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in book
Levels of Selection
edited by
Laurent Keller
Princeton Press
1999

11 Laws Governing Species Interactions? Encouragement and Caution from Figs and Their Associates

Edward Allen Herre

All organisms interact with members of other species. The diversity of forms that those interactions assume is overwhelming and offers the clearest reflection of the diversity of life itself. Directly or indirectly, parasitic organisms constantly affect virtually all ecological and evolutionary processes. In counterpoint, mutualistic interactions are ubiquitous, their members often comprise ecologically dominant members of communities, and, as with parasitisms, they exert a profound influence on essentially all levels of biological organization. However, the theoretical and empirical challanges presented by the ecology and evolution of interactions among species are equal to or greater than those presented by within-species or within-genome interactions.

For example, it is widely appreciated that mutualistic relationships usually incorporate parasitic aspects, and that the converse can be equally true for parasitisms. Furthermore, the mixed nature of some of these relationships, as well as the existence of transitional intermediates, strongly suggests that outcomes of species interactions can be both ecologically and evolutionarily quite fluid (e.g., Herre 1989; Compton et al. 1991; Thompson 1994; Bronstein and Hossaert-McKey 1996; Herre et al. 1996; Nefdt and Compton 1996; Pellmyr et al. 1996; Herre and West 1997). The fundamental question is whether there are any general rules that govern the ecological and evolutionary trajectories and outcomes of interactions, or if there is simply a large collection of special cases, with no overriding principles.

After mentioning some important general properties of parasitisms and mutualisms, I present a brief overview of factors that theory suggests ought to influence evolutionary outcomes of interactions, such as patterns of ecological transmission and degree of co-speciation. I then present relevant aspects of the natural history of a series of mutualists and parasites that are associated with figs. For each group of species, I examine whether the the predictions of the theory do or (in many cases) do not correspond to the degree to which an interaction is parasitic or mutualistic. Further, in keeping with one of the motivating themes of this book, I also discuss how selection

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at different levels of population structure influences both sex-ratio adaptations in the wasps, and the expression of virulence in the nematode parasites of those wasps (both of which influence the relationship of these organisms with the fig). Moreover, I emphasize that selection pressures resulting from different components of the fig-pollinator, parasite, nematode, and seed-disperser relationships can interact with each other in complex and often unexpected ways.

Parasitisms

In the case of parasitisms, it is the virulence (negative influence on host reproduction and survival) associated with parasites that drives their myriad influences. Therefore, central questions concerning parasitisms revolve around understanding factors that influence the expression and evolution of virulence (Levin and Pimentel 1981; Ewald 1987; Frank 1992; Herre 1993, 1995; Bull 1994; May and Nowak 1994; Nowak and May 1994; Ebert and Herre 1996). In order to frame such questions, much less answer them, it is fundamentally important to recognize that virulence is an attribute neither of the parasite nor of the host alone, but a result of the interaction between the two. It is particularly important to recognize that the outcome of that interaction usually depends on ecological context (see below). The responses to that ecological context are themselves embedded to a greater or lesser degree in evolutionary context. That is, organisms generally respond most "adaptively" to the situations most commonly encountered through their evolutionary history (Herre 1987). Nevertheless, in parasitisms, what is adaptive for the host clearly is often not adaptive for the parasite.

Furthermore, neither "host" nor "parasite" is a monolithic entity. Their populations are almost invariably composed of a variety of genotypes and strains. Because different parasite strains often have very different effects on a given host genotype, factors that influence the spatial or temporal distribution of parasite strains and of host genotypes will strongly affect the expression and evolution of virulence. Ultimately, changes in virulence observed in any particular system can result from changes selected in either the host or parasite populations, or, more likely, both. Moreover, virulence varies dramatically from system to system, and the virulence observed in any particular host-parasite system can change across space and time. All of this makes it inherently challenging to define, measure, and study virulence. Although the consequences of within-species variation have been more extensively studied in host-parasite systems (e.g., Ebert 1994; Thompson 1994), the situation with mutualisms is analogous, and all of the complexities outlined above for parasitic interactions also apply.

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Mutualisms

Given that mutualisms are best viewed as reciprocal exploitations that nonetheless provide net benefits to each of the involved parties, it follows that it is important to identify costs and benefits to each partner correctly and, if possible, to quantify them. Next, it is desirable to relate variation in those costs and benefits to variation in the factors that influence them (Herre 1989, 1996; Pellmyr 1989; Thompson and Pellmyr 1992; Anstett et al. 1996; Bronstein and Hossaert-McKey 1996). Finally, it is particularly important to identify the situations in which there exists a conflict of interest between the two (Herre and West 1997). Special attention should be given to the mechanisms that prevent the costs to either partner from exceeding the benefits, thereby maintaining the mutualistic nature of the interaction. For example, it appears that yuccas can curb parasitic tendencies in their mutualist moth pollinators by aborting fruits that the moths have overexploited (Pellmyr and Huth 1994).

Although there is no general theory of mutualism, several factors that can help align mutualists' interests have been tentatively identified. An important precondition for mutualisms is the potential for complementation or augmentation of functions and abilities among would-be mutualists. In such cases, the passage of symbionts from parent to offspring (vertical transmission), genotypic uniformity of symbionts associated with individual hosts, spatial structure of populations leading to repeated interactions between would-be mutualists or their descendents, and restricted options outside the relationship for one or both partners are thought to align interests and promote long-term stability. Conversely, movement of symbionts between unrelated hosts (horizontal transmission), multiple symbiont genotypes, and varied options are thought to promote the opposite effects (Trivers 1971; Axelrod and Hamilton 1981; Bull and Rice 1991; Frank 1992; Yamamura 1993; Leigh and Rowell 1995; Maynard Smith and Szathmáry 1995). It is no coincidence that many of the same situations are thought to influence the expression of virulence. Overall, this framework is logically appealing, and at least some cases appear to conform well with its predictions (e.g., Bull et al. 1991; Herre 1993, 1995; Clayton and Tompkins 1994). However, the attempt to assess the generality of this framework is necessary, and requires many carefully executed and interpreted case studies.

Fig-Associated Organisms

Here, I concentrate on the mutualistic and parasitic organisms associated with monoecious New World figs (with a few examples from Old World systems), and use them to examine the extent to which some of the proposed theories are or are not applicable. One justification for this seemingly narrow

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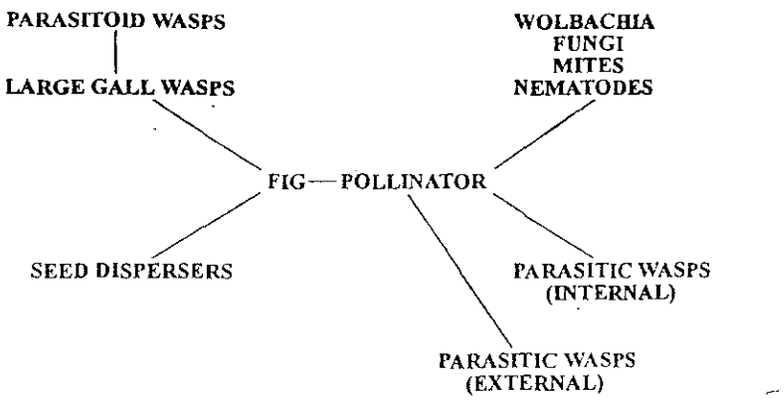

Fig. 11.1. Organisms associated with figs include: mutualist wasps, parasitic wasps (both internally and externally ovipositing) that appear to be primarily competitors with the pollinators, nematodes, fungi, mites, and Wolbachia (bacteria) that are phoretic or carried internally by the pollinating wasps, larger gall-forming wasps and their parasitoids, and frugivorous seed dispersers (see text).

approach is that figs and their associates provide both a wide range of types of interacting taxa (plants, insects, nematodes, fungi, bacteria, vertebrates) and a variety of types of interactions (Fig. 11.1; Corner 1940; Werren et al. 1995; Kalko et al. 1996). For most of these organisms, it is possible to make fairly direct measurements of fitness or major components of fitness. Often, variation in reproductive success of one member of these interactions can be related to variation in attributes of another at various levels (e.g., species, populations, individuals) (Herre 1989, 1993; Nefdt and Compton 1996; Herre and West 1997).

