How to be a Fig

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The 900-odd species of *Ficus* (20, 21) constitute the most distinctive of the widespread genera of tropical plants. Figs have (*a*) a complex obligatory mutualism with their pollinating agaonid fig wasps, yet are found in almost all tropical habitat types and geographic locations [this sets them apart from ant-acacias (63–65), euglossine-orchids (24, 26), moth-yuccas (45, 88, 89,), ant-epiphytes (66, 98) and ant-fungi (109)]; (*b*) fruits eaten by a large variety of vertebrates, most of which appear to be fig seed dispersers rather than seed predators; (*c*) minute seeds despite the adults' long-lived woody life form; (*d*) exceptionally numerous congeners in almost any mainland tropical forest habitat; (*e*) every woody life-form (deciduous, evergreen; tree, strangler, epiphyte, vine, scandent shrub, bush); (*f*) intra-population inter-tree asynchronous flowering and fruiting in many habitats, yet strong intra-tree synchronous flowering and fruiting; (*g*) heavy outcrossed pollination even when the density of flowering conspecifics is extremely low; (*h*) no inter-specific competition for pollinators within a habitat irrespective of the number of *Ficus* species present and the timing of sexual reproduction; (*i*) heavy visitation of fruiting crowns by seed dispersers even when the density of conspecifics is extremely low; and (*j*) over 50% predispersal seed predation of all seed crops.

There is a voluminous literature on the taxonomy and biology of fig flowers, fig fruits, and fig wasps (see reviews in 1, 9, 16, 20–22, 34–36, 41, 47, 52, 86, 90–96, 101, 112, 113), but each author focused on particular aspects of the system. Here I stress interactions among many parts of the system.

Wiebes' chapter in this volume is the most recent review of the details of the interaction of fig wasps with figs. However, a very brief overview of fig biology is useful here. First, ignore the atypical commercial fig, *Ficus carica,* since it occupies extra-tropical to sub-tropical habitats, has decidu-

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ous lobed leaves and large fruits in many parthenocarpic varieties, is gynodioecious, and has not been studied as a wild plant (11–13, 15, 17). A fig species much more representative of *Ficus* lives in tropical woody vegetation below 2000 m elevation, is a fast-growing woody plant, and has medium to large stiff oval leaves that are shed synchronously and then immediately replaced once a year (giving the illusion of being "evergreen" even in deciduous forest habitats). The bark is smooth, gray, and epiphyte-poor, and the trunk is fluted or otherwise contorted. Buttresses and surface roots are prominent. All above-ground parts (including immature fruits) are permeated near the surface with vessels (lactifers) containing white latex that in turn contains the powerful protease, ficin, among other defensive compounds (107). Fig trees have a small fauna of leaf-eating insects but are not generally subject to massive defoliation by leafcutter ants or caterpillars. As often as twice a year, a tree produces a crop of 500–1,000,000 1–5 cm diameter fruits (called "syconia" in other literature), each containing 100–1000 seeds. The small green fruits are borne on short peduncles in the leaf axils. They are entered through a scale-occluded pore (ostiole) by one or a few minute pollen-bearing wasps of the family Agaonidae. These wasps pollinate the hundreds of single-ovuled florets inside the monoecious fruit and lay one egg in each of many of the ovaries, reaching the ovary by inserting the ovipositor down the style. A wasp larva eats the developing seed and lives inside the seed coat. The plant therefore pays 50% or more of its offspring for outcrossing services. A month or so later, the wingless male wasps emerge and then mate with the females through holes they have cut in the sides of the ovaries. Since only one or a few pollinating wasps oviposit in one fruit, many matings are brother with sister. The winged females then emerge from the seed coat and pack pollen from newly dehisced anthers into recesses of the body to be carried off to another conspecific fig tree that bears fruit in the small green receptive stage. Females leave through a tunnel cut by the males in the wall of the nearly full-sized fig, or (rarely) through an expanded ostiole. Other minute wasps (parasitic Hymenoptera in the Agaonidae and Torymidae) parasitize fig seeds, fig wasps, or the combination, and oviposit either the same way the pollinators do or through the fig fruit wall. In gynodioecious species of *Ficus* (all Old World), some individuals or seasonal morphs bear fruits containing only florets with styles too long to allow the wasp to oviposit in the ovaries. The female wasps therefore pollinate the florets, but no seeds are lost to the wasps and no wasps are produced. Monoecious trees of these species tend to have a very high rate of fig-wasp seed predation and therefore act functionally as males. Various moth (Pyralidae) and weevil (Curculionidae) larvae prey on the developing seeds in maturing figs. The figs newly vacated by the pollinating wasps ripen rapidly and are avidly eaten by many species of vertebrates. These digest the fruit wall and the florets from which the wasps have exited, but the seeds undamaged by the wasps usually survive the trip through the gut. Apparently only *Treron* fruit pigeons and small parrots intensely prey on, as well as disperse, intact fig seeds. Mature seeds are also heavily preyed on by lygaeid bugs. Mature fig trees are most common in moderately disturbed sites such as riparian edges, tree crowns (as epiphytes), tree falls, secondary agricultural regeneration, and old landslides. Their lifespans are unknown, but probably do not exceed several hundred years in the wild state.

