

Conflict of interest in a mutualism: documenting the elusive fig wasp–seed trade-off

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SUMMARY

The generally accepted view that mutualisms represent reciprocal exploitations implies a greater or lesser degree of inherent tension between the partners. This view emphasizes the importance of identifying conflicts of interest between the partners, and then attempting to quantify the effects of factors that influence costs and benefits to each. The natural history of the speciose fig–fig wasp pollination mutualisms permits such measurements. However, previous attempts to document the presumed tensions, which are expected to result in a negative relationship between the production of viable seeds and pollinator wasp offspring, have met with mixed results, casting doubt on the existence of the conflict. Here, we present hierarchical analyses of 929 fruits sampled from 30 crops representing nine species of monoecious New World figs. These analyses control for the confounding influences of variation in (1) pollination intensity (numbers of foundress pollinators); (2) flower number per fruit; and (3) the proportion of those flowers that develop, on seed and wasp production, both among and within crops. We thereby show that a negative relationship between the production of viable seeds and wasps is, in fact, ubiquitous, thus documenting this underlying tension inherent in the mutualism. We suggest that complex interactions of variables that influence costs and benefits are likely to be a general property of most mutualistic systems.

1. INTRODUCTION

Current evolutionary thinking proposes that mutualisms are best viewed as reciprocal exploitations that nonetheless provide net benefits to each of the involved parties (Axelrod & Hamilton 1981; Thompson 1982, 1994; Futuyma & Slatkin 1983; Leigh & Rowell 1995). It follows that basic questions concern the identification and quantification of the variation in costs and benefits to each partner, and then the documentation of the factors influencing that variation. In particular, it is important to identify situations in which there exists a conflict of interest between the two parties (e.g. Herre 1989). Given such conflicts of interest, it is then desirable to identify mechanisms that prevent the costs to either partner from exceeding the benefits, thereby undermining the mutualistic nature of the interaction (Pellmyr & Huth 1994; West & Herre 1994). However, few such studies exist.

One notable set of mutualistic systems in which it is possible to identify and quantify costs and benefits to each partner, and relate their variation to several relevant ecological and evolutionary factors, are the numerous and generally species-specific fig–fig wasp pollination mutualisms (Wiebes 1979). For the purposes of this paper, there is an easily counted common

currency for assessing costs and benefits for each partner, namely viable seeds and those seeds that are consumed during the development of the wasp offspring. The patterns of viable seed and wasp production profoundly affect the reproductive success of both fig and pollinator wasps and lie at the centre of the mutualism (Herre 1989, 1996; Bronstein 1992; West & Herre 1994).

Figs and their wasps depend completely on each other in the long-term for pollination of the figs and the completion of the life cycle of the wasps. However, there is reason to believe that the short-term reproductive interests of the two partners are not identical with respect to the utilization of the fig's female flowers (Kjellberg *et al.* 1987; Herre 1989; West & Herre 1994). The monoecious figs need female flowers, both for producing intact, viable seeds, as well as for supporting the development of the pollinator wasps that will act as disperser agents for its pollen. In contrast, the pollinating wasps only benefit directly from the fig's production of female flowers that are eaten by their own offspring. Because wasps are produced at the expense of potentially viable seeds (Herre 1989; West & Herre 1994), a negative relationship between the production of viable seeds and wasp offspring is expected.

However, despite the expectation of a negative relationship between viable seeds and wasp offspring, that

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should itself be indicative of the inherent tension between the two mutualists, documentation of this expected trade-off has proved to be very elusive. Simple correlations between the mean viable seed and wasp offspring production across 22 crops of *Ficus pertusa* from Monteverde, Costa Rica, showed a significant *positive* relationship between the two; trees with seed-rich fruits also produced more wasps (Bronstein 1988, 1992). Similar patterns have also been reported across 13 crops of *F. aurea* collected in Florida (Bronstein 1992; Bronstein & Hossaert-McKey 1996). These observations are consistent with the suggestion that the seed-wasp trade-off and the attendant conflict of interest are not an intrinsic part of the system (Bronstein 1992).