These measurements can then be placed in a series of levels of ecological and evolutionary context that the above-mentioned framework suggests are important considerations. Specifically, from the basic natural histories, as well as more detailed genetic information, we know something about patterns of ecological transmission (e.g., Nason et al. 1996, 1998). Further, in most cases, we have genetic information that suggests phylogenetic relationships among many of the associated taxa, and we can therefore make inferences about longer-term associations or evolutionary tracking (Herre 1995; Herre et al. 1996; Machado et al. 1996).

Before examining the applicability of theory to these organisms, it is worth emphasizing the practical challenges to making both appropriate measurements and proper analyses that are posed by complex systems of interacting factors. For example, in the fig-wasp system many factors interact to affect the production of the basic currency of the mutualism: viable seeds and pollinator wasps (Herre 1989, 1996; see fig. 11.2). Unless the confounding effects of these factors are properly controlled for, it is very easy to

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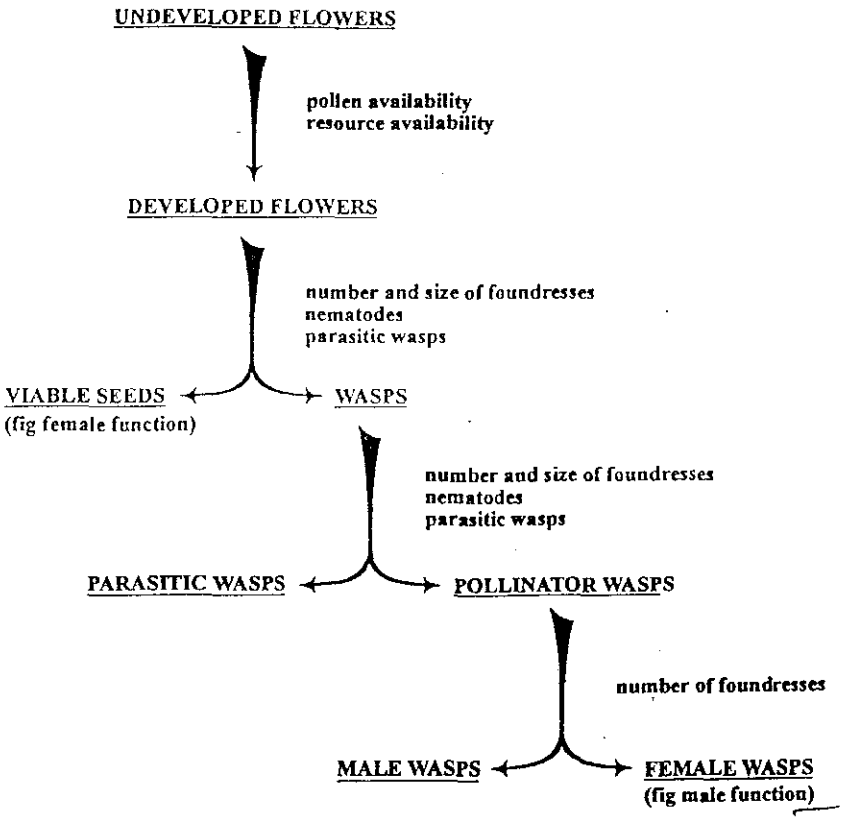

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FIG. 11.2. Flow chart showing stages at which different factors influence the production of viable seeds and pollinator wasps. The important point to recognize is that the production of the basic currency of the mutualism is influenced at many stages by a number of different factors, some of which are attributes of the fig, some of which are attributes of the wasp, and some of which are neither.

misinterpret the underlying relationships among variables of fundamental importance to the mutualism (West and Herre 1994; Herre and West 1997; see below).

Monoecious Fig-Pollinating Wasps

More than 750 named species of figs are found worldwide. All depend on minute wasps for pollination. The pollinator wasps, which are usually species-specific, are all members of the chalcidoid family Agaonidae, and all of them show similar life cycles (Wiebes 1979, 1995). It is important to note that the closest relatives of the wasps that pollinate figs appear to be the wasps that parasitize them (Boucek 1988; Machado et al. 1996). The monoecious figs belong to three of four recognized *Ficus* subgenera and comprise

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roughly half of all fig species. Both molecular and morphological evidence suggest that the life cycle of the monoecious species is ancestral to the more derived life cycles exhibited by the dioecious fig species (Ramirez 1969, 1980; Wiebes 1979, 1982; Corner 1985; Berg 1989; Herre et al. 1996; Kerdelhue and Rasplus 1996b; Anstett et al. 1997).

The reproductive cycle of the figs and the wasps begins when 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 and can thus be counted (Herre 1985, 1989, 1996; Compton et al. 1991; but see Gibernau et al. 1996). The numbers of foundresses per fruit can vary greatly both within and among species, and that variation can have a number of important effects on the outcome of the wasps' interactions with the fig (e.g., Herre 1989, 1993, 1996). Unpollinated fruit are usually, but not always, aborted.

After they are pollinated, some proportion of the female flowers begins to develop. Flowers that complete development eventually produce either an intact, viable seed or an adult wasp that consumes the contents of a single would-be 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 (fig. 11.2; Herre 1989, 1996; Anstett et al. 1996; Bronstein and Hossaert-McKey 1996; Herre and West 1997).

As final ripening of the fig fruit approaches, the wingless adult male wasps emerge from the seeds within which they matured. They crawl around the interior of the syconium, chew open seeds that contain females, and mate. The mated females enlarge the holes cut by the males, emerge from their seeds, gather pollen from male flowers, exit the fruit (through exit holes that in most species are cut by the males), and begin the cycle anew (Corner 1940; Galil and Eisikowitch 1968; Ramirez 1969; Frank 1984). After the female wasps leave, a wide range of animals eat the ripe fruit and disperse the viable seeds (Janzen 1979; Milton et al. 1982; McKey 1989; Windsor et al. 1989; Milton 1991; Kalko et al. 1996).

Ecological Patterns of Transmission and Evolutionary Patterns of Co-speciation

Recent genetic work has shown that the pollen-bearing wasps routinely disperse many kilometers, with the result that the areas covered by effective breeding populations of figs are usually a hundred or more square kilome-

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ters, an order of a magnitude larger than that documented for any other plant species (Nason et al. 1996, 1998; also see Compton 1990, 1993; Ware and Compton 1992). Therefore, the mutualistic fig-wasp system is largely characterized by an extreme horizontal transmission of the mutualist wasp. Furthermore, recent molecular data strengthens earlier morphological studies suggesting that, with a few exceptions, the wasps are species-specific (Herre et al. 1996). That specificity almost certainly arises from the species-specific chemical attractants that the figs release when receptive (van Noort et al. 1989; Ware and Compton 1992; Hossaert-McKey et al. 1994). Finally, the predominant evolutionary pattern shown is for co-speciation/co-cladogenesis among the wasp and fig lineages (Ramirez 1974; Wiebes 1979; Berg 1989; Herre et al. 1996).

Measuring Reproductive Success in the Figs and Wasps: Sorting Out the Effects of Confounding Variables

Many factors interact to affect the production of the basic currency of the fig-wasp mutualism: viable seeds and pollinator wasps (Herre 1996; see fig. 11.2). These factors include attributes of the fig (such as the number of flowers per fruit); attributes of the wasp (such as body size); attributes of the interaction between the two (such as the proportion of those flowers that develop, which is itself influenced by pollen availability [e.g., number or size of foundress pollinators] and resource availability); as well as attributes of neither (presence and densities of parasitic wasps and nematodes). It is critical to properly account for the confounding effects of these factors. Otherwise, misinterpretation of the underlying relationships among variables that are of fundamental importance to the mutualism is the likely result (West and Herre 1994; Herre and West 1997).

Specifically, the confounding of these factors often leads to the mistaken perception that there is either no relationship between viable seed and pollinator wasp production, or that the relationship exists and is positive. This would appear to be consistent with the interpretation that there is no conflict of interest between the two mutualists. Similarly, the relationship between parasitic wasp and seed or pollinator production often appears positive. This would appear consistent with the interpretation that there is no negative impact of the parasitic wasps (see below). In the absence of proper statistical control, the true underlying negative relationship between viable seed production and pollinator wasp production can be overlooked, and the underlying negative relationship between certain groups of parasitic wasps and pollinators can be missed (Herre 1989, 1996; West and Herre 1994; Herre and West 1997).