Such a natural history brings to mind many questions in population biology. This review is an effort to locate manageable questions, rather than to summarize an extensive body of information. I believe that at this stage in tropical biology it is more appropriate to try to make a few well-known systems better understood than to concentrate on the discovery of new systems (68).

TERMINOLOGY

I have deliberately avoided the word "*syconium.*" If we are to have a special word for every type of inflorescence or infrutescence, the proliferation of nouns would be astronomical. The fig syconium is nothing more than a globular inflorescence internally lined with several hundred female florets and fewer male florets. Ecologically, this structure is a fruit; *Ficus* has merely reinvented the multiple-ovuled ovary and many-seeded fruit. I call the cavity inside the fig a *pseudolocule;* the ostiole with its occluding scales is functionally analogous to the stigma and style of an ordinary flower. In fact, I suspect that the stigma of the fig floret has lost much of its physiological discriminatory ability. "No family has such small standarized flowers, yet such an astonishing array of infrutescences" (21). The plant probably relies on pollinator choice and behavior, ostiolar screening, and attractant allomones to get the correct pollen tubes to the ovules.

"Condit & Flanders (18) indicated that the term *gall flower* is a misnomer since this floral type represents nothing more than short-styled female flowers" (49) in which one of the occupants of the fig has oviposited [as also concluded by Rixford (101) and other early writers]. Gordh concluded that "the term will be retained, however, because it is convenient and well established" (49). I prefer to delete it. This is not a simple semantic problem. Certainly it is false that there are specific florets destined physiologically to be no more than food for the wasps, despite the impression given by earlier writers (e.g. 19). By cutting off the ovipositors of pollen-laden wasps, Galil & Eisikowitch (38) showed quite elegantly that pollination of any floret, long- or short-styled, results in normal-appearing seed if no egg is laid in the floret. As such, then, a "gall flower" can be identified only after the fact of seed predation, and should not be called a gall flower any more than should a *Hymenaea* flower bud with an *Anthonomus* weevil larva in it. If attached florets need a special name, *wasp flowers* would be more appropriate. If a pollinating agaonid is doing the ovipositing, it is the short-styled florets that usually get the egg simply because the animal can only reach the ovaries of short-styled florets (cf 37, 38). That about half of the florets in monoecious figs have short styles [e.g. about 1 : 1 in *Ficus religiosa* (78), and see (56)] could even be a product of the mechanics of floret packing in a small space. However, optimal ovary packing could also be achieved by differential pedicel growth after pollination as well as by differential style length before pollination.

