



Parasites of mutualisms

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Cooperation invites cheating, and nowhere is this more apparent than when different species cooperate, known as mutualism. In almost all mutualisms studied, specialist parasites have been identified that purloin the benefits that one mutualist provides another. Explaining how parasites are kept from driving mutualisms extinct remains an unsolved problem because existing theories explaining the maintenance of cooperation do not apply to parasites of mutualisms. Nonetheless, these theories can be summarized in such a way as to suggest how mutualisms can persist in the face of parasites. (1) For cooperation to occur, the recipient of a benefit must reciprocate, and the reciprocated benefit must be captured by the initial giver or its offspring. (2) For cooperation to persist, the mutualism must be re-assembled each generation. Because most mutualisms are of the 'by-product' type, broadly defined, the first condition is normally always fulfilled. Thus, the maintenance of mutualism usually requires enforcement of the second condition: reliable re-assembly. Hence, I argue that the persistence of mutualism is best understood by using theories of species coexistence, because each mutualist can be considered a resource for the other, and species coexistence theory explains how multiple taxa (e.g. parasites and mutualists) can stably partition a resource over multiple generations. This approach connects the study of mutualism to theories of population regulation and helps to identify key factors that have promoted the evolution, maintenance and breakdown of mutualism. I discuss how these ideas might apply to and be tested in ant-plant, fig-wasp and yucca-moth mutualisms.

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INTRODUCTION

"In every big transaction," said Leech, "there is a magic moment during which a man has surrendered a treasure, and during which the man who is due to receive it has not yet done so. An alert lawyer will make that moment his own, possessing the treasure for a magic micro-second, taking a little of it, passing it on."

God bless you, Mr. Rosewater by Kurt Vonnegut

Explaining the maintenance of cooperation in the face of cheating is a central problem for evolutionary biology (Darwin, 1859; Boucher, 1985; Dugatkin, 1997). Hamilton (1964a,b) showed that a loss of direct fitness due to an altruistic act could be compensated if the act were directed towards kin, thereby increasing the altruist's inclusive fitness. In contrast, among unrelated individuals, selection for cooperation occurs only if there

is a reciprocated benefit that outweighs the cost of the initial, proffered benefit (Trivers, 1971). However, such reciprocal altruism is open to cheating, which I define here as any behaviour that extracts, with minimal or no reciprocation, a benefit that is normally exchanged in a cooperative interaction, thereby reducing the fitness of one or both cooperating partners. Because reciprocation is assumed to be costly, all else being equal, a cheating strategy has a higher fitness than a cooperative strategy, and thus is expected to drive cooperation extinct. There is therefore widespread interest in understanding the mechanisms that limit the spread of cheating (Axelrod & Hamilton, 1981; Thompson, 1982; Boucher, 1985; Pierce, 1989; Bull & Rice, 1991; Bronstein, 1994; Connor, 1995; Dugatkin, 1997; Herre *et al.*, 1999).

Of particular interest here is cooperation between species, or mutualism (Boucher, 1985; Bronstein, 1994), in which each species has its fitness increased by the other. Cheaters, then, are species that extract benefits normally exchanged between mutualists. Thus, nectar-robbing birds (McDade & Kinsman,

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1980), galling fig wasps (West & Herre, 1994) and non-protecting plant-ants (Janzen, 1975) qualify, but herbivores of ant-plants and fig trees do not. Cheaters also include species that reciprocate only minimally, such as a bird that consumes many fruits but only rarely disperses the seeds (Howe, 1977), thereby imposing an opportunity cost, because the plant is denied the services of a more beneficial partner. These cheating species have been variously called *aprovechados* (Soberon & Martinez del Rio, 1985), interlopers (Bronstein, 1991), and parasites of mutualisms (Janzen, 1975). I favour the last term.

In this review, I survey ant-plant, fig-wasp and (briefly) yucca-moth mutualisms, which are well-characterized and host several kinds of parasites. I ask if the parasites reduce the fitness of their hosts and if the accumulation of these parasites would likely lead to the mutualism's dissolution. If so, I propose mechanisms that can act to constrain the spread of parasites.

It is useful to begin by reviewing existing models of cooperation, arranged in order of increasing applicability to mutualisms (Table 1). I will conclude that existing theory fails to explain how the spread of parasites is limited.

THE PRISONER'S DILEMMA

By far the dominant framework for modelling cooperation is the Prisoner's Dilemma (Trivers, 1971; Axelrod & Hamilton, 1981; Axelrod & D'Ambrosio, 1994; Dugatkin, 1997). A simple example is grooming. An individual can cooperate by investing time and energy into grooming a partner, or cheat by refusing to groom. The Prisoner's Dilemma game is set up so that both players receive a payoff (Reward) when they cooperate (groom each other). But if one player cooperates, and the second cheats, the cheater receives a bigger payoff (Temptation to Defect: gets groomed and does not pay the cost of grooming), and the second player pays a cost (Sucker's Payoff: does not get groomed, but still pays the cost of grooming). If both players cheat, then they receive an intermediate payoff (Punishment: neither gets groomed, but neither pays the cost of grooming). Thus, $\text{Temptation} > \text{Reward} > \text{Punishment} > \text{Sucker's Payoff}$. When the game is played for one round, the only theoretically viable strategy is for both players to defect (not groom) and to receive the Punishment payoff, thereby foregoing the higher Reward payoff (Axelrod & Hamilton, 1981), but avoiding the Sucker's Payoff, which can be negative and thus, fitness reducing.

MODELS OF COOPERATION

RETALIATION

When the Prisoner's Dilemma game is played for multiple rounds with no obvious final round (Iterated

Prisoner's Dilemma), a strategy called Tit-For-Tat can resist invasion by pure cheaters and maintain cooperation (Axelrod & Hamilton, 1981). In Tit-For-Tat, a player cooperates in the first round and in following rounds, mimics what the other player did previously (cooperate or cheat). Thus, cooperators are cooperated with, cheaters are cheated on, and in this way, a Tit-For-Tat player gains Rewards while avoiding (most) Sucker's Payoffs, thereby doing better than pure cheaters or cooperators. I refer to Tit-For-Tat and its (thousands of) variants (Nowak, Bonhoeffer & May, 1994) as retaliation strategies, because they are characterized by retaliation against acts of cheating.

For retaliation to work, each player must recognize other players individually and remember each player's action from the previous round of play together. Most mutualists, being non-hominoids, are not sufficiently intelligent to fulfil this assumption (Nowak & May, 1992; Nowak *et al.*, 1994). Also, retaliation strategies fail against highly mobile players (Dugatkin & Wilson, 1991; Enquist & Leimar, 1993), in large groups (Boyd & Richerson, 1988), in single rounds of play (Axelrod & Hamilton, 1981), and if the players are allowed to 'short-change' each other (see Parcelling below, Doebeli & Knowlton, 1998). Many, if not all, mutualisms exhibit all these characteristics.

PARCELLING

Even if interactants cooperate only once, an Iterated Prisoner's Dilemma can be created by 'parcelling' a single interchange of benefits into multiple, small exchanges (Connor, 1992). For instance, hermaphroditic fish alternatively donate small amounts of egg and sperm (Fischer, 1981). Cheating would take the form of donating sperm but not costly eggs. Because the cost of each bout is so small, there is almost no gain to be had from cheating, and therefore, there is little need for Retaliation. However, because Temptation always exceeds Reward by some (small) amount, parcelling can be invaded by a 'Short-Changing' strategy that fails to reciprocate at the final bout (Doebeli & Knowlton, 1998; Roberts & Sherratt, 1998), thereby degrading parcelling, even though a cheater could in theory be recognized by its short-changing behaviour.