When only one foundress wasp enters a fig fruit, counting the offspring gives a direct measure of that wasp's lifetime reproductive success (Herre

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1989, 1993). The variation in foundress's lifetime reproductive success can often be related to variation in a number of attributes of both the wasp and the fig fruit that it pollinated (Herre 1989; West and Herre 1994; Anstett et al. 1996; Bronstein and McKey-Hossaert 1996; Nefdt and Compton 1996; Herre and West 1997). Similarly, seed and wasp production can be measured, and their variation among fruit can be related to variation in the attributes of the individual foundress wasps (e.g., body size). Such measurements permit the documentation of how variation among individuals within both mutualist species has reciprocal effects on the reproductive success of the other.

Specifically, of the female wasps that are born in a given fruit, the larger ones appear to have a higher success rate of reaching the next fig, and, once there, the largest of these produce the greatest number of offspring (Herre 1989; Nefdt and Compton 1996; Herre and West unpubl.). Although there appears to be a slight heritable component, wasp body size is mostly explained by the dry weight of the seeds from the fruit in which they hatch. Combined, these observations suggest that wasp body size can shift the outcome of the fig-wasp interaction toward the production of wasps, but that wasp body size is most clearly affected by the fig (Herre 1989; Herre and West in prep.).

In essence, although both the wasp and the fig depend on each other for long-term survival and reproduction, their short-term interests are not necessarily aligned. An individual fig needs the foundresses to pollinate its flowers in order to produce seeds of its own. It also needs the foundresses' female offspring to disperse its own pollen. Those female offspring are useful only insofar as they produce seed with the pollen of the fig that produces them. In contrast, the foundress wasps only benefit from would-be fig seeds that are consumed by their offspring. That is, although there is a mutual, long-term interdependence between the two partners, there are clear conflicts of interest, some of which would appear to have the potential to undermine and ultimately destabilize the relationship.

Fig-Wasp Sex ratios and Their Influence on the Fig

Because only female wasp offspring provide pollination services for the fig, the tendency of the wasps to shift sex ratio away from extreme female bias with increasing foundress numbers is not in the fig's interest. Although the details of the relationships vary among fig species, single foundresses, particularly in larger-fruited figs, often do not provide sufficient pollen to saturate the receptive flowers and maximize seed set. Generally, increased numbers of foundresses are associated with increases in both seed and wasp

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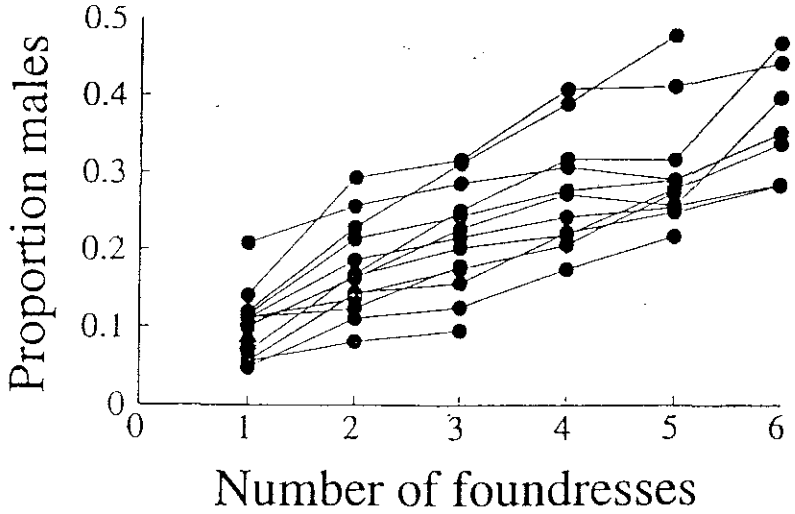

FIG. 11.3. The relationship between brood sex ratio and number of foundresses in 15 species of Panamanian fig-pollinating wasps. Within species, the brood sex ratio becomes less female-biased as the number of foundresses increases. Between species, species that have higher average foundress numbers (suggesting more outbreeding) show less female-biased sex ratios for any given number of foundresses. Because only female wasps can transport pollen, decreasing female bias runs counter to the fig's reproductive interests (see text).

production (Herre 1989). Of the wasps that are produced, however, an increasing proportion tends to be wingless males, which are of no use as fig pollen vectors (fig. 11.3; Herre 1989, 1996)

These sex-ratio shifts represent the wasps' responses to varying intensities of local mate competition (Hamilton 1967, 1979; Frank 1985; Herre 1985). Interestingly, local mate competition represents one of very few examples of a Prisoner's Dilemma-style game known from a natural system in which the payoff values can be derived from first principles. Furthermore, the key to understanding how much greater or lesser degrees of female bias are favored lies in understanding how among- and within-group selection are balanced (Colwell 1981; Wade 1985).

The payoff matrix below (table 11.1) shows the relative fitnesses of two outbred foundresses that contribute equal-sized broods to fig fruits. By "playing" a female-biased strategy (0.25 males), the foundress maximizes its absolute fitness. By "playing" an even sex ratio (0.50 males), however, the foundress insures that the relative fitness of the other wasp within the same fig fruit (deme) does not exceed her own. Cooperation (which in this case is represented by female-biased sex ratios) is only enforced by the existence of many sets of competing foundresses in multiple fruits (demes). That is, the among-deme

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TABLE 11.1
Local Mate Competition Game Payoff Matrix

	Sex Ratio of Wasp B	
Sex Ratio of Wasp A	*0.25*	*0.5*
0.5	22(19)	15(15)
0.25	25(25)	19(22)

Note: The first value gives the payoff to wasp A for any combination of brood sex ratios empoyed by A and B. The value inside the parentheses gives the payoff to wasp B for the same situation. Values were calculated assuming two outbred foundresses contributing equal numbers of offspring to a common brood from which mated female offspring emigrate (Herre 1985). Notice that the female-biased ratio (0.25) "loses" to an even sex ratio (0.50) within the deme (payoff of 19 versus 22), yet female-biased sex ratios are observed because of the advantage across demes. The average payoff in demes with two even sex-ratio broods is 15; a rare genotype with a sex ratio of 0.25 (and average payoff of 19) can therefore invade, if the number of demes is high (see Colwell 1981; text).

advantage of increased productivity allows the selection for female-biased sex ratios to override the within-deme selection for even sex ratios (Taylor and Bulmer 1980; Colwell 1981; Frank 1985; Herre 1985).

Population structure also appears to play a similar role in selecting for nematode virulence, with populations characterized by higher foundress numbers permitting and even promoting increased virulence (Herre 1993, 1995). Both of these effects of increased foundress number are detrimental to the fig. These examples support the plausibility of arguments that the effects of population structure and within-deme (within-host) genetic homogeneity can be important in maintaining the beneficial effects of some types of mutualisms (see Levin and Pimentel 1981; Herre 1985; Bull and Rice 1991; Frank 1992; Leigh and Rowell 1995; Maynard Smith and Szathmáry 1995).

THE SEEDS

In monoecious figs, the flowers that develop into viable seeds (usually 40–50%) represent a large portion of the fig's investment in female function. Flowers that support the development of the pollinator wasps, in particular the females, represent a large portion of the fig's investment in "male" function (fig. 11.2; Herre 1989). Therefore, although the investment in female and male function on the part of the monoecious fig is largely reflected in seed and wasp production, respectively, the interests of the wasps are only directly aligned with the fig's investment in its male function. This raises the question of why selection on the much more numerous, and much shorter-lived, wasps to increase their own fecundity has not come at the expense of the production of any viable seeds. We might expect that selection on the

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pollinator wasps would, in the short term, lead to increasingly male-biased sex allocation in figs, and, in the long term, to the complete suppression of viable seed production and eventual collapse of the system. However, after at least 40 million years of possibly frantic coevolution with the wasps, monoecious figs still produce seeds (Collinson 1989; Herre and West 1997).

The mechanisms that prevent pollinators from overrunning the seeds are still not understood. In contrast with some well-studied yuccas in which overexploited fruit are generally aborted (Pellmyr and Huth 1994), there is no evidence that figs abort overexploited fruit (contra Axelrod and Hamilton 1981; also see Addicott et al. 1990; Bull and Rice 1991). In particular, some figs will retain large portions of their crops that have not been pollinated in the event of infestation by certain types of parasitic wasps (see below). Another idea had been that pollinator wasps did not possess ovipositors long enough to reach ovaries on "long-styled" flowers, and thus were only capable of producing offspring in flowers with short styles. Because measurements of pollinator ovipositors show that most ovaries are within the wasps' reach, it now seems clear that differences in style length of seed-destined and wasp-destined flowers is not a sufficient explanation for maintaining seed production (Bronstein 1992; Compton 1993; Kjellberg et al. 1994; West and Herre 1994; Nefdt and Compton 1996; see below).