However, simple correlational analyses in complex systems that are characterized by the interactions of several variables are apt to confound the effects of those variables and obscure the functional relationships among them. The interaction between figs and their wasps presents such a system (Herre 1996). In particular, analyses performed across fig crops have been shown to confound the effects of many variables that have been shown to influence both seed and wasp production, potentially obscuring their true underlying relationships (Herre 1989, 1996; West & Herre 1994). In fact, simple correlations between viable seed and wasp production conducted even *within* crops of several species have been inconclusive, showing a mix of both positive and negative relationships (Herre 1996). Therefore, in order to determine whether a trade-off exists as a general property of this mutualism, and, if so, its form, it is necessary to examine the seed-wasp relationships both among and, in particular, within crops, while controlling for variables that, both singly and collectively, have been identified as influencing both seed and wasp production.

Here, we examine the relationship between seed and wasp production in nine species of monoecious New World figs. The fruits of these species range from among the smallest to among the largest found in the New World, and a molecular phylogeny suggests that they represent widely divergent lineages within *Ficus* (Herre *et al.* 1996). In order to document the underlying relationship between viable seed and pollinator wasp production, we show that it is crucial to recognize and statistically control for the confounding effects of differences in (1) pollination intensity (the number of foundress pollinator wasps); (2) the total number of flowers per fruit; and (3) the proportion of flowers that develop. These factors have been previously shown to interact in complex, but systematic, ways to influence variation in pollinator wasp and viable seed production both between and within crops (Herre 1989, 1996; West & Herre 1994; Anstett *et al.* 1996; Bronstein & Hossaert-McKey 1996; West *et al.* 1996). Without an appreciation of the effects of these variables, the relationships that influence the costs and benefits to each partner cannot properly be understood. Specifically, by controlling for the effects of these confounding variables we show that the negative relationship that is indicative of the inherent tension between the two partners is, in fact, ubiquitous.

2. BACKGROUND BIOLOGY

The pollinator wasps are all members of the chalcidoid family, Agaonidae, and all of them show similar life cycles (Wiebes 1979, 1995). Generally, some number of mated, pollen-bearing, foundress wasps enter a receptive fig syconium (the enclosed inflorescence that defines the genus, *Ficus*, and ultimately develops into the fig fruit), pollinate the uniovulate female flowers that line the interior, lay eggs in some of these flowers, and then die. Usually, the foundress wasps die inside the one fig fruit that they pollinate (Herre 1996; Gibernau *et al.* 1996). After being pollinated, some proportion of the female flowers begin to develop. Those flowers that complete development eventually produce either an intact, viable seed, or an adult wasp that consumes the contents of a single seed during the course of its own development. Previous studies have shown that the proportion of the flowers that develop can be strongly influenced by a combination of pollen and resource availability (Herre 1989, 1996; Anstett *et al.* 1996; Bronstein & Hossaert-McKey 1996).

As final ripening of the fig fruit approaches, the wingless adult males emerge from the seeds within which they matured. They crawl around the interior of the syconium, chew open seeds that contain females, and mate with them. Then, the mated females emerge from their seeds, gather pollen from male flowers, exit the fruit, and disperse to begin the cycle anew (Frank 1984; Herre 1989, 1996; Compton 1993; Herre *et al.* 1997). After the female wasps leave, a wide range of animals eat the ripe fruit and disperse the viable seeds (Milton 1991; Kalko *et al.* 1996).

In this study, we examined eight fig species in the subgenus *Urostigma*, and one in the subgenus *Pharmacosycea* (*F. yoponensis*) that occur naturally in the vicinity of the Panama Canal (table 1; see also Herre 1989, 1996). The *Urostigma* species are each pollinated by a single species-specific wasp from the genus *Pegoscapus*, and the *Pharmacosycea* species by a single species-specific wasp from the genus *Tetrapus* (Wiebes 1979, 1995; Herre *et al.* 1996). Individual trees of all these fig species may produce 1–3 fruit crops per year. The development and maturation of the fruit within the crop of a single tree in these populations are largely synchronous with the vast majority of fruits maturing over two or three days (Milton *et al.* 1982; Windsor *et al.* 1989; Milton 1991; Kalko *et al.* 1996).