Roberts & Sherratt (1998) show that if investment is increased in each subsequent round ('Raise-the-Stakes'), the 'Short-Changing' strategy can be kept from invading. A human example is the Confidence-Building Measure (Fisher & Ury, 1981). Two antagonists (China and the US) start by making multiple, small exchanges (Ping-Pong teams and pandas), setting the psychological stage for larger, more substantive exchanges (diplomatic recognition). Note that 'Raise-the-Stakes' now assumes players who remember past behaviours. Thus, application to mutualisms is as questionable as are Retaliatory strategies.

Table 1 Mechanisms enforcing cooperation among unrelated individuals, listed roughly in order of increasing applicability to mutualisms**RETALIATION**

Definition: Punishing or refusing future interactions with a partner after an act of cheating.

Theory: Trivers (1971), Axelrod & Hamilton (1981), Bull & Rice (1991)

Example: Predator inspection in guppies (reviewed in Dugatkin, 1997)

PARCELLING/RAISING THE STAKES

Definition: Partitioning benefits from a single interchange into amounts small enough to make cheating unprofitable and/or increasing investment in each subsequent round

Theory: Connor (1992), Roberts & Sherratt (1998)

Examples: Mutual grooming, gamete transfer in hermaphroditic fish (Fischer, 1981)

TRAIT-GROUP SELECTION

Definition: Demes with more altruistic alleles have disproportionately higher fitness than demes with fewer altruistic alleles

Theory: Wilson (1975), Dugatkin & Mesterton-Gibbons (1996)

Example: Foraging by one of a group of pleometrotically founding ant queens (Rissing *et al.*, 1989)

NEIGHBOURHOOD INTERACTIONS

Definition: Interaction with only one's nearest neighbours, leading selfish players to suffer low fitness when abundant

Theory: Nowak & May (1992), Doebeli & Knowlton (1998)

Example: None

FILTERING

Definition: Avoiding investment in likely cheaters

Theory: Bull & Rice (1991)

Example: Floral abortion in yucca–moth interactions (Pellmyr & Huth, 1993)

VERTICAL TRANSMISSION

Definition: Symbionts are passed from parent to offspring, aligning selective pressures

Theory: None, but see Herre *et al.* (1999) for a review

Example: Aphids and *Buchnera* bacteria Margulis & Fester (1991)

BY-PRODUCT

Definition: Selfish activity by one partner inadvertently creates an indirect benefit for the other partner that outweighs the cost of the selfish act

Theory: Brown (1983), Connor (1986)

Example: Ants tending Homoptera on plants also attack herbivores (Benson, 1995)

HOSTAGE TRADING

Definition: By-product mutualism achieved via the simultaneous exchange of benefits

Example: Presence of domatia and/or food bodies on the newest leaves in ant-plants, sticky pulp on seeds which must be swallowed for pulp to be extracted

TRAIT-GROUP SELECTION

In trait-group selection (Wilson, 1975), alleles for cheating are assumed to spread unchecked. Cooperation is maintained by the regular subdivision of a population into reproductively isolated demes, with fecundities that increase nonlinearly with the proportion of cooperative alleles or individuals. Altruistic foraging by one of a group of unrelated, but cooperatively founding conspecific ant queens (Rissing *et al.*, 1989) is thought to be an example. However, no mutualism has yet been shown to conform to this scenario.

NEIGHBOURHOOD INTERACTIONS

A result similar to trait-group selection can be achieved when cooperators are allowed to interact only with their nearest neighbours. Cooperation is maintained, even in the absence of recognition (Nowak & May, 1992) and in the presence of short-changing strategies (Doebeli & Knowlton, 1998). This is because as cheaters increase in density, they interact mainly with each other, driving their fitnesses down, whereas cooperator fitnesses increase with density, but are then subject to invasion by cheaters. Again, no mutualism has been shown to

conform with the assumption of nearest neighbour-only interactions.

FILTERING

Bull & Rice (1991) outline an alternative to the Iterated Prisoner's Dilemma, called Partner-Choice, which can maintain cooperation in systems lacking retaliation. Partner-Choice mechanisms are those which 'filter' out or prevent likely cheaters from entering a cooperative game, so I refer to Partner-Choice as filtering (Table 1). An example is *noD* recognition genes, which exclude pathogenic bacteria but allow nitrogen-fixing bacteria to enter the roots of leguminous plants (Dénarié, Debelle & Rosenberg, 1992). I consider filtering to occur when a player chooses among various partners before significant amounts of resources have been exchanged. Thus, the selective abortion of flowers in which seed-laying pollinators (e.g. yucca moths) have laid an overabundance of eggs is filtering, and not retaliation (pace Pellmyr & Huth, 1994), because the plant has not yet invested in costly seeds. Thus, investment in an overabundance of flowers represents a cost of filtering. In Dugatkin's (1997) review of cooperation theory, only filtering is listed as applicable to mutualisms. However, as we will see below, even filtering is overcome by parasites of mutualisms.

VERTICAL TRANSMISSION

An extreme form of the Iterated Prisoner's Dilemma occurs when symbionts are passed from parents to offspring, termed vertical transmission (reviewed in Herre *et al.*, 1999), the most notable examples being endosymbionts (Margulis & Fester, 1991; Douglas, 1996). In vertical transmission, because the fitness of one partner lineage is increased with the fitness of the other, cooperation is promoted.

However, most mutualisms are horizontally transmitted (Jordano, 1987; Herre *et al.*, 1999), meaning that the offspring of one mutualist disperse separately from the offspring of the other mutualist(s) (e.g. seeds of ant-plants and queens of ant colonies, Yu & Davidson, 1997), and the mutualistic interaction must be re-assembled each generation. Also, cheating can still arise in the context of vertical transmission. For example, lichen symbioses host several parasites (Richardson, 1999).

BY-PRODUCTS

Brown (1983) describes how a selfish act by one species can inadvertently 'rebound' to produce a net 'by-product' benefit for a second species. For example, ants parasitize plants by tending aphids on them (Way, 1963). If the same ants deter other herbivores, and if this benefit is greater than the cost of lost plant sap,

then the ant has provided a net by-product benefit to the plant (Benson, 1985). Connor (1986) extends this model by pointing out that one species can invest resources into another to trigger a by-product benefit (giving the hypothetical example of a bird fertilizing a bush to obtain valuable shade), and calling this "investing in pseudo-reciprocity". In some mutualisms, this investment is one-sided (e.g. seed dispersal, where the investment is fruit pulp), and in others, the investment is mutual (e.g. ant-plants, see below). Nonetheless, despite the broad applicability of by-product mechanisms to mutualisms (Connor, 1995), parasites produce no discernible by-product benefits.

HOSTAGE-TRADING

The final model of cooperation reviewed here relies on Trivers' (1971) observation that the time delay between a cooperative act and its reciprocation is what allows cheating to invade. Consequently, cooperation can be enforced by exchanging benefits simultaneously. I call this hostage trading, after spy movies in which two parties simultaneously exchange captured prisoners. For example, many monkey-dispersed fruits coat their seeds in a sticky pulp. To extract the pulp, the monkey must also swallow the seed, guaranteeing dispersal (D. Yu, pers. obs.). The possibility of hostage trading suggests that transitions from parasite to mutualist should often be marked by innovations that produce simultaneity in the transfer of benefits. Note that, by definition, hostage trading works only within generations.