Nonetheless, there currently appear to be at least two types of viable explanations for the stability that has allowed seed production in figs to persist. One possibility is that there are chemical or physical differences among flowers within a fruit that prevent a portion of them from receiving eggs or prevent them from supporting wasp development if an egg is laid on them (Verkerke 1989; West and Herre 1994; S. G. Compton pers. comm.). This explanation is based on considerations of floral anatomy and inferences from patterns of flower utilization of New World parasitic wasps (West and Herre 1994; West et al. 1996). In essence, it suggests that the figs have hit upon an as yet undescribed "unbeatable" mechanism that prevents wasp oviposition and/or development in some of the flowers, but allows it on others.

A second possibility is suggested by what is clearly the best study currently available on mechanisms of stability of the fig-wasp mutualism (Nefdt and Compton 1996). This study of a series of African figs suggests that, although the foundresses have physical access to most flowers, they possess too few eggs to exploit all of them. Access was determined by comparing ovipositor lengths with style lengths of the flowers. The ovaries of most flowers were found to be within the reach of the wasps' ovipositors in most species examined, and most flowers within reach were found to be able to support a wasp's development. Furthermore, wasp egg loads were also determined in a subset of species. The norm was too few foundresses carrying too few eggs to exploit all of the available flowers, and thus a large fraction of flowers escaped oviposition.

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In essence, assuming the egg counts were accurate, this explanation depends on as yet undescribed trade-offs that prevent wasps from producing enough eggs and/or from developing ovipositors that provide access to all flowers (e.g., Kathuria et al. 1995), as well as figs that can effectively limit the number of pollinators that enter any given fruit. It should be noted that slightly modified versions of this "trade-off" hypothesis and the "unbeatable seed" hypothesis are not mutually exclusive. One very intriguing possiblity is that different fig wasp systems have achieved stability through different mechanisms.

Finally, figs usually expend roughly half of their seeds in feeding wasps, many of which will carry pollen. In yuccas, there is much less chance that a yucca moth developing from a yucca fruit will carry the plant's pollen. It is probably no coincidence that in yuccas only (roughly) one-fourth of seeds go to developing moths (Pellmyr and Huth 1994; Pellmyr et al. 1996). In fact, the allocation patterns (seeds and wasps) and foundress distributions appear to reflect more closely the interests of the fig rather than those of the wasps, implying that the fig is generally the dominant member in the relationship (Herre 1989, 1996; Nefdt and Compton 1996).

Effect of the Seed/Wasp Trade-off on Fig Reproductive Success

Because there is a fundamental negative trade-off between seed and pollinator wasp production (Herre and West 1997), offspring of female wasps dispersing from a given fig tree will come at the expense of seeds that would otherwise be fathered by that fig's pollen. Therefore, the fig that produces the wasps would benefit most if its wasps arrived as foundresses at another receptive fig, pollinated the flowers, induced seed production, but were themselves sterile (see fig. 11.4). One theatre in which this conflict can potentially play out is wasp body size. Increased body size appears to influence a wasp's success by increased likelihood to reach another tree, and increased reproduction (Herre 1989; Nedft and Compton 1996). Depending on the relative importance of these two effects, it appears that wasps would benefit from being as large as possible, but that the fig might benefit most from intermediate-sized wasps (Herre and West in prep.). It is worthwhile to emphasize again that more of the variation in wasp body size appears to be attributable to the environment (the fruit that they are born in) than the size of the mother (Herre 1989).

These different aspects of fig-wasp conflict are analogous to certain types of parent-offspring conflict (Godfray, chap. 6), conflict between mates (Lessells, chap. 5), as well as basic sex-allocation problems piggybacking along for the ride (Herre 1989, 1996). Some of these conflicts almost certainly

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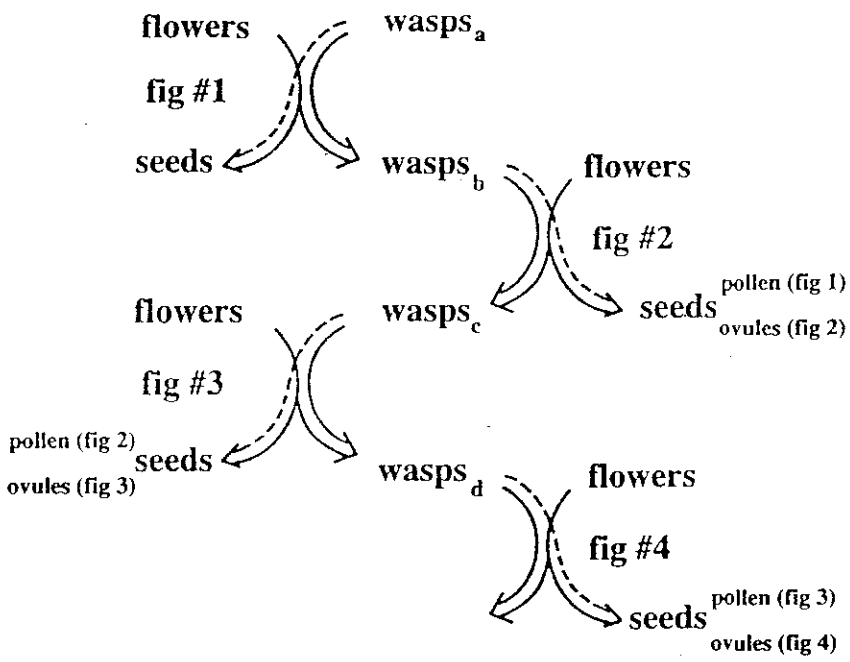

FIG. 11.4. Diagram of reproductive interests of both fig and wasp over three generations of fig pollination and wasp reproduction. Wasps (a) carry pollen to fig #1 for the production of its viable seeds, some of which are consumed to produce the wasp offspring (b). These wasps, in turn, carry pollen from fig #1 to pollinate flowers on fig #2. Some portion of those flowers develop as viable seeds (with genetic contribution from fig #1), others are eaten by the developing offspring of the wasps, and so on. The important point is that in monoecious figs, the pollinators that carry pollen from any tree reproduce directly at the cost of potential offspring of that tree. It would be in the fig's short-term interests to produce sterile wasps to carry its pollen, just as it would be in the wasp's short-term interest to be able to exploit all of the fig's seeds for the development of its offspring.

provide the selective background that has produced dioecy in figs on at least two occasions over the course of evolution. The interested reader should consult the increasing literature concerning the ecology and evolution of dioecious figs (Ramirez 1969, 1980; Wiebes 1979, 1982; Kjellberg et al. 1987; Berg 1989; Herre 1989; Kjellberg and Maurice 1989; Gibernau et al. 1996; Kerdelhue and Rasplus 1996b; Patel 1996; Spencer et al. 1996; Anstett et al. 1997).

THE REASON FOR WASP POLLINATION

Across the different species of fig-pollinating wasps, both active and passive pollination are found. In wasp species that actively pollinate, there are usu-

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ally specialized morphological structures in which pollen is stored, and there are deliberate behaviors for collecting pollen in the ripe, natal fruit and then depositing it on the stigmatic surfaces in the receptive syconia (Ramirez 1969; Frank 1984). In species with passive pollination, specialized structures and behaviors appear to be absent. Recent work has discovered structures and behaviors that were previously missed, however, so that specialized structures and active pollination are perhaps more common than has been thought (Ramirez and Malavasi 1997.

Superficially, there appear to be several reasons why the pollinators perform these services for the figs. First, the fig trees usually abort unpollinated fruit. Given that, in most cases, the foundresses do not leave the fruit they enter, this binds the fate of the foundress wasp's progeny to that of the fruit it enters. Second, 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 (Herre 1989; Herre and West 1997). Third, pollinated flowers may provide a better resource for developing wasps (Verkerke 1989). Furthermore, this relationship between pollination success and wasp success may be linked to the species-specificity that is generally observed in these systems; usually the "right" pollinator species does the best job both in terms of seed and wasp production (Compton 1990; Ware and Compton 1992; see Kerdelhue and Rasplus 1997).