3. METHODS

Fruits were sampled from 30 different crops representing nine different species (table 1). Individual fruits were collected at a stage in which the male wasps had emerged from their consumed seeds, but before an exit hole had been chewed in the fruit. Each fruit was then cut open and the number of female foundresses that had pollinated the fruit determined. Each individual fruit was then sealed between two matching Petri dish halves, and all the immature wasps were allowed to emerge. The dishes containing the contents of the fruits were then frozen. Later, the total number of wasp offspring and viable seeds that each fruit contained were counted, as were the number of developed and undeveloped female flowers in a randomly selected section that represented between

Table 1. *Characteristics of the fig species examined in this paper*

(Species is followed by the proportion of fruit pollinated by a single foundress (taken from Herre 1987, 1989, 1993), the number of crops sampled, the number of fruit sampled, and the average contents per fruit. Standard deviations are given in parentheses.)

species (<i>Ficus</i>)	proportion single foundress broods	crops sampled	fruit sampled	number female flowers	proportion developed flowers	number viable seeds	number pollinator wasp offspring
<i>F. bullenei</i>	0.82	2	70	296 (67)	0.86 (0.06)	118 (36)	113 (38)
<i>F. citrifolia</i>	0.78	16	417	331 (62)	0.85 (0.09)	118 (30)	146 (35)
<i>F. columbrinae</i>	0.99	1	23	197 (18)	0.91 (0.03)	90 (18)	90 (11)
<i>F. nymphaefolia</i>	0.55	2	75	634 (153)	0.95 (0.05)	324 (120)	242 (51)
<i>F. obtusifolia</i>	0.83	4	191	889 (129)	0.92 (0.05)	404 (86)	373 (107)
<i>F. pertusa</i>	0.90	1	29	201 (45)	0.84 (0.07)	90 (22)	52 (23)
<i>F. nr. trigonata</i>	0.31	2	62	777 (203)	0.89 (0.07)	373 (125)	272 (73)
<i>F. turbinata</i>	0.75	1	44	299 (38)	0.87 (0.07)	128 (27)	115 (23)
<i>F. yoponensis</i>	0.58	1	18	514 (183)	0.46 (0.15)	86 (50)	105 (24)

one-quarter and one-half of each fruit. The proportion of developed flowers in each fruit was estimated by dividing the number of developed flowers (those that produced a viable seed or that supported the development of either a pollinator or a parasitic wasp) by the total number of female flowers in that section. The total number of female flowers in each fruit was estimated by dividing the total number of developed flowers in the entire fruit by the proportion of developed flowers (see also Herre 1989).

Four general types of analyses relating the production of viable seeds to that of pollinator wasp offspring were conducted. (1) Simple correlations of seed and wasp means across 16 crops of one species (*Ficus citrifolia*) were conducted in order to compare with positive correlations previously reported across crops for *F. pertusa* and *F. aurea* (Bronstein 1992; Bronstein & Hossaert-McKey 1996). (2) Across-crop analyses of *F. citrifolia* while controlling, both separately and jointly, for the effects of crop differences in flower number and proportion of developed flowers were conducted in order to determine the influence of those variables at the level of crop. (3) Simple correlations of seed and wasp production within each of the 16 crops of *F. citrifolia* as well as within each of the crops from the other eight species (table 1) were conducted for comparisons with the simple correlations within crops reported in Herre (1996). (4) Within-crop analyses of all crops, while controlling for the effects of fruit differences in flower number and proportion of developed flowers, were conducted in order to determine the influence of these variables at the level of fruit.

We investigated the correlations between these variables using the regression and multiple regression techniques implemented in the GLIM statistical package (Crawley 1993). For the within-crop analyses here, we selected only those fruits that contained one foundress, and thereby controlled for effects of differential pollination (Herre 1989, 1996; West & Herre 1994). However, analyses of multiple foundress fruits showed no qualitative differences to the results of seed-wasp relationships that we present here for the single foundress analyses.