CONDITIONS FOR THE OCCURRENCE AND PERSISTENCE OF MUTUALISM

The above models of cooperation can be usefully summarized in two conditions, the first being: (A) for cooperation to occur, the recipient of a benefit must reciprocate, and the reciprocated benefit must be captured by the initial giver or its offspring. To a first approximation, Retaliation, Parcelling, Filtering, and By-product mechanisms enforce the first half of this condition and tend to assume the second, and Vertical transmission, Trait-group, and Neighbourhood interactions mechanisms can be seen as enforcing the second half and assuming the first. Hostage trading enforces both.

An example is given by ant-plants. Ant colonies invest workers in plant protection, and ant-plants invest in food and housing. Both investments trigger growth in the other symbiont (Janzen, 1966). In another example, fig wasps pollinate fig flowers, which provide endosperm for wasp larvae (Galil & Eisikowitch, 1968), and fig plants invest ovaries into wasp offspring, which carry pollen to conspecific plants (Herre & West, 1997). In

both cases, there is the reciprocation of benefits and the capture of those benefits by the initial giver (ant and plants) or offspring (fig wasps).

However, because mutualistic interactions take place (by definition) between or among different species, there must also be a second condition: (B) *for cooperation to persist, the mutualism must be re-assembled each generation*. One way to guarantee re-assembly is by vertical transmission (Herre *et al.*, 1999), but most mutualisms are horizontally transmitted, such that offspring disperse separately and then reunite (Jordano, 1987; Yu & Davidson, 1997; Herre *et al.*, 1999).

Axelrod & Hamilton (1981) recognized this problem when they noted that Tit-for-Tat players would likely only be able to invade a population of cheaters if the initial inoculum of cooperators were aggregated. Neighbourhood interactions therefore also help to enforce the second condition. However, it will be seen that limiting cooperation to nearest neighbours is an overly stringent way to achieve re-assembly.

It will also be seen that most parasites of mutualisms interfere primarily with the re-assembly of mutualisms. Thus, any theory of mutualism must concern itself with the mechanisms that allow the offspring of different mutualist lineages to reunite reliably, despite the presence of parasites, over very long timescales (up to millions of years, Machado *et al.*, 1996; Pellmyr, Leebens-Mack & Huth, 1996a). I propose here that this challenge can best be met by utilizing theories of species coexistence. For each mutualist, the other mutualist can be thought of as a resource, and parasites are competitors for that resource (Soberon & Martinez del Rio, 1985). Stable coexistence of competitors can then translate to persistence of mutualism. Two examples from the literature, one empirical and one theoretical, illustrate this point.

McDade & Kinsman (1980) measured the impact of nectar and pollen robbers on two plant species: *Aphelandra golfodulcensis* and *Justicia aurea*. Only two hummingbird species were able to extract nectar 'legitimately', by passing their recurved bills along the recurved floral corollas. Eight bird species and several ant species damaged corollas so as to extract nectar, and two bee species removed pollen for consumption. These 'non-legitimate' visitors never pollinated flowers and, importantly, reduced nectar and pollen availability so severely that legitimate visitors virtually stopped visiting, preventing re-assembly of the mutualism. None of the cooperation mechanisms listed above (Table 1) was effective. In particular, the recurved corollas failed as filters, and parasites did not produce by-product benefits.

The authors hypothesize that the system persists because only mutualists appear to visit the natural,

scattered and smaller clumps of *Aphelandra* and *Justicia* located in primary forest canopy gaps, whereas the studied population was a large clonal clump on a roadside. Thus, persistence of the mutualism is thought to depend on the coexistence of parasitic and mutualistic floral visitors via divergent habitat selection.

Kinzig & Harte (1998) modelled the persistence of mutualistic microbes that consume soil nitrogen at less than their maximum possible rate, thereby releasing more nitrogen to nearby plants, which then, because of increased growth, release more carbon into the soil. This carbon is in turn consumed by the microbes ('investing in pseudo-reciprocity'). In contrast, parasitic microbes release little or no nitrogen and gain an increased population growth rate in the short-term. They can thereby invade and competitively displace mutualists, preventing the latter from associating with plants over the long term, but reducing plant (and microbe) biomass to below levels achieved by mutualists. Kinzig and Harte showed that mutualistic microbes are able to persist only if the environment is subdivided so that subpopulations of mutualists are allowed to build up the high levels of nitrogen necessary to foment rapid plant growth, which produces and by-product benefit of higher carbon availability, resulting in high mutualistic microbe abundances that allow them to outcompete parasitic microbes for empty areas. Thus, spatial refuges from competition allow succeeding generations of mutualists to stably re-unite with plants. Spatial structuring has long been known to promote species coexistence (Tilman & Kareiva, 1997).

Thus, both studies argue that species-coexistence mechanisms allow the persistence of mutualisms. We now assess the empirical support for this hypothesis in ant-plants.

ANT-PLANT INTERACTIONS

Hundreds of tropical plant species worldwide provide housing for ants, called domatia, in the form of hollow stems, tubers, tendrils, petioles or leaf pouches (Davidson & McKey, 1993). These plants are known as ant-plants or myrmecophytes, and in most cases, both ant and plant cannot establish, survive or reproduce in the absence of the other. Removal of resident ants leads to increased herbivory, and/or decreased growth, fecundity and survivorship (Janzen, 1966, 1969; Letourneau, 1983, 1998; McKey, 1984; Schupp, 1986; Fiala *et al.*, 1989, 1994; Vasconcelos, 1991; Fonseca, 1994; Moog, Drude & Maschwitz, 1998; Yu & Pierce, 1998).

Ant-plant symbioses are characterized by horizontal transmission, leading the majority of these associations to have arisen by *de novo* colonization, rather

than through co-cladogenesis (Ward, 1991, 1993; Davidson & McKey, 1993; Chenuil & McKey, 1996; Yu & Davidson, 1997). As a result, partner identity is labile, such that a number of myrmecophytic plants and plant-ants associate with multiple partner species (Wheeler, 1942; Benson, 1985; Huxley, 1986; Longino, 1989; Ward, 1991, 1993; Davidson & McKey, 1993; Fonseca & Ganade, 1996; Yu & Davidson, 1997; Fiala, Jakob & Maschwitz, 1999). It is not surprising therefore that ant-plants also host many parasites.

PARASITES OF ANT-PLANTS

PARASITIC ANTS

An early example of a parasite of a mutualism comes from the classic ant-acacia symbiosis. Workers of the ant species *Pseudomyrmex nigropilosa* hide when disturbed, do not attack herbivores, vines or competing plants, and consume the food bodies provided by the plant (Janzen, 1975). Hostplants inhabited by *P. nigropilosa* thus suffer high mortality. A typical colony of a mutualistic *Pseudomyrmex* species dedicates a third of its workers to protecting the plant (Janzen, 1975). *Pseudomyrmex nigropilosa* avoids this cost. *Pseudomyrmex nigropilosa* colonies also reduce rates of establishment of mutualistic acacia-ants (i.e. the parasite impedes re-assembly).

Similarly, in Cameroon, the ant *Cataulacus mckeyi* inhabits but rarely protects saplings of the ant-plant *Leonardoxa africana* (McKey, 1984; Gaume & McKey, 1999), which is normally inhabited by the truly mutualistic ant, *Petalomyrmex phylax*. *Petalomyrmex phylax* dedicates 60 times the number of workers to the task of protecting new leaves than does *C. mckeyi*. Host-plants inhabited by the latter suffer high rates of herbivory.