Style length, the defining trait of gall flowers, is only relative. A long ovipositor with the associated ability to oviposit in a floret with a style of any length is certainly possible, as demonstrated by the nonpollinator *Sycophaga sycomori* in *Ficus sycomorus* (39, 44). I suspect that whenever intraspecific competition begins to select for longer ovipositors in pollinating agaonids, counterselection occurs in the fig for traits that reduce the number of competing wasps that enter the fig. Such traits might be a tighter ostiole, shorter period of receptiveness by the fig, more florets per fig, etc. The wasp might counter these traits by the production of more but smaller eggs. However, smaller eggs would probably slow the development time of the wasp larvae, thereby raising the probability that they will be eaten by a dispersal agent before they can complete development and emerge. The fig can exacerbate this problem for the wasp by evolutionarily shortening the time to ripening of the fruit. Furthermore, the evolution of more seeds per fig would change the parameters of the disperser interaction.

The world is even more complicated. A gall is a proliferation of tissue abnormal for a site and generated by physiological manipulation of the plant through release of chemicals by the insect. A fruitlet containing a pollinating agaonid rather than a seed is therefore a gall. If the entering wasps are nonpollinators, such as *Sycophagus sycomori* in *Ficus sycomorus* (39, 44), the mere act of oviposition in the fruitlets leads to sclerification of the pericarp, to development of the endosperm and nucellus (which the larvae eat) (see 78), and to retention and ripening of the seed-free fig (and florets). Furthermore, the male florets do not develop in such a seed-free fig unless there are wasps developing in some female florets (44). The evolution of the ability to cause fig retention is expected in *S. sycomorus* since it never pollinates a fig and is derived from a pollinating agaonid ancestor (J. T. Wiebes, personal communication). However, in *Ficus religiosa,* if the incoming agaonids (*Blastophaga quadraticeps*) are deprived of pollen and thus can only oviposit, the tree aborts the seed-sterile figs (37). However, abortion may not occur in seed-free figs that were entered by the pollinating agaonid in Florida *Ficus aurea* and *F. laevigata* (see later discussion of host-specificity). The mere application of single hormone-like chemicals (e.g. naphthaleneacetic acid) to unpollinated *Ficus carica* figs will prevent their abortion (23). I suspect that the wasp or its larva manipulates the fig tree in the same manner. Since the normal course of events is to abort unpollinated figs, the entire fig has to be viewed as a gall when occupied by *S. sycomorus,* and each fruitlet containing a wasp larva should also be viewed this way. Unfortunately, this is not the context in which "gall" was applied originally to the system. In fact, it is not at all clear to me why the word "gall" was ever applied to the fruitlets with wasps in them since they usually look like normal fruitlets with a contained seed predator rather than like galled plant tissue. We do not speak of "gall leaves" or "gall stems," so why "gall flowers"?

The larva of a pollinating agaonid is clearly a seed parasitoid, and the adult wasp is a seed predator in analogy to the bruchid beetles and other insects whose larvae develop inside seeds and fruits (67). However, the large suite of other wasps that oviposit in the floret ovary from both inside and outside the fig may be either parasitoids of the pollinating wasps or seed predators or both. Recent studies of the biology of these animals (52, 113) make it obvious that it would be premature to conclude anything other than that they kill seeds and pollinating agaonids.