(a) *Variation across F. citrifolia fruit crops*

Samples of between 17 and 49 fruits were collected from the crops of 16 *F. citrifolia* trees. For each crop we calculated the average number of pollinating wasps and viable seeds that

developed in a fruit, the average number of female flowers per fruit, and the average proportion of female flowers in a fruit that either developed into a viable seed or supported the development of a wasp. We carried out four regression analyses on the crop means, with the number of viable seeds in a fruit as the dependent variable, and the number of pollinator wasp offspring in a fruit as the independent variable. The covariates included in these four regression analyses were, respectively: (1) no covariates (similar to analyses presented in Bronstein 1992); (2) the proportion of female flowers developed in a fruit; (3) the total number of female flowers in a fruit; (4) both the proportion of female flowers developed in a fruit and the total number of female flowers in a fruit.

(b) *Variation within fruit crops of F. citrifolia and eight other species*

In addition to the 16 *F. citrifolia* crops described above, we collected samples of between 18 and 57 fruits from 14 fruit crops representing eight other fig species (tables 1 and 5). Only fruits that had been pollinated by a single foundress were considered to control for any confounding effects due to variable foundress numbers (Herre 1989, 1996; West & Herre 1994). The data from each crop were analysed separately. For each crop we carried out the same four types of regression analyses, with the number of viable seeds in a fruit as the dependent variable, and the number of pollinator wasp offspring as the independent variable, as with the among-crop analyses.

4. RESULTS

The nine species represent widely divergent lineages within the genus *Ficus* (Herre *et al.* 1996, unpublished data), and average characteristics of all species examined are given in table 1. The different species represent a broad range of average fruit sizes (numbers of female flowers per fruit), proportions of developed flowers, numbers of viable seeds, numbers of pollinator wasp offspring, and average number of foundresses, that are characteristic of monoecious species of *Ficus* (see also Herre 1989). There is also considerable variation in these variables among fruit within species (see table 1). It is worth noting that the different

fecundities observed in the different wasp species, as well as the different per fruit production of viable seeds, demonstrate the very different coevolutionary outcomes characteristic of the different fig wasp species pairs (see also Herre 1989, 1996; Herre *et al.* 1996; Thompson 1994).

(a) Variation between *F. citrifolia* fruit crops

Summaries of across crop analyses are given in table 2. There was a non-significant positive relationship between the average number of viable seeds and the average number of pollinator offspring in the fruit of a crop ($F_{1,14} = 2.03$, $p > 0.05$, $n = 16$; figure 1a), similar to cross-crop analyses in other species (see Bronstein 1992; Bronstein & Hossaert-McKey 1996). Further, there was still no significant relationship between the crop means of viable seeds and pollinator offspring when either mean proportion of developed flowers ($F_{1,13} = 2.33$, $p > 0.05$) or mean numbers of flowers ($F_{1,13} = 0.72$, $p > 0.05$) were included singly as covariates in the analysis. However, when both of these variables were included as covariates, the relationship between the crop means of viable seeds and pollinator offspring was significantly negative ($F_{1,12} = 21.27$, $p < 0.01$, slope -0.89 , s.e. = 0.19; figure 1b, table 2).

The latter result is explained by multiple regressions that showed significant positive correlations between (1) the average number of viable seeds and both the mean proportion of developed flowers ($F_{1,12} = 23.33$, $p < 0.01$, slope 343, s.e. = 71), and the mean numbers of flowers ($F_{1,12} = 50.27$, $p < 0.01$, slope 0.82, s.e. = 0.12); and (2) the average number of pollinator offspring and both the mean proportion of flowers developed ($F_{1,13} = 18.99$, $p < 0.01$, slope 285, s.e. = 65), and the mean number of flowers ($F_{1,13} = 43.25$, $p < 0.01$, slope 0.53, s.e. = 0.08).