In two other ant-plant systems, the resident ant protects the hostplant against herbivory, but parasitizes the host by preventing flowering (a "castration parasitism", Baudoin, 1975). In Kenya, Young, Stubblefield & Isbell (1997) have shown that the ant *Crematogaster nigriceps* prevents flowering and fruiting in the ant-plant *Acacia drepanolobium* by chewing and destroying the hostplant's axillary vegetative shoots on which inflorescences are normally produced. In comparison to plants inhabited by three other, non-castrating ant species, plants inhabited by *C. nigriceps* have a higher density of terminal shoots, which sprout the hollow thorns in which ants nest, and a higher density of extra-floral nectaries, from which the ants feed. *A. drepanolobium* persists because over 80% of hostplants are inhabited by one of three other mutualistic ant species.

Yu & Pierce (1998) have also described a castration parasitism of the ant-plant *Cordia nodosa* in Peru. Workers of the most common ant associate, *Allomerus*

cf. *demerarae*, protect new shoots from herbivory, but also attack and destroy floral buds, reducing population fruit production by almost 80%. *Cordia nodosa* inhabited by any of four mutualistic *Azteca* species are responsible for the majority of the fruit and pollen production. *Allomerus demerarae* benefits from castrating its hostplants because senescence of branches (and thus, domatia) is slowed, leading in turn to faster-growing plants, and more fecund resident colonies (Yu & Pierce, 1998). Similar to *Crematogaster nigriceps*, *A. demerarae* relies exclusively on its hostplant for food and nesting space. Workers do not leave their hostplant, as revealed by baiting experiments, whereas *Azteca* colonies construct carton nests and regularly forage off the hostplant (Yu & Pierce, 1998).

To summarize, ants can parasitize ant-plants by failing to invest in sufficient workers to protect the hostplant or by re-allocating host plant resources from reproduction to growth. Although only two species of the former kind of parasite have been well characterized, they are likely to be quite common. Many ant-plant species support a number of non-protecting, opportunistic plant-cavity and litter-dwelling ant species (Fiala & Maschwitz, 1992; Tennant, 1994; Fiala, Maschwitz & Linsenmair, 1996). It is reasonable to expect that if these parasites were to occupy all or even most of the hostplants, the extinction of the mutualism would result.

A PARASITIC BEETLE

The ant *Pheidole bicornis* associates mutualistically with several species of myrmecophytic *Piper* plants in Costa Rica. Risch & Rickson (1981) reported a striking filtering mechanism, in which hostplants produce food bodies only in the presence of *Pheidole*. However, Letourneau (1990) later found that larvae of the clerid beetle *Phyllobaenus* sp. are also able to stimulate food body production, having 'broken the code' of the filter. Furthermore, not only do *Phyllobaenus* beetles not protect hostplants, their larvae kill *Pheidole* workers and consume the ant brood, resulting in an almost four-fold increase in the rate of herbivory (Letourneau, 1990). It is thus conceivable that *Phyllobaenus* populations could grow large enough to destroy the *Piper-Pheidole* mutualism.

THE LIMITATIONS OF FILTERS

Filters are able to exclude some potentially parasitic species from ant-plant mutualisms. For example, ant-plants appear to attract their ant symbionts with volatile compounds (Longino, 1989; Vasconcelos, 1993). Foundresses of ant species not sensitive to those volatiles are put at a disadvantage when searching for saplings of myrmecophytes. Even after arrival, closed

entrances in a number of species impede entry, restricting the number of ant species associated with each ant-plant species (Fiala & Maschwitz, 1992). For example, the ant-plant *Cecropia obtusifolia*, recently introduced into Hawaii, never hosts ant colonies there, despite the fact that five ant species regularly patrol plant surfaces, some of which have congeners associated with *Cecropia* in South America (Wetterer, 1997). In contrast, Fiala *et al.* (1996) describe a *Macaranga* species which, unlike its congeners, has an open domatium entrance, and associates with 12 ant species, as contrasted with the one or two ant species in typical *Macaranga* species.

About half of myrmecophytic *Macaranga* also display a slippery wax coating on their stems (Federle *et al.*, 1997), impeding all but specialized ant species from walking on them. The wax appears to be adaptive, because only the specialist ants prune encroaching vines, and because the wax can prevent aggressive ant species from preying on colonies of the specialists. Nonetheless, the wax is only partially effective, as exemplified by one of the waxy species, *M. pruinosa*, which hosts in addition to the specialists, a variety of other ant species that nest in the domatia, under the stipules, or in carton nests (Federle *et al.*, 1997).

More intricately, a form of chemical camouflage appears to restrict the entry of the ant *Azteca australis* into the ant-plant *Cecropia pungara*. Colonies of *A. australis* are never found in adult *C. pungara* (Davidson & Fisher, 1991). However, experimental placement of *A. australis* queens on saplings of *C. pungara* caused the queens to engage in the entire suite of colonizing behaviours: antennation, running and chewing (Yu & Davidson, 1997). Nonetheless, not one queen was able to locate and open an entrance to a domatium, even though they all rapidly entered the entrances of *Cecropia* species in which they normally establish.

Saplings of *C. pungara* are also unique in producing food bodies before domatia develop (Folgarait & Davidson, 1994, 1995), favouring foundresses of its normal ant associate *Pachycondyla luteola*, which require external food sources when maturing brood, over *Azteca* foundresses, which use only internal resources when founding colonies (Yu & Davidson, 1997). Importantly, *P. luteola*, which uses a nitrogen-based sting venom, appears to be *C. pungara*'s optimal symbiont. *Azteca* workers use carbon-based sprays for attack and defence, which are unsuitable for *C. pungara*'s slow growth and subsequent long periods of low carbon availability when temporarily overtopped by neighbouring vegetation (Yu & Davidson, 1997).

However, the apparent effectiveness of *Cecropia pungara*'s two filters reveals an important constraint: for filters to be effective, parasites and mutualists must differ significantly from each other. *Pachycondyla luteola* and *Azteca australis* belong to widely separated

clades (Holldobler & Wilson, 1990), have different colony founding requirements and, probably, different sensory biases. Thus, no filter seems likely to prevent the entry of parasites over evolutionary time, as suggested by the studies showing that ant-plants are characterized by multiple *de novo* colonizations by multiple ant lineages (Ward, 1991, 1993; Davidson & McKey, 1993; Chenuil & McKey, 1996; Yu & Davidson, 1997).

In fact, with specialized parasites, filters are not at all effective, the most obvious example being the ability of *Phyllobaenus* to 'break the code' of myrmecophytic *Pipers* (Letourneau, 1990). Another example is *Acacia drepanolobium*, the flowers of which have ant-repellant chemicals that inhibit resident ants from deterring pollinators (Willmer & Stone, 1997). However, the ant-plant's castration parasite *Crematogaster nigriceps* attacks shoots. Finally, neither Janzen (1975) nor McKey (1984) has reported that ant-plants in any way obstruct colonization by foundresses of parasites. Clearly, none of these parasites is being filtered out.