Nonetheless, there are some problems with this straightforward view of factors that align the fig-wasp interests and thus potentially stabilize their relationship. At least three fig species are known to have more than one species of associated pollinator (Galil and Eiskowitch 1968, 1969; Wiebes 1979; Michaloud et al. 1985; Kerdelhue and Rasplus 1997). In fact, of the two "pollinators" associated with *Ficus sycomorus*, *Ceratosolen arabicus* and *C. galili*, the females of the latter species do not pollinate. *Ceratosolen galili* has pollen pockets, yet does not use them and is not normally associated with any viable seed production. The clearest interpretation is that *C. galili* has lost the behavioral component needed for pollination. It is the sole member of the genus, indeed among all of the known pollinator species, that has effectively become a parasite on the system (Galil and Eizikowitch 1968, 1971; Compton et al. 1991). *Ceratosolen galili* is not the sister taxon to the actual pollinator (Herre et al. 1996). Interestingly, this is also the case with nonmutualistic yucca moths (Pellmyr et al. 1996). In contrast, a reversion to nonpollinating has happened more than once among the group of moths that pollinate yuccas.

The existence of a pollinator-turned-parasite raises several questions. One concerns how this wasp has bypassed mechanisms that seem to keep other systems in check. The parasitic *C. galili* does not depend on the pollinator, *C. arabicus*, to pollinate the fruit. Seedless fruit will not abort in the absence

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TABLE 11.2
Attributes of Pollinator Wasp-Fig Systems

Wasps that pollinate figs form a monophyletic group
Within the pollinator clade, only one case is known in which the species no longer pollinates
Closest sister taxa are all parasites of mutualism of fig and fig pollinator wasp
With few exceptions, pollinator wasps are species-specific
Preliminary analyses suggest a high degree of co-speciation with host figs
Pollinator wasps are horizontally transmitted from host to host
All pollinate and oviposit from inside the fig fruit
Many factors influence the outcome of the fig-wasp interactions
Complex system of alignments and conflicts of interest between partners
Partial alignment of interests with figs occurs in male function of fig
Female (seed production) function of figs at odds with wasp short-term interests

of the pollinator if *C. galili* wasps are present (Compton et al. 1991). Is this due to some special trick of *C. galili* or could a nonpollinating *C. arabicus* wasp accomplish the same result? In fact, in the most carefully studied sites, roughly 66% of all fruits were occupied by *C. galili*, whereas only 40% of the fruit were occupied by the legitimate pollinator, *C. arabicus*. Although there are possible disadvantages in fecundity and survival that comes with the smaller size of *C. galili*, it is not clear that these are sufficient to prevent them from completely displacing the pollinator, at least locally. Finally, if this pollinator-turned-parasite wasp cannot only succeed in parasitizing but even come to dominate, why does this not occur more often? In *F. sycomorus*, *C. arabicus*, and *C. galili*, are we witnessing an ongoing collapse that could occur in any of the other fig-wasp mutualisms?

The ability of the "correct" pollinator species to consistently outcompete the odd crossover may be an important component in preventing this (e.g., Compton 1990; Ware and Compton 1992; Kerdelhue and Rasplus 1997). It may also be important that *F. sycomorus* is a relatively large-fruited fig. Generally, large-fruited figs receive several foundresses (Herre 1989; Compton et al. 1991), and the consequences of what any one foundress does in any particular fruit (e.g., not pollinate) are, on average, covered to a greater extent than in systems in which there are normally fewer foundresses. Such a situation may facilitate a pollinator's evolutionary experimentation with increasing degrees of parasitism (also see Thompson and Pellmyr 1992). (See table 11.2.)

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FIG. 11.5. Photograph of the pollinator (*Pegoscapus hoffmeyeri*), externally ovipositing parasitic wasp (*Idarnes* sp.), large gall-forming wasp (*Apocerus* sp.), and parasitoid of the gall former (*Physothorax* sp.) associated with *Ficus obtusifolia*.

Fig-Parasitizing Wasps

Figs also support a diverse community of parasitic nonpollinating wasps (Gordh 1975; Hamilton 1979; Janzen 1979; Ulenberg 1985; Boucek 1988, 1993; Bronstein 1991; Compton et al. 1991; Compton and Hawkins 1992; Compton and van Noort 1992; Hawkins and Compton 1992; Compton 1993; West and Herre 1994; Cook and Power 1996; Kerdelhue and Rasplus 1996a; van Noort and Compton 1996; West et al. 1996). All chalcidoid wasps that depend on the tissues of the syconium for completing their life cycles (both the pollinators and the majority of nonpollinators) have been grouped in the family Agaonidae. According to this classification, all pollinating fig wasp genera belong to the subfamily Agaoninae, whereas nonpollinators are grouped into five different subfamilies (Epichrysomallinae, Otitesellinae, Sycorictinae, Sycophaginae and Sycoecinae) (Boucek 1988). This scheme is largely supported by molecular data (Machado et al. 1996; Machado and Herre unpubl.). Thus, given the phylogenetic relationships, an understanding of the biologies of these parasitic groups is very likely to contribute to understanding the evolutionary origins and mechanisms underlying the stability of the mutualism between the figs and the pollinators (West and Herre 1994; Kerdelhue and Rasplus 1996a).

In the New World, all nonpollinating wasps oviposit from the exterior of the syconium. These externally ovipositing wasps seem to comprise three very ecologically distinct groups (see fig. 11.5): (1) a group that is similar in body size to the pollinators and that appears to compete with them for the same resources for larval development (e.g., *Critogaster* and some groups of *Idarnes*); (2) a group of relatively larger wasps that lay their eggs in the flowers or fruit walls, inducing the formation of large galls in which the larvae develop. The presence of these galls appears to prevent unpollinated fruit from being aborted (e.g., *Aepocerus* and *Idarnes* (incerta)); (3) a group

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of true parasitoids of the larger gall-formers (e.g., *Physothorax*) (West and Herre 1994; West et al. 1996). In addition to wasps of these types, some Old World nonpollinators enter the syconia to oviposit. These wasps include all members of the subfamily Sycoecinae, a few members of the subfamily Otitesellinae, and the genus *Sycophaga* from the subfamily Sycophaginae (Abdurahiman and Joseph 1967; Boucek 1988).

Externally Ovipositing Competitors of the Pollinators

Idarnes (subfamily Sycophaginae) is a genus of nonpollinating wasps associated with figs in the New World subgenus Urostigma (Americana), and *Critogaster* (subfamily Sycorictinae) is a genus of nonpollinating wasps associated with figs of the New World subgenus Pharmacosycea. Unlike pollinator wasps, *Idarnes* and *Critogaster* females do not enter the fig. Instead, they penetrate the fig wall from outside with their characteristically long ovipositors and lay eggs in the interior seed layers of the fruit. Like the pollinators, individual larvae of these parasites develop at the expense of one flower within the fig fruit. *Idarnes* and *Critogaster* females emerge and leave without collecting pollen. Although their ecologies and effects on host wasps and figs appear to be quite similar, *Idarnes* and *Critogaster* are only very distantly related (Boucek 1988; Machado et al. 1996; West et al. 1996). In fact, in both cases, these wasps are more closely related to other genera of nonpollinator wasps that have very distinct ecologies (e.g., large gallers or internally ovipositing parasitic wasps; see below) than they are to each other (Herre 1996; Machado et al. 1996; West et al. 1996).

Idarnes (and *Critogaster*) parasites have a detrimental effect on the reproductive success of their hosts. Specifically, after statistically controlling for confounding variables (e.g., foundress number, etc.), there is a clear negative correlation between the number of *Idarnes* (and *Critogaster*) wasps emerging from a fruit and pollinator wasp production (West and Herre 1994; West et al. 1996). In contrast, there is no significant correlation between the number of *Idarnes* wasps emerging and viable seed production. *Idarnes* also are found to develop in unpollinated fruit that are retained, apparently because of the influence of large galling wasps (Bronstein 1991; West and Herre 1994). Therefore, *Idarnes* are not obligate parasitoids of the pollinators, nor do they depend on them to pollinate the flowers.

Implications for Fig-Pollinator Stability

Both the pollinators and the externally ovipositing parasites in the New World figs tend to develop in seeds closer to the interior of the fruit, which are predominantly derived from flowers with short styles (Herre 1989; West and Herre 1994). It is odd that the parasites that are oviposit from the outside of the fig do not preferentially develop in seeds derived from longer-styled

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flowers that are closer to outside of the fruit, closer to where these wasps oviposit. This suggests that the longer-styled flowers are not available for use or that they provide a considerably inferior resource for developing wasps than do short-styled flowers. Therefore, considering the observed negative relationship between these parasites and pollinator production, and the lack of any relationship between these parasites and good seed production in New World figs, it is difficult to embrace the idea that all flowers are equally available for oviposition or equally conducive to wasp development.