Therefore, across crops, those with higher average numbers of flowers per fruit and those that developed a higher average proportion of their flowers tended to produce both more viable seeds and more wasp offspring per fruit, creating a positive correlation between seed and wasp productions.

(b) Variation within fruit crops of *F. citrifolia* and eight other species

Summaries of the relationships between the number of viable seeds and the number of pollinator wasps developing in a fruit, when the various covariates are included in the analyses, are given in table 3 for the 16 crops of *F. citrifolia*, and in table 4 for 14 crops of eight other species. Table 5 shows the slopes between the number of viable seeds in a fruit and the number of pollinator wasp offspring in a fruit for each crop, when both the number of female flowers in a fruit and the proportion of female flowers developing in a fruit were included as covariates.

When no other covariates, or only the proportion of female flowers developing in a fruit were included in the analysis, there was no significant trend for the slope between viable seed and wasp production to be negative (tables 3 and 4). However, if the number of female

Table 2. Summary of multiple regression analyses among 16 *F. citrifolia* crops

(The table indicates whether the correlations between the crop mean number of viable seeds in a fruit (dependent variable) and the crop mean number of pollinator wasp offspring per fruit (independent variable) were negative or positive, and significant ($p < 0.05$) or non-significant (n.s.). The first column shows the covariates that were included in each analysis, where PDEV is the crop mean proportion of female flowers developing per fruit, and FTOT is the crop mean total number of female flowers per fruit.)

covariates	slope of viable seeds versus wasp offspring			
	negative significant	negative n.s.	positive n.s.	positive significant
none	0	0	—	0
PDEV	0	0	—	0
FTOT	0	—	0	0
PDEV + FTOT	—	0	0	0

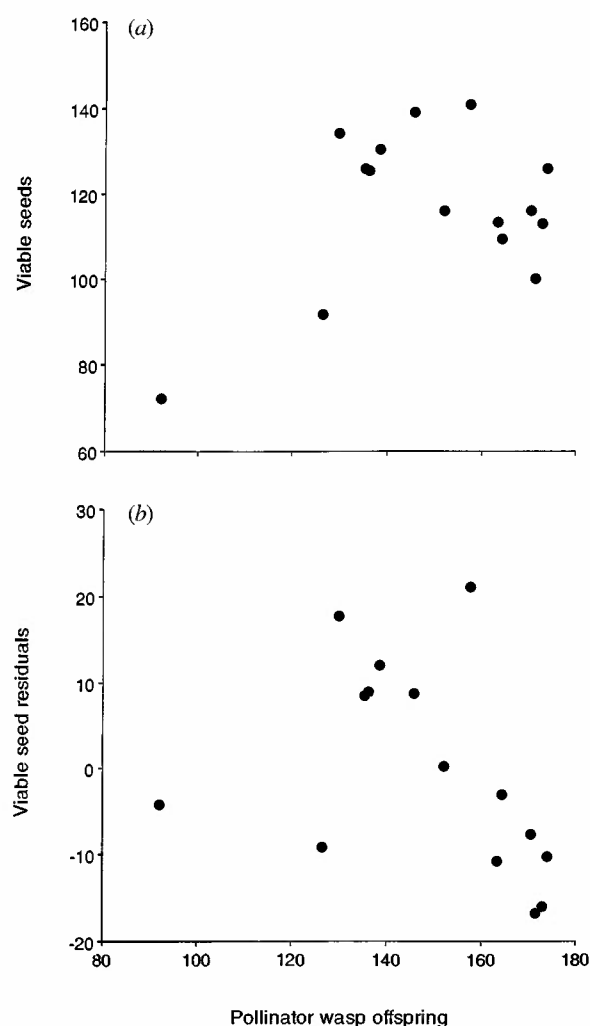


Figure 1. The relationship, across 16 crops of *F. citrifolia*, between average number of viable seeds in a fruit, and average number of pollinator wasp offspring in a fruit. (a) The raw averages of viable seeds. (b) The residuals after controlling for average number of flowers in a fruit, and average proportion of female flowers developed. After controlling for the effects of confounding variables, the relationship is seen to be clearly negative (see text).