HOSTAGE TRADING IN ANT-PLANTS

To understand how cheating is prevented in ant-plant interactions, it is important first to understand how hostage trading normally prevents cheating between ants and plants and how it breaks down. Plant morphology and ontogeny create situations in which ant and plant exchange benefits simultaneously. For example, in all ant-plants involved in defence mutualisms, the production of each new domatium is tied to the successful defence of attached plant parts. Thus, domatia are located in shoots (e.g. *Cecropia* and *Triplaris*), tendrils (e.g. *Nepenthes bicalcarata*), leaf laminae (e.g. *Tococa*) and petioles (e.g. *Pourouma myrmecophila*) containing or supporting domatia. Extra-floral nectaries and food bodies are also disproportionately active and abundant on or near new leaves (Huxley, 1986; Folgarait, 1994, 1995, but see McKey, 1984). Hostage trading also applies to ant-epiphytes, which host ant colonies in hollow tubers and are in turn fertilized by the colonies (Janzen, 1974; Huxley, 1978, 1980; Treseder, Davidson & Ehleringer, 1995). The more nutrients deposited in the appropriate root cavities, the larger the tuber (and the ant colony) can grow. Importantly, the ant inhabitants are not reported to defend hostplant leaves against herbivory (Janzen, 1974; Huxley, 1978); leaf production is only indirectly tied to tuber growth. Along these lines, hostage trading could help to explain why ant-plants are not found in the temperate zone. Any temperate-zone ants overwinter in a root cavity in order to avoid winter freezing. Under these circumstances, such a plant would no longer be able to trade domatia for protection of leaves, analogous to ant epiphytes.

In summary, hostage trading ensures that ants reciprocate when they receive plant-provided benefits and that the plant can capture that reciprocated benefit. An interesting example of what seems to be an incipient form of hostage trading is found in *Cordia nodosa* (Yu & Pierce, 1998). Occasionally, floral buds are found on new shoots (containing leaves and a domatium). The entire package is protected by *Alloeris* workers, and as a result, floral buds escape destruction. However, after the leaves mature, the ants often attack the flowers, rendering this strategy only partially successful. In fact, in rare cases, workers destroy both the new shoot and the flowers, a form of 'spiteful behaviour' (Trivers, 1985)!

CHEATING OCCURS WHEN HOSTAGE TRADING BREAKS DOWN

Parasitic ants that fail to protect their hostplants simply do not engage in hostage trading. Instead, these ants nest in the few domatia produced by ant-plants awaiting colonization by mutualists. Rapid allocation to reproduction allows these ants to escape before the sapling dies (Janzen, 1975). Castration parasites do hostage trade for vegetative benefits (domatia for leaves). However, a parasitic relationship arises because the ants avoid exchanging *fitness* benefits (ant reproductives for seeds).

THE COEXISTENCE OF PARASITES AND MUTUALISTS

We see here that neither filters nor hostage trading can reliably prevent parasites from entering ant-plant mutualisms. Furthermore, parasites do not engage in parcelling nor provide by-product benefits as a result of their selfish activities, and vertical transmission, trait-group dynamics and neighbourhood interactions are not occurring. At an abstract level, it could be argued that Retaliation is occurring when ants fail to protect their hostplants. By not growing, both ant and plant reap Punishment benefits (neither cooperates, neither gains the benefit of cooperation). However, because ant-plants must make some domatia in order to allow mutualists to colonize (initial investment in cooperation), parasites are able to invade because of the large number of players, the 'large group' effect (Boyd & Richerson, 1988). And of course, plants are not retaliating against castration parasites, providing more, not fewer, domatia after castration. In summary, ant parasites sidestep the first condition of cooperation, the reciprocation of benefits.

However, ant-plant mutualisms can persist because mutualistic ant species, which do fulfil the first condition of cooperation, can reliably establish in a portion of hostplants in each generation, thereby also fulfilling

the second condition of cooperation, re-assembly. As ant-plants can be thought of as a resource for competing ant species (Soberon & Martinez del Rio, 1985; Davidson, Snelling & Longino, 1989), the problem of the maintenance of cooperation becomes a problem of the maintenance of species coexistence.

COLONIZATION OF ANT-PLANTS

In ant-plant systems, the species of resident ant colony is determined at the sapling stage, when multiple queens colonize saplings (Davidson *et al.*, 1989; McKey, 1988; Vasconcelos, 1993; Yu & Davidson, 1997). Coexistence among ant species is largely achieved via niche partitioning at this stage, known in plant ecology as regeneration-niche partitioning (Grubb, 1977). For example, a non-random pattern of association among five ant species and five *Cecropia* species reflects patterns of queen dispersal to saplings (Yu & Davidson, 1997). Some ant species colonize any *Cecropia* species, but only in particular habitats, and others colonize all habitats, but prefer particular host species. Such niche partitioning could allow the stable coexistence of competing parasitic and mutualistic ant species.

However, host- or habitat-based regeneration-niche partitioning does not apply to most ant-plant systems, which host multiple ant species within a seemingly homogeneous habitat (McKey, 1984; Davidson *et al.*, 1989; Fonseca & Ganade, 1996; Yu & Pierce, 1998; Fiala *et al.*, 1999). For these systems, coexistence appears to depend on more subtle forms of regeneration-niche partitioning.

COMPETITION-COLONIZATION TRADEOFFS

Recent work has suggested that ant-plant symbioses serve as ideal empirical examples of spatial models of species coexistence (Vasconcelos, 1993; Yu *et al.*, in press). A well-known example of a spatial model of coexistence is the competition-colonization tradeoff model (Levins & Culver, 1971; Tilman, 1994), which is summarized by these two equations.

$$\frac{dp_1}{dt} = c_1 p_1 (1 - p_1) - m_1 p_1 \quad (1a)$$

$$\frac{dp_2}{dt} = c_2 p_2 (1 - p_1 - p_2) - m_2 p_2 - c_1 p_1 p_2 \quad (1b)$$

p_i represents the relative abundance of adults of species i , c_i the *per capita* colonization rates, and m_i the *per capita* density-independent mortality rates. Species 1 is the superior competitor because it can colonize any site not occupied by a conspecific ($1 - p_1$), whereas species 2 can colonize only empty sites ($1 - p_1 - p_2$). As a result, species 2 suffers competitive

displacement by species 1 ($-c_1p_1p_2$), but can still persist by having a higher rate of colonization ($c_2 > \frac{c_1^2}{m}$ when mortality rates are equal).

For example, colonies of the parasitic ant *Pseudomyrmex nigropilosa* can be displaced from hostplants by colonies of mutualistic acacia-ants establishing *de novo* in the same plants or residing in neighbouring plants (Janzen, 1975). *Pseudomyrmex nigropilosa* coexists with the competitively superior mutualistic acacia-ants by being a better colonizer of new saplings and of adult plants in which mutualistic colonies have died (Janzen, 1975). High colonization rates of *P. nigropilosa* are made possible by the production of new queens within 2 months of colony establishment, contrasting with the 2 years or more of growth that mutualistic acacia-ants require before producing queens (Janzen, 1975). The competition-colonization tradeoff is self-reinforcing because early allocation to reproductiveness necessarily reduces allocation to workers, reducing both hostplant survivorship and the ability to deter displacement.

Similarly, the parasitic *Phyllobaenus* beetle can be considered a superior competitor, able to colonize empty hostplants and to displace mutualistic *Pheidole* colonies. The competition-colonization model predicts that *Pheidole* should have a higher *per capita* colonization rate, c_i , of empty plants and/or a lower adult mortality rate, m_i (Nee & May, 1992). *Pheidole* itself lowers the rate at which *Phyllobaenus* can colonize and displace ant colonies, by removing the beetle's eggs (Letourneau, 1983, 1990).

More speculatively, since *Piper* plants only survive in the presence of their mutualistic ants, coexistence of *Phyllobaenus* and *Pheidole* might be mediated at a regional scale. Levels of *Phyllobaenus* infestation differ from one region of Costa Rica to another (29% of *Piper cenocladum* petioles occupied by *Phyllobaenus* larvae in one population vs. <1–2% of petioles at two other sites, Letourneau, 1991). Subpopulations might crash due to excessive *Phyllobaenus* infestation and subsequently be recolonized from other subpopulations, as described in a model for spatially-structured diseases (Rand, Keeling & Wilson, 1995).