FIG SEED PARASITOIDS

Besides the pollinating agaonids, the two types of parasitic Hymenoptera found in fig seeds are competitors and parasitoids of the pollinating agaonid and are seed predators of the fig tree. Those that oviposit through the wall of the green fig and into an ovary in which a pollinating agaonid has already oviposited [Torymidae—e.g. *Apocrypta longitarsus* in *Ficus sycomorus* in Israel (38)] have an ovipositor many times the body length. The larva eats the endosperm and other seed tissues directly, and the agaonid larva starves or is eaten directly. The success ratios are unknown in this competition; they matter to the parent fig only in that the parasitoid is not a pollinator nor does it carry pollen when it leaves the fig. These wasps tend to have normal-appearing males, depend on the male pollinating wasps for an exit hole in the fig, and kill something less than 20% of the agaonids in a fig. There is strong selection for a low rate of oviposition per fig by these wasps: If too many emerge, there will not be enough agaonid males to cut the exit hole. I suspect these parasitoids to be the least fig-species–specific of the fig wasps; but, as in those that enter the fig to oviposit, strong host specificity will be selected for because the development times (which vary among fig species) must closely match those of the wasps that cut exit holes in the fig. Furthermore, ovipositor length must be appropriate for the species-specific distance between the green fig epidermis and ovaries containing agaonids. It is rumored that the brown spots on fig surfaces mark the sites of torymid oviposition punctures (52). If so, the number of oviposition attempts on a fig is much greater than the number of torymid wasps it produces.

Parasitoids that enter the pseudolocule to oviposit are much more numerous in individuals than are those that oviposit from the outside. *Sycophagus sycomori* is the best known (37–39, 44, 47) owing to its introduction to Israel along with *Ficus sycomorus* but without the pollinating agaonid. Incidentally, its survival in unpollinated figs calls into question the dogma that pollinating fig wasps pollinate the florets in which they oviposit as well as others. The ovipositor of *S. sycomorus* is long enough to oviposit in both long- and short-styled florets. In East Africa, where the pollinator is present, it oviposits in florets irrespective of whether they have pollinator eggs in them (the outcome of the ensuing competition is unknown).

S. sycomorus has no pollen pockets and does not carry pollen (J. T. Wiebes, personal communication), and the wasps leave the fig even before the anthers open. Parasitoids of this type may constitute as many as half of the wasps to emerge from a fig (J. T. Wiebes, D. Janzen, unpublished data). A continuous strong evolutionary conflict must exist between them and the fig. Any adaptation of the fig that lowers the intensity of seed predation by these parasitoids will also lower the number of pollinating agaonids incoming or outgoing with pollen. Since their males can cut their own exit from the fig, it is not obvious what keeps these parasitoids from eliminating figs from a habitat in contemporary and evolutionary time.

Both kinds of parasitoids discussed above seem to be slightly less host-specific than are the pollinating agaonids (111). Hill (56, 57) found 16 of 51 species of Hong Kong fig parasitoids to emerge from 2 or 3 species of figs. However, such comparisons are premature until more taxonomic work has been done with the wasps.

FIG PSEUDOLOCULE STERILITY

The pseudolocule of a developing fig, like the locule of any other young fruit, must be protected internally against pathogens. The ostiole constitutes a selective filter; like the stigma and style, it must admit appropriate gametes but retard passage of detrimental organisms.

The most external mechanism of pseudolocule sterility is ostiolar tightness. It is well known that ostiolar scales are so tightly appressed that they strip off wings and antennal segments as female fig wasps force their way through the ostiole. I hypothesize that this amputation is an incidental by-product of a major ostiolar scale function: wiping the wasp clean of fungal spores, pollen grains, bacteria-rich clumps of detritus, yeast, and other microorganisms. The fitness of the wasp (parasitoids as well as pollinators) should be raised if she is clean of microbes as well as wings when she arrives in the pseudolocule of the green fig. There should be strong selection, therefore, for an external morphology that is easily wiped clean. Break-away wings and antennal segments may be viewed as an adaptation allowing passage through the very tightly appressed wipers as well as an adaptation to the cramped quarters in which she will have to work; the sequestration of pollen in the corbiculae, pockets, or integumental folds (40, 42, 43, 45, 46, 90) may be viewed as a device for getting it past the wipers as well as a way of carrying it. Fig pollen is exceptional in not being exposed to airborne pathogens as it moves from anther to stigma: Pollen is acquired by the wasp before the fig is opened, and the young fig pseudolocule should contain nearly sterile air since the ostiolar scales serve as a series of air locks. This hypothesis is not falsified by the observation that pollinating agaonids have specialist mites riding on them that get past the wipers (J. T. Wiebes, personal communication) any more than beaver ear mites negate the hypothesis that the split toe-nail of a beaver functions in fur cleaning. There should also be selection against free-flying wasp females' obtaining food at contaminant-rich sites such as the accumulation of fermenting figs beneath a fruiting fig tree. Other functions of ostiolar tightness will be discussed later.