At least in the New World systems, these externally ovipositing parasitic wasps appear to be competing with the pollinators for a subset of the flowers (predominantly short-styled) that either have the potential to develop as seeds or to support the development of wasps. These observations suggest that these wasps are exploiting the opportunities that the fig presents to the pollinators and form the basis of the inference that figs have some unexploitable flowers that cannot be used by either of these groups of wasps, and that the mechanism involved is not simply spatial position within the syconium (West and Herre 1994; West et al. 1996). A modified form of this idea consistent with the Nefdt and Compton (1996) observations on the African systems is that some subset of flowers is only marginally exploitable, or provides a potential, but inferior, resource for developing wasps.

Published reports suggest that the Old World genera *Sycoscapter* and *Philotrypesis* have similar ecologies and similar effects (Compton et al. 1991, 1994; Compton and van Noort 1992; Kerdelhue and Rasplus 1996a,b; F. Kjellberg pers. comm.). However, directly comparable studies need to be conducted in both New and Old World fig systems in order to determine clearly whether these different wasps are in fact exploiting their host figs in a similar manner, and, more interestingly, whether the host figs rely on different mechanisms to maintain the stability with their associated wasps (Herre 1989; Nefdt and Compton 1996; West et al. 1996; Herre and West 1997).

EVOLUTIONARY PATTERNS OF CO-SPECIATION

Both morphological and molecular data suggest that these and other parasitic wasps have co-speciated with their hosts (Gordh 1975; Ulenberg 1985; Machado et al. 1996). Both the *Idarnes* and *Critogaster* parasites also show similar degrees of co-cladogenesis (suggesting co-speciation) with the figs when compared to the pollinators (Herre et al. 1996; Machado et al. 1996). As is the case with the pollinators, these parasites are also horizontally transmitted. Thus, neither evolutionary nor ecological patterns of transmission tell us anything with respect to the parasitic/mutualistic nature of these wasps.

The major difference between these wasps and the pollinators appears to result from the fact that the parasitic wasps lay eggs from the outside of the fruit, and further that these wasps tend to lay eggs in several different fruits. Beyond making it difficult for these wasps to perform any pollination ser-

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TABLE 11.3
Externally Ovipositing Parasitic Wasps, "Competitors"

External oviposition
Members of different families of nonpollinators
Often nearest relatives show very different ecologies (e.g., large gall formers)
Predominant negative effects on pollinators, not seed production
Pollination and pollinators are not needed for these wasps to exploit the fig
Do not appear to be parasitoids of pollinators
Appear to exploit a similar subset of the fig's flowers as the pollinator
Suggests that fig controls access to flowers, and not by spatial arrangement alone
Co-speciation with hosts (as with pollinators)
Horizontal transmission (as with pollinators)

vices, perhaps this decouples the parasites' interests from those of any particular fig fruit that it lays its eggs in, and thereby helps explain the relative mutualistic and parasitic tendencies of these different wasps. Unfortunately for this attractive idea, other groups of parasitic wasps have life histories that caste doubt on this notion (see below). (See table 11.3.)

INTERNALLY OVIPOSITING PARASITIC WASPS

All members of the subfamily Sycoecinae, a few members of the subfamily Otitesellinae, and the genus *Sycophaga* of the subfamily Sycophaginae, are reported to oviposit from the inside of the fruit, much as the legitimate pollinators do. Furthermore, these species generally appear to be using the flowers that the pollinators would otherwise use (much as external competitors) (Galil and Eisikowitch 1968, 1969, 1971; Compton et al. 1991; Kerdelhue and Rasplus 1996a,b). The females of these species emerge and leave without collecting pollen, and thus, with a few possible exceptions in which pollen may be passively transferred (see Newton and Lomo 1979), they are parasitic on the system, as are the externally ovipositing species.

Interestingly, parasites of this type are found to be associated only with Old World fig species (Abdurahiman and Joseph 1967; Boucek 1988; Compton et al. 1991; van Noort and Compton 1996). Either these types of wasps did not arrive or had not yet evolved when the New World was colonized by the *Ficus* groups now present, or they subsequently became extinct. Combined with the observations and inferences mentioned above, the interesting possibility that New and Old World figs differ in fundamental ways with respect to their interactions with their associated wasps deserves considera-

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tion (West and Herre 1994; Kerdelhue and Rasplus 1996a; Nefdt and Compton 1996; West et al. 1996; Herre and West 1997).

Like the pollinators and the externally oviposting parasites, internally ovipositing Sycoecines associated with a diverse group of African figs are generally species-specific. Furthermore, both pollinators and parasites associated with any given fig show remarkably similar head morphology. Although an independent test (e.g., molecular-based phylogenies) is desirable, this pattern suggests co-speciation and co-evolution with their hosts (see van Noort and Compton 1996). Thus, as with the other wasps, both mutualistic and parasitic, it appears that these wasps are horizontally transmitted and show a high degree of co-speciation with their host figs.

That these *parasites* enter the fig fruit in order to oviposit undermines the idea that *pollinators* entering the fruit to oviposit helps to explain the maintenance of the mutualism. In a certain sense, it would seem obvious why the external ovipositing species are parasites, but it is unclear why the internally ovipositing species (*Sycophaga*, etc. or the *C. galili*, for that matter), which are often the most abundant insects found in the fruit, do not establish mutualistic relations with the fig (but see Newton and Lomo 1979).

It is also unclear why these internal parasites do not take over the systems and drive the pollinators (and ultimately the figs) to extinction. One testable explanation combines the observation that, within species, large body size gives advantages in wasp survival and reproduction (Herre 1989; Nefdt and Compton 1996), with the suggestion that pollinated flowers provide better nourishment for developing wasp offspring (Verkerke 1989). Clearly, many, if not all, species of both internal and external parasitic wasps can develop in the absence of pollination or pollinators. These wasps may develop to larger size on flowers that have been pollinated. This could provide a mechanism for maintaining the pollinators in these systems, depending on the strength of the effects. Thus, if short-styled flowers also provided superior resources for developing wasps, then the combination of the two effects would have the potential to maintain both seed and pollinator wasp production in figs. (See table 11.4.)

Large Gall-Forming Wasps

A diverse group of relatively larger wasps is also associated with figs of the New World section Urostigma (e.g., *Aepocerus*, *Heterandrium* (Otiteselinae), and *Idarnes* (incerta) (Sycophaginae); see fig. 11.5). These wasps can be more than 10 times the size of the pollinators. They lay their eggs in the flowers or fruit walls, inducing the formation of large galls in which their larvae develop. Ecologically, they appear to drain resources and decrease both pollinator (fig male) and seed (fig female) production in the fruits in

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TABLE 11.4
Internally Ovipositing Parasitic Wasps

Internal oviposition
Members of different families of nonpollinators
Old World taxa
Often nearest relatives show very different ecologies (e.g., large gall formers or external ovipositers)
Predominantly negative effects on pollinators, not seed production
Pollination and pollinators are not needed for these wasps to exploit the fig
Appear to exploit a similar subset of the fig's flowers as the pollinator
Apparent co-speciation with hosts (as with pollinators)
Horizontal transmission (as with pollinators)

which they are present (West et al. 1996; see also Cook and Power 1996; Kerdelhue and Rasplus 1996a). As with the pollinators and other parasites, the large-gall formers also generally appear to be species-specific, and generally show co-cladogenesis with the host (Machado and Herre unpubl.). Like the other species in these systems, these wasps are also horizontally transmitted.

Interestingly, molecular work supports the proposition that the different species that share this type of ecology are also only distantly related to each other. Wasps that form large galls have therefore arisen independently several times during the radiation of the five families that comprise the fig parasites (as have the "competitors"). That work further suggests that the closest relatives to some of these wasps (e.g., *Idarnes* (incerta)) are the "competitor-type" parasitic wasps that often parasitize the same groups of figs (the *Idarnes* already discussed). Both morphological and molecular studies of these genera indicate that these "competitor" and "large-gall-forming" members of *Idarnes* are more closely related to the Old World genus *Sycophaga*, whose ecology entails entering the fig syconium to lay eggs, than they are to other externally ovipositing wasps that show similar, if not identical ecologies (Boucek 1988, 1993; Herre 1996; Herre et al. 1996; Machado et al. 1996; West et al. 1996). Thus, it appears that the various basic ecologies associated with parasitizing figs have evolved separately on several occasions in both the New and Old World. Given this pattern in the parasites, it is conspicuous that the pollinators form a monophyletic group and that pollination has apparently evolved only once (Ramirez 1974; Wiebes 1979, 1982; Boucek 1988, 1993; Machado et al. 1996; Herre et al. 1996; West et al. 1996; but see Newton and Lomo 1979).