DISPERSAL-FECUNDITY TRADEOFFS

The competition-colonization tradeoff model (Eqn 1) requires that the superior competitor be able to displace adults of the inferior competitor. If this assumption is not met, then stable coexistence cannot be achieved in a homogeneous environment (Armstrong, 1976; Chesson & Warner, 1981; Comins & Noble, 1985; Yu & Wilson, in press). The reason is that when adults are invulnerable and competition is limited to the juvenile stage, such as amongst queens, any increase

in juvenile competitive ability merely has the effect of increasing effective fecundity (the production of new adults), and the species with the highest effective fecundity eventually wins.

Adult colonies of the castration parasite *Allomerus demerarae* are largely invulnerable to displacement by the mutualistic *Azteca* species competing for the same hosts (Yu & Pierce, 1998). As a result, coexistence of parasites and mutualists in these systems via the standard competition-colonization tradeoff (Eqn 1) appears highly unlikely (Yu & Wilson, in press).

Instead, coexistence can be explained by a model that invokes a tradeoff between colony fecundity and foundress (queen) dispersal ability (Yu, Wilson & Pierce, in press). In any given sapling, the winning foundress is the first one to survive and produce workers, which attack and kill any other live queens on the same sapling. As colonization is defined as the production of a new adult by an existing adult, colonization rates (c_i) are determined by colony fecundity, individual foundress dispersal abilities, post-arrival mortalities, and colony growth rate to reproductive maturity.

Measurements of these rates in the ant-plant *Cordia nodosa* reveal that *Allomerus* colonies are more fecund than are *Azteca* colonies and that *Azteca* foundresses are longer-distance dispersers (Yu, Wilson & Pierce, in press). As a result, the two species are able to coexist in an environment where hostplant density varies spatially. The more fecund *Allomerus* can dominate sites characterized by high hostplant density, but *Azteca*'s foundresses are better at finding saplings in low-density sites and thereby win most saplings there by default. Each species is thus a superior colonizer over a range of patch densities, and migration across sites with different hostplant densities maintains local mixing of *Azteca* and *Allomerus*. In short, the mutualism can persist because *Azteca* can reliably associate with a portion of hosts.

In support of this model, censuses from widely separated localities in Peru revealed that, as hostplant density decreases from 100 to 10 per hectare, the relative abundances of both *Azteca* foundresses in saplings and of *Azteca* colonies rise. Moreover, the rise in the relative abundance of foundresses is significantly steeper, as expected if *Azteca* gains a dispersal advantage in sites of lower hostplant density (Yu, Wilson & Pierce, in press).

The dispersal-fecundity tradeoff model can be generalized to reveal a simple general criterion of competitive exclusion (Yu & Wilson, in press), namely that the species with the highest value of c_i/m_i (essentially, population growth rate or fitness) competitively excludes the other species. Coexistence occurs over spatial or temporal heterogeneity in c_i/m_i , such that each species has the highest population growth rate in some

place or at some time (Chesson & Warner, 1981; Comins & Noble, 1985). In the *C. nodosa* system, spatial variation in patch densities (and thus, in values of c_i) provides the necessary heterogeneity.

Application of the c_i/m_i criterion might also be used to explain the stable coexistence of parasites in two other ant-plant mutualisms. For instance, coexistence of the castration parasite *Crematogaster nigriceps* with its mutualistic competitors (Young *et al.*, 1997) could depend on the fact that ant-acacia stands are regularly disturbed by elephants, which would produce spatial heterogeneity in hostplant density and/or colony mortality rates. In another example, saplings of the host-plant *Leonardoxa africana* are found in small, dense stands on slopes, often around groves of adults or adjacent to inundated areas, and also as widely scattered individuals in forest on level terrain (McKey, 1984). In one population surveyed by McKey (1984), where numbers of adult *L. africana* are 'substantial', the parasitic ant species *Cataulacus mckeyi* is rare (2%) and mutualistic *Petalomyrmex phylax* is common (98%). Where trees are less common, 10 to 60% of *L. africana* are inhabited by *C. mckeyi*. The dispersal-fecundity explanation predicts queens of the parasitic ant, *Cataulacus mckeyi*, to be better colonizers of isolated *L. africana* saplings, but colonies of the mutualist, *Petalomyrmex phylax*, to be more fecund. The application of the dispersal-fecundity explanation here is admittedly speculative, and alternative or additional explanations are likely, but it is clear that a species-coexistence approach promises to explain the stable coexistence of parasite and mutualist in ant-plant systems. Following Yu, Wilson & Pierce (in press), empirical tests of dispersal-mediated coexistence would take the form of colonization experiments over a range of environmental conditions, such as host-plant density.

FIGS AND YUCCAS

The species coexistence approach outlined here can also be applied to the obligate mutualisms between *Ficus* plants and their pollinating wasps, and between *Yucca* plants and their pollinating moths. The wasps and the moths pollinate the flowers of their host-plants and oviposit in a portion of those flowers, and the larvae consume the endosperm of developing seeds. In this way, fig and yucca plants end up 'paying babies to make babies' (Janzen, 1979a), and both mutualisms, like ant-plants, therefore involve 'investment in pseudo-reciprocity' (Connor, 1986).

Pollination mutualisms exhibit an obvious conflict of interest. Pollinators should be selected to oviposit in all ovaries, since pollinators receive no short-term benefit by allowing any ovary to produce seeds. However, the spread of such a strategy would eliminate

seed production and doom the mutualism to extinction. The search for mechanisms to stabilize the pollinator-seed conflict has therefore stimulated much fig and yucca research (Janzen, 1979a,b; Kjellberg, Michaloud & Valdeyron, 1987; Bronstein, 1988a,b; Frank, 1989; Addicott, Bronstein & Kjellberg, 1990; Ganeshaiah *et al.*, 1995; Anstett, Bronstein & Hossaert-McKey, 1996; Herre, 1996; Nefdt & Compton, 1996; Herre & West, 1997; Pellmyr & Huth, 1994; Addicott, 1998; Addicott & Bao, 1999).

POLLINATION PARASITES

There are also specialized parasites in both systems, which do not pollinate, but do lay eggs. In figs, these parasites include gallers, parasitoids, and inquilines. Gallers oviposit in fig flowers but do not pollinate them, and are so called because their larvae feed on galled ovaries, that is, nucellar tissue that has been made to proliferate parthenogenetically (Galil & Eiskowitch, 1968; Kerdelhué & Rasplus, 1996b). Parasitoid larvae feed on the larvae of pollinators or gallers, and inquilines feed on the gall tissue induced by either galler or pollinator larvae. In this article, I will treat only gallers, which have been demonstrated to compete with pollinators for ovaries, and of these, the discussion will primarily concern gallers that oviposit from outside the fig, in contrast to pollinators, which enter figs in order to pollinate and lay eggs. Externally ovipositing gallers comprise by far the majority of galler species (Machado *et al.*, 1996). Parasitoids are treated elsewhere (West *et al.*, 1996; Weiblen, Yu and West, 2001), and little is known about inquiline biology.

Because ovaries used by galler larvae are rendered unavailable to pollinators (Galil, Dulberger & Rosen, 1970), gallers represent a pure cost to the plants, and in most systems studied, galler and pollinator abundances are negatively correlated, supporting the hypothesis that they compete (strong evidence: West & Herre, 1994; West *et al.*, 1996; Kerdelhué & Rasplus, 1996b; weak evidence: Bronstein, 1991; Compton *et al.*, 1991; no evidence: Cook & Power, 1996). The galler-pollinator dichotomy can be thought of as an extreme version of the pollinator-seed conflict, and the balance of the evidence suggests that gallers have the potential to exclude pollinators in many fig species.