Table 3. Summary of multiple regression analyses within 16 *F. citrifolia* crops

(The table indicates the number of crops for which the correlation between the number of viable seeds per fruit (dependent variable) and the number of pollinator wasp offspring per fruit (independent variable) were negative or positive, and significant ($p < 0.05$) or non-significant (n.s.). The first column shows the covariates that were included in each analysis, where PDEV is the proportion of female flowers developing per fruit, and FTOT is the total number of female flowers per fruit.)

covariates	slope of viable seeds versus wasp offspring			
	negative significant	negative n.s.	positive n.s.	positive significant
none	1	8	7	0
PDEV	1	10	5	0
FTOT	8	7	1	0
PDEV + FTOT	13	3	0	0

Table 4. Summary of multiple regression analyses within crops of all species other than *F. citrifolia*

(The table indicates the number of crops for which the correlation between the number of viable seeds per fruit (dependent variable) and the number of pollinator wasp offspring per fruit (independent variable) were negative or positive, and significant ($p < 0.05$) or non-significant (n.s.). The first column shows the covariates that were included in each analysis, where PDEV is the proportion of female flowers developing per fruit, and FTOT is the total number of female flowers per fruit.)

covariates	slope viable seeds versus wasp offspring			
	negative significant	negative n.s.	positive n.s.	positive significant
none	1	6	6	1
PDEV	1	8	5	0
FTOT	8	5	1	0
PDEV + FTOT	12	2	0	0

flowers in a fruit was included as a covariate, then there was a negative slope between viable seed and wasp production in 15 out of 16 *F. citrifolia* crops, and in 13 out of 14 other species crops (tables 3 and 4). This relationship was significant ($p < 0.05$) in eight of the *F. citrifolia* crops and in eight of the other species crops (tables 3 and 4). Moreover, when both the number of female flowers and the proportion of female flowers developing in a fruit were included as covariates, the slope between viable seed and wasp production in all 16 of the *F. citrifolia* crops and all 14 of the other species crops is negative (tables 3–5). This relationship was significant ($p < 0.05$) in 13 of the *F. citrifolia* crops and 12 of the other species crops (tables 3–5).

5. DISCUSSION

In order to determine what general principles, if any, apply to mutualistic interactions, a clear understanding

Table 5. Details of the multiple regression analyses within crops of all species

(The table indicates the slope between the number of viable seeds per fruit (dependent variable) and the number of pollinator wasp offspring per fruit (independent variable), when both the total number of female flowers per fruit, and the proportion of female flowers developing per fruit were included as covariates. (n.s., non-significantly different from 0; ^a $p < 0.05$; ^b $p < 0.01$).

species (<i>Ficus</i>)	crop	number of fruit	slope of viable seeds versus wasp offspring	
			estimate	standard error
<i>F. bullenei</i>	1	26	-0.28 ^a	0.14
<i>F. bullenei</i>	2	44	-0.85 ^b	0.09
<i>F. citrifolia</i>	1	17	-0.30 n.s.	0.23
<i>F. citrifolia</i>	2	22	-0.28 n.s.	0.15
<i>F. citrifolia</i>	3	39	-0.43 ^b	0.08
<i>F. citrifolia</i>	4	29	-0.99 ^b	0.04
<i>F. citrifolia</i>	5	37	-0.73 ^b	0.07
<i>F. citrifolia</i>	6	36	-0.83 ^b	0.13
<i>F. citrifolia</i>	7	13	-0.83 ^b	0.13
<i>F. citrifolia</i>	8	26	-0.76 ^b	0.13
<i>F. citrifolia</i>	9	19	-0.30 ^a	0.15
<i>F. citrifolia</i>	10	26	-0.72 ^b	0.13
<i>F. citrifolia</i>	11	22	-0.23 n.s.	0.14
<i>F. citrifolia</i>	12	26	-0.77 ^b	0.16
<i>F. citrifolia</i>	13	25	-0.58 ^b	0.12
<i>F. citrifolia</i>	14	26	-0.76 ^b	0.13
<i>F. citrifolia</i>	15	27	-0.31 ^b	0.09
<i>F. citrifolia</i>	16	27	-0.40 ^b	0.13
<i>F. columbrinae</i>	1	23	-0.84 ^b	0.06
<i>F. nymphaeifolia</i>	1	42	-1.04 ^b	0.18
<i>F. nymphaeifolia</i>	2	33	-0.68 ^b	0.16
<i>F. obtusifolia</i>	1	57	-0.63 ^b	0.05
<i>F. obtusifolia</i>	2	42	-0.48 ^b	0.07
<i>F. obtusifolia</i>	3	50	-0.91 ^b	0.04
<i>F. obtusifolia</i>	4	42	-0.91 ^b	0.03
<i>F. pertusa</i>	1	29	-0.34 n.s.	0.18
<i>F. nr. trigonata</i>	1	38	-1.02 ^b	0.07
<i>F. nr. trigonata</i>	2	24	-0.84 ^b	0.10
<i>F. turbinata</i>	1	44	-0.19 n.s.	0.13
<i>F. yoponensis</i>	1	18	-0.89 ^a	0.36