The presence of these gall-forming wasps seems to prevent unpollinated fruit from being aborted, and thus these wasps do not seem to require the

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TABLE 11.5
Large External "Galler" Parasitic Wasps

Induce the formation of large galls from fruit wall or flower tissue
Drain resources away from both seed and wasp production
Can prevent the abortion of unpollinated fruit
Taxonomically diverse set of species
Closest relatives often exhibit very distinct ecologies
Horizontally transmitted
Generally high degree of species-specificity
Predominance of co-speciation with host

presence of the pollinators in order to utilize the syconium. Although it is not clear how the large gallers prevent the abortion of unpollinated fruit, it is likely that these wasps can produce substances that mimic (or interfere with) hormonal signals in the fig. If so, cracking the hormonal code of the fig must have been a great (and possibly ongoing) evolutionary achievement for these wasps (as well as a great threat to the figs). Given the multiple origins of parasitic wasps with such different ecologies, it appears that the hormonal manipulation developed by the different types of wasps must allow a great deal of evolutionary flexibility associated with the multiple radiations into what appear to be a multiply repeated suite of fig-exploiting ecologies (Herre 1996; Machado et al. 1996). Deciphering both the fig and wasp hormonal codes and then placing them in a phylogenetic context would be a fascinating research challenge. (See table 11.5.)

PARASITOIDS OF GALL-FORMING WASPS

The wasps that are parasitoids of the large-gall makers (e.g., *Physothorax*) are almost certainly mutualists for the fig and the pollinators to the extent that they control the abundances of the parasites. Theoretical analysis of aggregation patterns of the parasitoids on gall-forming hosts suggests that they have this capability (West et al. 1996). Thus, it appears that ecological control of one of the most obvious threats to the New World fig-pollinator mutualisms can be acounted for.

As with the other taxa discussed, preliminary molecular data suggest that these also appear to be species-specific and also appear to be co-speciating with their hosts (Machado and Herre unpubl.). As with the others, these wasps are horizontally transmitted. Furthermore, as is the case in the majority of the nonpollinating wasps that are parasitic on figs, these beneficial (to the fig) parasitoids oviposit from the outside the fig fruit. Therefore, if we

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TABLE 11.6
Parasitoids of Gall-Forming Wasps

Parasitoids of large-gall-forming wasps
Appear to be capable of controlling gall-former populations
Horizontally transmitted
Predominantly species-specific
Appear to co-speciate with hosts

consider the wasps associated with the figs collectively, none of the factors that theory suggests might be important in influencing relative benevolence of mutualists or parasites gives any consistent pattern. Mutualist or parasite, all are horizontally transmitted, all are for the most part species-specific, and all of their radiations show a strong tendency to co-speciate with the figs (Herre et al. 1996; Machado et al. 1996; Machado and Herre, unpubl.). Have these ideas just declared bankruptcy? (See table 11.6.)

Nematode Parasites of the Pollinators

Just as distinct species of fig-pollinating wasps are generally associated with distinct species of host figs, morphological and molecular work on the Panamanian species has established that distinct species of nematodes of the genus *Parasitodiplogaster* are associated with distinct species of host fig wasps (Poinar and Herre 1991; Herre 1995, unpubl.). In nematode-infested fig fruits, immature, dispersal-phase nematodes crawl onto newly emerged female fig wasps and are thereby carried to the next fig. Before the host wasp leaves its natal fruit, the nematodes enter the body cavity of the wasp and, at some point, begin to consume it and grow. Later, up to 20 or more adult nematodes (with a median of roughly 6 or 7) emerge from the dead wasp's body (Herre 1993, 1995), mate, and lay eggs within the fig fruit in which the host wasp has laid her eggs. The nematodes' eggs hatch before the emergence of the next generation of fig wasps, and the nematodes begin *their* cycle anew (Poinar 1979; Poinar and Herre 1991; Herre 1993, 1995; Giblin-Davis et al. 1995).

The natural histories of fig-pollinating wasps and the nematodes that parasitize them (Poinar 1979; Poinar and Herre 1991; Giblin-Davis et al. 1995) permit the direct measurement of several parameters that theory identifies as important to the evolution of virulence (Herre 1993, 1995). Specifically, in nearly ripe fig fruits that have been pollinated by only one foundress wasp, the presence of immature nematodes can be used to determine whether that individual wasp was infected. Therefore, within species of fig wasps, the

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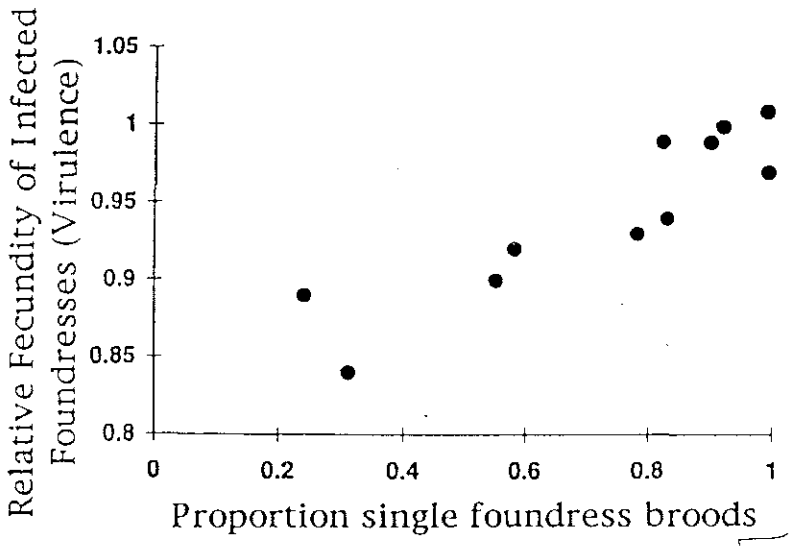

FIG. 11.6. The relationship between virulence (calculated as the proportion of offspring that nematode-infected foundresses produce relative to uninfected foundresses) and average proportion of single foundress broods for 11 species of fig-pollinating wasps. As foundress number increases, opportunities for horizontal transmission increase. Species in which the opportunities for transmission are increasingly horizontal harbor more virulent species of nematodes.

number of wasp offspring associated with nematode-infected single foundress wasps can be compared to the number of offspring associated with uninfected single foundresses in order to estimate the nematodes' effects on the fecundity (one major component of lifetime reproductive success) of their host fig wasps (i.e., virulence). Across species of fig wasps, virulence estimates can be compared with differences among them in the opportunities for nematode transmission.

Long-term studies indicate that fig wasp species vary characteristically in population structure (number of foundresses). Studies initiated over 15 years ago (roughly 180–200 fig wasp and nematode generations) in the vicinity of the Panama Canal show that the different host wasp species present a continuum of population structures (distributions of numbers of foundresses per fig fruit) (Herre 1985, 1987, 1989, 1993, unpubl.). Species in which the average number of foundresses is consistently higher present their parasitic nematode populations with relatively increased opportunities for horizontal transmission. Additionally, increased opportunities for horizontal transmission are linked with the increased mixing of unrelated nematodes within individual hosts. As previously reported, these are the situations in which the nematode species with the greatest estimated virulences are found (fig. 11.6; Herre

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TABLE 11.7
Nematode Parasites of the Pollinators

High degree of species specificity with host wasps
High degree of concordance (implying a predominance of co-cladogenisis) with host wasps
Ancient association with the wasps
Range of opportunities for transmission
Range of negative effects (virulence) on host fitness
Most virulent species are associated with highest opportunities for transmission

1993, 1995). Finally, theory can enjoy a modest success. But what is really going on here? (See table 11.7.)

Figs and Seed Dispersers

In the vast majority of cases, pollinator wasps are required in order for figs to develop fully ripe fruit. Without the wasps to catalyze the usually bountiful fruit production, a wide array of frugivorous animals would be that much closer to starvation. In turn, the various frugivores disperse the fig seeds (Janzen 1979; Milton 1991; Kalko et al. 1996). Although fig fruit have been characterized as low-quality resources for frugivores, more recent and careful analyses show that fig fruits can be quite high in certain nutrients (e.g., calcium, protein, as well as sugars) (Kalko et al. 1996; Herre 1996; O'Brien et al. 1998; Wendln et al. unpubl.). Figs invest a great deal of energy and resources into their fruit. Why?

