopterans on *F. sur* benefit the tree by reducing the number of non-pollinating wasps developing in fruit (Compton & Robertson, 1988). Future work could examine the possibility that non-pollinating wasps may have influenced the evolution of factors such as fruit morphology, fruiting phenology and even dioecy (see also Frank, 1989; Patel, Hossaert-McKey & McKey, 1993; Compton *et al.*, 1994).

It is perhaps puzzling that figs have not merely evolved thick or tough fruit walls which could exclude the ovipositors of these 'evil' non-pollinating wasps. A possible solution to this problem may be that the evolution of such a fruit wall would conflict with other important roles the fruit wall must play. For example, the fruit wall must be able to allow the transpiration of enough water to keep the fig cool enough for the pollinator larvae to survive (Patino, Herre & Tyree, 1994). Alternatively, a fruit that is tough enough to exclude non-pollinators ovipositing from the outside may not be particularly attractive to frugivores.

We have also shown that the parasitoids may play a significant part in reducing the populations of their galling host wasps (section 4). Just as non-pollinating wasps may have been an important selective pressure shaping many aspects of fig biology, these parasitoids are likely to have affected many aspects of their host's biology (Godfray, 1994). For example, we have discussed how parasitoids may have influenced the evolution of their hosts' population structure, and therefore their reproductive strategies (section 4). These observations add to the many ways in which parasites have been implicated to influence the biology of their hosts (e.g. Price, 1980; Hamilton, 1980; Hamilton & Zuk, 1982).

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