of many specific cases is critical. For each case, this involves characterizing costs and benefits to each partner, and determining the functional relationships among variables that influence those costs and benefits. Specifically, it is important to correctly identify potential conflicts of interest. If the relationships among mutualists in individual case studies are misunderstood, the task of making useful generalizations is severely hampered. In the case of the mutualism between figs and their pollinator wasps, the functional relationships among factors that influence costs and benefits to each member have only recently begun to be understood. In fact, even the fundamental question of whether or not trade-offs and conflicts of interest between the partners exist, has been unclear (Herre 1989, 1996; West & Herre 1994; Bronstein 1992; Bronstein & Hossaert-McKey 1996).

We have shown that a simple regression across 16 fruit crops from *F. citrifolia* trees provided no evidence

for a negative relationship between viable seed and pollinator wasp production. This pattern is similar to that previously found in two other fig species (Bronstein 1988, 1992; Bronstein & Hossaert-McKey 1996). Even simple correlational analyses within 30 crops collected from nine species do not consistently show a negative relationship. This pattern is similar to previously published results of simple correlational analyses that have been conducted within crops (Herre 1996). However, when the confounding effects of total flower number and proportion of flowers developed per fruit were controlled for statistically, the negative trade-off between pollinator wasp and viable seed development was found to be ubiquitous.

In order to understand the interactions of factors underlying this result, it is important to appreciate the fact that variation in seed and wasp production is related to variation in both the number of flowers in a fig fruit and the proportion of them that develop. These patterns have been found across species, across crops within species, and among fruit within crops of individual trees (Herre 1989, 1996; West & Herre 1994; Bronstein 1992; Bronstein & Hossaert-McKey 1996; Anstett *et al.* 1996). What then affects the number of flowers and the proportion of them that develop?

Variation in the number of flowers initially found in receptive fruits within crops appears to be due at least in part to local availability of resources (Bronstein & Hossaert-McKey 1996; Herre 1996, unpublished data). This interpretation is suggested by experiments in which radioactive carbon dioxide was introduced to leaves on fig trees with developing fruit crops. Labelled carbon from the subtending leaves accumulated predominantly in adjacent fruits, showing the subtending leaf to be a major source of carbohydrate for developing fruit. Further, fruit of both *F. insipida* and *F. yoponensis* developing at the bases of larger leaves show higher numbers of total flowers, as well as disproportionately higher productivity of viable seeds and pollinator wasps (Herre 1996, unpublished data). In another series of studies, fruit of *F. aurea* growing adjacent to leaves contained significantly more female flowers than fruit located further from a leaf (Bronstein & Hossaert-McKey 1996). What then influences the proportion of those initial flowers that develop?