Although the fruits of many different species of figs are eaten by a wide range of frugivorous animals, closer inspection in New World systems shows at least two types of specificities. First, different sets of frugivorous species are associated with the fig species possessing relatively small fruits that ripen to a red color, and the species with green-ripening fruits that are much more variable in size. Mainly birds take the former during the day, and bats predominantly take the latter during the night (Kalko et al. 1996; Korine, Kalko, and Herre, in prep.). Furthermore, within the species with green ripening fruit, there is a very clear association between size of the fruit of a given species and the body size of the bat species that prefer them. In general, the bat species that constitute the principal frugivores/seed dispersers of larger species of figs are larger, travel longer distances with the fruit, and have larger home ranges. The implication is that, on average, they disperse seeds over larger areas (Herre 1989, 1996; Kalko et al. 1996). Assuming that

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increased seed dispersal is advantageous, selection for dispersal may favor larger fruit.

Fruit size is related to a wide variety of what would otherwise appear to be unrelated traits. Both across and within species, fruit size (specifically, the number of flowers per syconium) affects the wasp reproductive success; with all else equal, more flowers generally lead to greater wasp reproductive success (Herre 1989; Herre and West 1997). In most large-fruited species, however, foundress number is relatively high. High foundress numbers are associated with wasp sex ratios that are less female-biased, which means less efficient pollen dispersal for the fig (Herre 1985, 1987, 1989). Because wasp offspring generally do not increase proportionately to foundress number, higher foundress number also means lowered reproductive success of the average foundress (Herre 1989). In addition, higher foundress numbers are related to increased opportunities for nematode transmission, increased genetic heterogeneity of nematodes that infect single foundresses, and consequently higher nematode virulence (Herre 1993, 1995).

Larger fruit also show an increased absolute and relative dependence on evaporation in order to produce fruit temperatures cool enough to maintain viable wasps (Patiño et al. 1994). The result is that producing the wasps that carry the pollen is also more expensive in terms of water loss in large-fruited species. Moreover, in both the Old World (Compton and Hawkins 1992) and New World (West and Herre unpubl.) figs, larger-fruited species generally harbor more parasitic wasps, both in number of species and often in number of individuals. Finally, as mentioned before, large, multifoundress fruit may present an open door to internal parasites such as *Sycophaga*, or to pollinators with overt parasitic tendencies, such as *Ceratosolen galili*. Given what appear to be a number of disadvantages associated with larger fruit size, why do large-fruited species exist? Perhaps the advantages from increased seed dispersal balance the multiple disadvantages mentioned above. All of this is consistent with the interpretation that selection generated from seed dispersers produces changes (fruit size) that impinge on other aspects of the fig biology. That is, one set of mutualists associated with figs appears to impose selection that can oppose the interests of others.

Conclusions

In the introduction I noted the great importance and diversity of parasitic and mutualistic interactions and asked if there were some simple rules that govern them. After stating some of the candidates for simple rules, I discussed a great deal of very detailed natural history concerning the different mutualists and parasites associated with figs. The presentation of this detail is crucial for several reasons.

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First, in order to test the applicability of theory, it is essential to understand the mechanics that underlie these interactions. In order to do that, it is critical to understand that these are complex systems and that multiple factors influence outcomes. For example, taking the simple (usually positive) correlations between pollinators and seeds, or those between parasites and pollinators, at face value, it is difficult to understand that the relationships are in fact either partially or completely dominated by antagonistic elements. Failing that, with respect to understanding the relationships or using those relationships to test theory, you are lost.

Furthermore, it is frequently important to understand the interactions among several different types of species in order to provide the context to properly pose and test evolutionary hypotheses about any of them. For example, understanding the biology of the different types of parasites is almost certainly important in understanding either the stability of the fig-pollinator interactions, or the evolutionary shifts of figs from monoecy to dioecy. It is not an accident that different facets of natural history relevant to the discussion of fig-pollinator stability were discussed over several sections concerning several different wasp taxa associated with the figs.

Moreover, the degree of interrelationships among what would seem to be unconnected characteristics of the figs and their associates is both extraordinary and unexpected. In essence, the central message is the importance of viewing any one attribute of this system (and by implication any system) within the context of the other aspects, and of clearly understanding the functional interrelationships among them.

It should be noted that the examples presented as tests of theory have involved analyses at very different scales of biological organization. Specifically, I have considered how differences (and similarities) among broadly defined taxa (pollinators, competitors, etc.) in characteristics such as ecological dispersal or evolutionary tracking are associated with parasitism or mutualism. I have considered how differences among species within a taxon may be associated with differences that increase or decrease detrimental effects on an interacting species (virulence in the nematodes, sex ratios in the pollinator wasps). Finally, I have considered how differences among individuals within one species may affect the other (e.g., body size in the pollinators). With respect to the latter, it appears that analyses of the consequences of variation among individuals may provide the key to understanding the mechanisms underlying fig-wasp stability.

At the level of the stereotyped entities such as "pollinator wasps," "externally ovipositing parasitic wasps," "internally ovipositing parasitic wasps," "large gall forming wasps," "parasitoid wasps," the "rules" relating ecological transmission patterns or evolutionary tracking to greater or lesser beneficial effects simply fail. In contemplating this failure, other, more general, examples should also be considered. For example, it is worth bearing in

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mind that gonorrhea, syphilis, herpes, and HIV all have similar transmission patterns (mostly horizontal) but very different effects on their hosts. Similarly, mycorrhizal fungi, zooxanthellae (symbiotic algae associated with corals), and nitrogen-fixing bacteria are also mostly horizontally transmitted. Yet, the effects they have on their hosts range from commensal to beneficial to indispensable. The nematode example provides the most clear-cut case for making a statement about a connection between mode of transmission and virulence. Why do "the rules" work in the one case and apparently not in the others?

In the specific case of the fig-pollinating wasps and their nematode parasites, increased opportunities for horizontal transmission decouple the parasite's reproductive interests from those of its host. Therefore, in this system, opportunities for horizontal transmission per se only serve to release a constraint against virulence. It is within-host competition of different parasite genotypes that is identified as the driving selective force toward virulence, much as within-deme selection favors less female-biased sex ratios in the pollinator wasps (Frank 1985, 1992; Herre 1985, 1993, 1995).

More generally, the much maligned rules are much more helpful in understanding differences among species within a group of very similar organisms (e.g., differences in virulence among nematodes, or differences in sex ratio among pollinator wasps), in which a few variables that theory identifies as key shift (respectively, transmission, local mate competition), than they are with respect to explaining differences among much more dissimilar entities (Read and Harvey 1993). As is the case with making single-factor analyses within complex systems, among-taxa comparisons confound many factors.

These examples suggest that "rules" (e.g., links between transmission and virulence, links between long-term association and niceness, etc.), are subject to contravening influences. For many reasons, it is unlikely that rules governing among-species interactions across a wide diversity of types of interactions will be found that will even approach the power of Hamilton's Rule in explaining within-species interactions. Instead, the task appears to be to carefully document many systems, especially very similar systems in which only a few key variables change, and then to attempt to determine if there is a hierarchy of rules. Ultimately, a great deal of attention will need to be paid to differences in details of the natural history of the different systems.

This piece started out as an exploration of applicability of rules. It has evolved by necessity into a discussion of details of the natural history of a series of unexpectedly interrelated examples of interactions involving figs. The central message should not be the lack of rules with any explanatory power concerning the outcomes of species interactions. Instead, understanding why the rules work in the cases that they do is crucial, as is the apprecia-

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tion that context and scale determine the applicability of those rules we presently recognize.

Acknowledgments

For extensive discussion and useful coments during the writing of this paper, I thank Betsy Arnold, Elisabeth Kalko, Egbert Leigh, and Stuart West. The empirical and conceptual foundations contributing to this work were laid during the course of a series of very enjoyable collaborations with Elisabeth Kalko, Carlos Machado, John Nason, Sandra Patiño, Mel Tyree, Don Windsor, and Stuart West. For additional useful discussions and comments, I thank Steve Compton, Cees Berg, Koos Wiebes, William Hamilton, Drude Molbo, Dieter Ebert, John Thompson, Finn Kjellberg, Judie Bronstein, and Rhett Harrison. Laurent Keller has circumnavigated the Sea of Patience on my behalf.

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