A second line of defense is needed against pathogens that gain entry to the immature fig pseudolocule. Some are bound to enter on the wasp, and in some cases so many wasps enter the ostiole that a tunnel is worn through it. This tunnel must allow entry of both dirty wasps and contaminated air. In the case of *Ficus sycomorus* in Egypt, "as soon as the eggs are laid, the fig commences to secrete a watery fluid which eventually fills the cavity to about one-fourth its capacity. Before the time arrives for the young insects to emerge from their cells, the fluid is again absorbed" (8). I have noted the same phenomenon for *Ficus insipida* and *Ficus ovalis* in Costa Rica. This fluid without doubt contains antibiotic compounds. It is analogous to the phytoalexin-rich fluid that is secreted into the bean locule when this cavity is invaded by microbes or fungi. A protective role for this fluid is further suggested by the observation that microbial or fungal clones are never found growing in the pseudolocule of undamaged developing figs; the corpses of the female wasps remain relatively intact for many weeks unless mashed by the enlarging florets.

Once the new generation of wasps has emerged from the fig [either through the self-opening ostiole (few species) or through a tunnel in the fruit wall made by male agaonids (most species)], the pseudolocule is easily accessible from the outside. However, by this time the seeds are hard and mature, and the fig will usually ripen within a few days.

POLLINATOR SPECIFICITY

There is general agreement that in most cases there is only one species of pollinating agaonid for each species of fig and that this wasp pollinates only one species of fig (2, 3, 56, 91, 111). (Instructive exceptions will be discussed later.) Both the significance for the plant and the mechanism of this extreme pollinator specificity are terra incognita.

Assume that a fig wasp can live for one week when moving between figs (but see later section). If the trees in a fig population are truly random with respect to intra-population flowering times but are highly synchronous within the tree (as they are generally believed to be), a breeding fig population is only actually 1/52 of the actual population of adult figs with respect to flowering conspecifics—if each fig tree bears receptive figs for a week and liberates wasps for a week once a year. This puts even the more common species of figs among the rarest of trees when it comes to pollination dynamics. The rare species are being pollinated at a phenomenally low density (and probably great inter-tree distances). This implies that fig wasps are extremely competent at locating their fig trees. The wasps are able to search far for a plant in which they can develop rather than fail in any nearer allospecific fig tree with figs of receptive age. On the other hand, their high specificity requires the evolution of a great ability to locate figs of the correct species. The fig tree should also be strongly selective in admitting wasps to its figs. Great ability to locate a receptive fig could easily result in a bombardment of the young figs with wasps bearing allospecific pollen. Even if these wasps develop, they would not be likely to carry the pollen to a conspecific if they were so sloppy as to enter the wrong species of fig in the first place.

There are many potential mechanisms for reinforcement of fig-wasp specificity. Most simply, the wasps are probably cued to a unique mix of chemical signals produced by each species of fig. However, incoming wasps have never been censused at a receptive fig. All specificity records are based on emergences from figs. Therefore no information exists on the species purity in the cloud of pollinators that must arrive. Mistakes do occur. In an isolated Venezuelan *Ficus turbinata* tree, Ramírez (91) found that 5% of 121 figs (syconia) produced the wrong species of agaonid. The florets in these fruits did not, however, produce viable seed. In a second case, he found a single mature fig to contain 209 individuals of the wrong species of agaonid. Again, the seeds did not develop but the wasps did.