In yuccas, the situation with non-pollinating parasites is more complicated. Some moths pollinate only occasionally (Aker & Udovic, 1981; Powell, 1992; Tyre & Addicott, 1993; Addicot & Tyre, 1995). Others pollinate, but mainly with pollen from the same plant (geitonogamy), even though self pollen has very low success and selfed seeds suffer severe inbreeding depression (Pellmyr *et al.*, 1997; Richter & Weis, 1998; Marr *et al.*, 2000). Finally, some moth species never pollinate and are proper parasites of the yucca-moth

mutualism (Powell, 1992; Addicott & Tyre, 1995; Addicott, 1996; Pellmyr *et al.*, 1996a), which, following Addicott & Tyre (1995), I call 'secondaries'. Secondaries lack the maxillary tentacles used to transport and pollinate yucca flowers.

Secondaries oviposit in developing fruits after the critical period of floral abortion that is thought to select against heavy oviposition in pollinating moths (Pellmyr & Huth, 1994; Pellmyr *et al.*, 1996a). Fruits utilized by secondaries are noted for heavy larval loads (Addicott, 1986). Populations of *Yucca filamentosa* with secondaries suffer average seed destruction levels of 75% (Pellmyr *et al.*, 1996a), and in one population with two species of cheaters, all seeds in 85% of fruits were destroyed (Pellmyr *et al.*, 1996a).

WHY NOT POLLINATE?

Pollination triggers the development of seed endosperm, a strong sink for plant resources (Haig & Westoby, 1991), thereby allowing larvae to benefit from increased resource availability, and making pollination, whether achieved actively or passively, a selfish strategy on the part of both wasps and moths. If so, why should so many species not pollinate, or pollinate geitonogamously? For yucca moths, several authors have suggested that moth dispersal to a new plant is costly (Aker & Udovic, 1981; Tyre & Addicott, 1993; Addicott & Tyre, 1995; Pellmyr *et al.*, 1997; Marr *et al.*, 2000). Moths are active for only a few hours in the early evening and typically live for only three to five days (Dodd & Linhart, 1984) with a maximum lifespan of up to 8 or 9 days (Powell, 1984). Dispersal to a new plant might significantly reduce time and energy available for oviposition bouts and egg production and expose dispersing moths to bat predation (Addicott & Tyre, 1995). Thus, high-quality pollen (i.e. pollen from plants other than the host) is costly to give away (Marr *et al.*, 2000). Moths should therefore be selected either to be conservative in their use of pollen or not to disperse. As we see here, moths follow both strategies. At the extreme, some moth lineages should lose pollination behaviour, and therefore, parasitism should be a derived strategy, as is seen (Pellmyr *et al.*, 1996a,b; Pellmyr & Leebens-Mack, 2000). In the fig system, the origin of externally-ovipositing gallers has a simpler explanation. They appear to be descended from fig-associated wasps that never evolved the ability to enter the closed chamber of the fig, where the flowers and their stigmas are located (Machado *et al.*, 1996).

THE COEXISTENCE OF PARASITES AND MUTUALISTS

As with ant-plants, the standard mechanisms proposed to limit the spread of cheating in a mutualistic system

(Table 1) do not appear to apply to the fig-pollinator-galler interaction. Successful production of parasite offspring is not dependent upon pollination (Retaliation, Parcelling, Hostage trading), there is no evidence that mutualists and parasites subdivide into isolated demes (Trait-group selection), and the dispersal of pollinators precludes Neighbourhood interactions and Vertical transmission. Neither fig nor yucca plants derive any benefits from the presence of gallers (By-product mutualism). In some fig species, figs entirely lacking in pollinator foundresses are aborted (Filtering), but in other cases, gallers can prevent abortion of figs even in the absence of pollination (Galil *et al.*, 1970; Bronstein, 1991; Compton *et al.*, 1991; Compton, 1993; West *et al.*, 1996). In yuccas, secondaries oviposit after floral abortion is no longer possible (Pellmyr *et al.*, 1996a). What, then, prevents the competitive exclusion of pollinators by gallers and secondaries? As in ant-plants, persistence depends on reliable re-assembly: mechanisms allowing pollinators access to some proportion of host ovaries from generation to generation.

I list several hypotheses here, with the intention to encourage empirical tests. This discussion will be limited to figs because little is known about the population dynamics of secondaries (but see Addicott, 1998 regarding different kinds of pollinating yucca moths).

NEGATIVE FEEDBACK

In many fig species, emerging gallers cannot escape figs without the aid of male pollinators, which dig exit tunnels for female pollinators (and thus, gallers also) (Godfray, 1988; Bronstein, 1991; Weiblen, Flick & Spencer, 1995; Cook & Power, 1996; Kerdelhué & Rasplus, 1996b). If pollinator populations decline due to competition from gallers, most emerging galler wasps should find themselves in figs without pollinators, and thus unable to escape. Similarly, as mentioned, some gallers need the presence of pollinator foundresses to prevent fig abortion (Bronstein, 1991). Thus, galler dependence on male fig wasps and/or pollination creates 'negative feedback' that promotes coexistence (Weiblen *et al.*, 1995).

However, in some *Ficus* species, figs open an entrance automatically before wasp eclosion (Ramirez, 1974; Verkerke, 1989), and in other *Ficus* species, gallers (e.g. *Aepocerus*, *Sycophaga*, *Philotrypesis*) can exit without the aid of male pollinators (Hill, 1967; Galil & Eisikowitch, 1968; Galil *et al.*, 1970; Bronstein, 1991; Compton *et al.*, 1991; Compton & van Noort, 1992; Cook & Power, 1996; Machado *et al.*, 1996; West *et al.*, 1996). Negative feedback clearly is not acting in these systems.

NICHE PARTITIONING

In some fig species, galler offspring are found primarily in the outer layer of ovaries of a fig, and pollinators are found in the inner layer (Compton & Nefdt, 1990; Kerdelhué & Rasplus, 1996a; Cook & Power, 1996). However, in other species, gallers and pollinators both preferentially use the inner ovary layer (West & Herre, 1994; West *et al.*, 1996; Kerdelhué & Rasplus, 1996b), and there are also gallers (West *et al.*, 1996) that are able to pre-empt entire figs. Niche partitioning is absent in these systems.

PREDATOR-MEDIATED COEXISTENCE

Ants, birds, staphylinid beetles and parasitoid wasps attack pollinator and galler foundresses and larvae (Bronstein, 1988c; Compton & Robertson, 1988; Compton, 1993; Kerdelhué & Rasplus, 1996b; West *et al.*, 1996). Galler foundresses are disproportionately attacked, especially by ants, because they oviposit from outside figs, and predation therefore reduces galler relative abundances and increases seed and pollinator abundances (Bronstein, 1988c; Compton & Robertson, 1988; Kerdelhué & Rasplus, 1996b). If the galler-predator interaction is stable, predators could regulate the abundance of gallers below the level needed for gallers to exclude pollinators competitively. West *et al.* (1996) and Weiblen, Yu & West (2001) have found that parasitoid-galler attack rates are host-density dependent, which stabilizes the interaction, supporting this possibility.

TRADEOFFS AND ENVIRONMENTAL HETEROGENEITY

Application of the c_i/m_i criterion reveals that gallers and pollinators exhibit a number of tradeoffs that might produce coexistence, given the appropriate environmental heterogeneity.