Several studies indicate that variation in the proportion of flowers that develop to produce pollinator wasps and viable seeds represents a combination and interaction of variable resource and pollen availability (Herre 1989, 1996; West & Herre 1994; Bronstein & Hossaert-McKey 1996). Specifically, in many cases, increased numbers of foundresses per fruit are associated with increased flower development, suggesting that flower development within a fruit can be limited by pollen availability (Herre 1989, 1996; West & Herre 1994; West *et al.* 1996; Anstett *et al.* 1996; Bronstein & Hossaert-McKey 1996). In this study, we controlled for the effects of differential pollination of this sort by considering only fruit that were pollinated by only one foundress for the within-crop analyses. Additionally, there is a strong suggestion that, in some cases, flowers that have been pollinated will not develop due to resource limitation, either among fruit within

crops (see above; Herre 1989, 1996; Anstett *et al.* 1996; Bronstein & Hossaert-McKey 1996), or across fruit crops (Herre 1989, 1996; Bronstein 1992). Nonetheless, in most cases in which either resource or pollen availability can be shown to increase, flower development and both seed and wasp production increase. Ongoing work addresses the quantitative links between resource and pollen availability and resulting patterns of seed and wasp production, as well as the identification of the underlying mechanisms generating those patterns (E. A. Herre, unpublished data; F. Kjellberg, personal communication).

It is worth emphasizing that, in these monoecious fig species, the production of wasps is generally linked to the proportion of flowers that develop. Therefore, to the extent to which flower development is linked to pollination, the reproductive success of the wasps is linked to their own capacity to pollinate the fig tree's flowers. This property of the system causes the interests of the two partners to coincide in this respect. It also is interesting to note that, as mentioned above, in most cases viable seed production increases more rapidly with increased flower development than does wasp production.

The analyses presented here show that both flower number and the proportion of female flowers that develop are positively correlated with the production of pollinator wasps and viable seeds. Fruit in which there are more female flowers, and a higher proportion of them, produce both more viable seeds and more pollinator wasp offspring. Moreover, the slopes of the relationships of these variables with seed production are generally greater than they are with wasp production. When the confounding effects of these variables were statistically controlled for, the negative trade-off between pollinator wasp and viable seed production is shown to be ubiquitous. This same pattern occurs both across and within crops, documenting the inherent conflict of interest between the two partners of this mutualism.

Analyses of trade-offs in other pollination mutualism systems in which, as with the figs, some of the seeds are consumed by the developing offspring of the pollinators also often show positive relationships between seed and pollinator production (Thompson & Pellmyr 1992; Pellmyr *et al.* 1996). We suggest that the interaction of several variables in determining ecological and evolutionary outcomes is likely to be a general property of most mutualistic systems (Herre 1989, 1996; Bronstein 1992; Thompson & Pellmyr 1992; West & Herre 1994; Thompson 1994; West *et al.* 1996; Pellmyr *et al.* 1996), and that at least in some of them it is likely to play an important role in maintaining the stability of the mutualism (Pellmyr & Huth 1994; Pellmyr *et al.* 1996).

One remaining question is why the pollinating wasps do not exploit more or even all of the flowers at the expense of the figs' viable seed production? The most carefully studied fig-wasp systems suggest that while some flowers can only support the development of a seed, others have the potential to develop either into a seed or a wasp, if an egg is laid in them. While the underlying mechanisms are not entirely clear, they appear to involve physiological, structural, and/or

chemical differences in the flowers. Nonetheless, various studies suggest the possibility that the mechanisms differ in different species of figs and their associated pollinators (Murray 1985; Kjellberg *et al.* 1987; Bronstein 1988; Verkerke 1986; Compton & Nefdt 1990; West & Herre 1994; Kathuria *et al.* 1995; Nefdt & Compton 1996; Herre 1996). Definitive answers require further in-depth studies within species, as well as tests of the generality of identified mechanisms across distantly related species. However, our analyses clearly demonstrate the negative relationship between the production of viable seeds and pollinator wasps that represents the inherent conflict of interest between the two partners of this mutualism. It is this inherent conflict that makes mechanisms for excluding wasps from access to some of the seeds necessary for the continued stability of the mutualism.

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