DIURNAL-NOCTURNAL FLIGHT TRADEOFF

In *Ficus sycomorus*, the galler *Ceratosolen galili* is a diurnal flier, and the pollinator *C. arabicus* is a nocturnal flier (Compton *et al.*, 1991). Because figs cease to be attractive to wasps shortly after foundress arrival, entry by *C. arabicus* at night could reduce the rate of daytime entry by *C. galili*, and vice versa, accounting for the statistical under-representation of figs with both species (Compton *et al.*, 1991). Coexistence can therefore be facilitated by temporal heterogeneity in fig-opening times.

DISPERSAL-FECUNDITY TRADEOFF

The extremely small sizes of fig wasps cause them to be carried passively by wind, limiting their ability to direct dispersal toward receptive fig plants (Ware

& Compton, 1994). In addition, mortality of pollinator foundresses during dispersal can reach 95% due to predation and dehydration (Ware & Compton, 1994; Compton, Rasplus & Ware, 1994a; Compton, Ross & Thornton, 1994b). As a result, pollinator foundress limitation should be widespread, as is seen (Bronstein, 1988a; Herre, 1989, 1996; Corlett, Boudville & Seet, 1990; Hawkins & Compton, 1992; Anstett *et al.*, 1996; Bronstein & Hossaert-McKey, 1996; Kerdelhué & Rasplus, 1996b; Nefdt & Compton, 1996). Low pollinator arrival rates have been mooted as a mechanism for stabilizing the pollinator-seed conflict because most figs would not receive sufficient foundresses to exploit all available ovaries, allowing the remaining ovaries to produce seeds (Corlett *et al.*, 1990; Ware & Compton, 1994; Anstett *et al.*, 1996; Bronstein & Hossaert-McKey, 1996; Nefdt & Compton, 1996).

Unfortunately, similarly comprehensive data for gallers are not available. However, because the life-spans of gallers appear to exceed those of pollinators, at least in some cases (Compton *et al.*, 1994a), gallers should be superior dispersers and suffer less foundress limitation.

On the other hand, pollinators might have higher *per capita* fecundities, in large part because they are internal ovipositors, which gives them a refuge from the predators that prey on and chase off externally-ovipositing gallers. In support, Weiblen, Yu & West (2001) have found that abundances of galler offspring are approximately an order of magnitude lower than pollinator offspring in several fig species. Clearly more data on relative fecundities and dispersal abilities are necessary.

The fig system thus shows the makings of a dispersal-fecundity tradeoff, coexistence being produced by spatial heterogeneity in the abundance of receptive plants. Different rates of mortality during and after dispersal should result in widely varying relative abundances of gallers and pollinators across fig species, populations and individual plants, as has been seen (Bronstein, 1988a; Herre, 1989; Corlett *et al.*, 1990; Hawkins & Compton, 1992; West *et al.*, 1996). For example, the numbers of galler foundresses arriving at different *F. pertusa* plants vary by orders of magnitude, with each of the three species of gallers dominating numerically on at least one tree (Bronstein, 1991). A further prediction of the dispersal-fecundity tradeoff is that gallers should reach isolated plants in high numbers, but more fecund pollinators should be relatively more abundant at plants near their birth sites.

FECUNDITY-FECUNDITY TRADEOFF

A complementary hypothesis is that gallers and pollinators can coexist over variation in *per capita* fecundities (part of c_i) caused by spatial variation in the

attack rates of galler foundresses, primarily by ants. Gallers would have higher fecundities in plants lacking predators, and pollinators would do better on plants with predators. Accordingly, a broad survey showed that only 46% of 429 fig trees over 20 species had ant-attended figs (Cushman *et al.*, 1998), demonstrating the necessary spatial heterogeneity in ant attendance.

COMPETITION-COLONIZATION TRADEOFF

Addicott (1998) has alluded to a competition-colonization tradeoff in yucca moths in which the larvae of mutualistic moths have a competitive advantage over secondaries, because the former are laid earlier on flowers and thereby have a head start in development.

EVOLUTION OF PARASITISM VS. MUTUALISM

In summary, the species coexistence perspective, with an emphasis on trade-offs, can provide insight into the mechanisms allowing parasites and mutualists to coexist. The examples given above constitute a roadmap for further empirical work. In addition, viewing parasites as competitors with mutualists can shed light onto the evolution of cheating in cooperative systems.

For example, Herre *et al.* (1999) are surprised to find high degrees of genetic and taxonomic diversity in many mutualistic systems, such as in corals and root rhizospheres. They suggest, by analogy to the evolution of virulence in parasites (Herre, 1993; Mosquera & Adler, 1999), that competition among symbionts for the resources or services of a host should favour the evolution of parasitism. The reasoning goes that because virulence corresponds to reproductive effort (i.e. the rate at which parasites convert host soma to parasite offspring, Ewald, 1988), under competitive pressure, selection should favour higher virulence (Mosquera & Adler, 1999).

However, the species-coexistence approach argues that there is no *a priori* reason to expect that competition among mutualists should lead to cheating. For instance, while the ant *Allomerus demerarae* has apparently evolved its castrating behaviour as a way of competing for hostplants, the mutualistic *Azteca* species appear to compete via superior dispersal ability (Yu, Wilson & Pierce, in press), and so there is little to no selection pressure to castrate. The point here is that we need not expect that competition amongst symbionts must promote cheating.

Instead, the divergent behaviours of mutualism and parasitism can be seen as reflecting the divergent ways by which mutualists can respond to competition. Firstly, mutualists can offer increased benefits, such

as bigger fruits and more nectar, to attract more partners (the 'market effect', Noë & Hammerstein, 1994), or higher rates of patrolling to increase reciprocated benefits ('investing in pseudo-reciprocity' Connor, 1986). In either case, competitive ability is increased, and competition has led to increased transfers of benefits, that is, 'more mutualism'. Secondly, as suggested by Herre *et al.* (1999), mutualists might extract more benefits (e.g. castration) or reduce reciprocated benefits (e.g. fail to protect or pollinate). In either case, net fitness has increased, and competition has led to 'more parasitism'. And finally, different mutualists (and mutualists and parasites) can coexist by specializing on different subsets of the host resource spectrum (Rowan *et al.*, 1997). Which of the three outcomes obtains depends on several factors, including, but certainly not limited to, the strength of tradeoffs, which promote niche partitioning, historical factors (Pellmyr & Leebens-Mack, 2000), and life-history considerations.

In particular with ant-plants, the evolution of parasitism can be viewed as one of many possible resolutions to a life-history conflict between ant and plant over when to start reproducing. For instance, non-protecting ants begin reproduction at small colony sizes, removing any incentive to invest colony resources into plant protection and growth. On the other side of the coin, *Cordia nodosa* can begin to flower when it has only five domatia, but *Allomerus* colonies do not consistently produce reproductives until the plant has 25 domatia or more (Yu & Pierce, 1998). Here, there is obvious selection pressure for *Allomerus* to delay the onset of reproduction in its host. In contrast, mutualistic *Azteca* are able to build carton nests, thereby overcoming plant constraints on colony size. Moreover, many ant-plant species, especially trees, fruit only after many years of growth, reducing or eliminating the conflict in these cases. There are also tantalizing hints that plants can resolve conflict with symbiotic ants by fiat. Myrmecophytic *Tachigali* trees are monocarpic, which would greatly impede the evolution of castration (W. D. Hamilton, pers. comm.), and the ant-plant *Crypteronia griffithii* does not host ants as an adult (Moog *et al.*, 1998). Under this conception, the multiple factors that decide the optimal sizes of first reproduction (Stearns, 1992; Rees *et al.*, 1999), rather than competition *per se*, underlie the evolution of cheating or cooperation.

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