If the wrong wasp appears at a receptive fig, the ostiole constitutes the next barrier. If the ostiole served only as a wasp-wiper and excluder of foreign macro-organisms, it and its scales should be adjusted just to the size of the wasp. Figs with identical-sized seeds and florets should have identical ostioles. Actually, however, ostiolar size, scale tightness, scale surface sculpture, and thickness of the scale pile vary greatly (e.g. 93). This variation probably reflects in part the selective exclusion of all but the correct pollinating wasp species and a morphology to minimize the number of individuals of parasitoids that enter.

Once inside the wrong fig, I would guess that a pollinating agaonid (or other fig wasp) can oviposit and develop normally if its dimensional morphology allows it. Ramírez's example cited above supports this hypothesis, as does the apparently nontoxic nature of fig seeds. No special detoxification chemistry is likely to be needed to eat fig endosperm and associated tissues since there is no reason to suspect that mature fig seeds escape from seed predators by chemical defenses. However, escape from the wrong fig by the next generation of pollen-laden adults will be complicated if the pollen-presentation behavior is not that of the usual host, if the fig wall is too tough for the wrong males to penetrate, or if the fig development time does not match that of the wrong wasp.

A fig pollinated by the wrong wasp is a bad investment for the parent tree on two counts: (*a*) The seeds will not develop, and therefore the wasps are acting solely as seed predators; (*b*) the wasp will not carry pollen to a conspecific even if it can emerge from the fig. I therefore expect the parent tree to abort fruits pollinated by the wrong wasps (though perhaps some outcrossing with congenerics is a valuable source of novel genetic information). This again means that the purity of the wasps that emerge from a fig seed crop is not evidence of fig-wasp specificity. It would be of great interest to examine the founding wasps for a set of aborted figs from a tree in a habitat rich in species of figs.

In addition to fig pollination at a very low density of flowering individuals, extreme pollinator-specificity among fig wasps also has the consequence that as new fig species are stacked into a habitat, there is no danger of exclusion through competition for pollinators. There is the possibility of a newcomer fig producing allomone messages that overlap with those of the resident fig species, but this overlap should quickly select for character displacement of this trait. I doubt that the upper limit of fig intra-habitat species richness is set by filling of this communication channel, since the vocabulary of pheromone communication is enormous.

Since there are some 900 species of *Ficus* (21), it is probably safe to guess that there are as many species of pollinating agaonids. The most parsimonious hypothesis for the generation of these wasp species is probably the classical process of speciation in allopatry followed by later reinvasion of siblings' habitats. Since there is no pool of more generalist pollinators to service a mutant fig and its offspring, sympatric speciation processes seem unlikely. Furthermore, a rather large population of conspecific fig trees would be required to sustain a mutant population unless there are numerous simultaneous behavioral changes in the fig–wasp interaction as presently understood.

There are two places in the world where I expect agaonid pollinator specificity to break down or the fig species to stop acting like the fig described in the introduction: on islands and in very harsh environments. "There is hardly any tropical island of any size but possesses one or more species of *Ficus.* . . . In Fernando de Noronha was an endemic fig, *Ficus noronhae.* In Christmas Island *F. retusa* was abundant, and reproduced itself. Both of these, as I found, possessed abundance of gall wasps. . . . The genus is absent from the Hawaii Islands [(and see 80)], but there is a species in Fanning Island, 900 miles south, and it is absent too, from Cocos-Keeling Island, 700 miles from Java. Most of the Polynesian islands, however, possess one or more species" (99). "On the small San Andres Island (Colombia) *F. aurea* and an unknown species of fig were each represented only by a few mature trees. Very few trees showed synchronized development of syconia; usually each tree had syconia in all phases of development. Thus wasps emerging from ripe figs could find figs in the receptive stage in the same tree. Apparently in small populations selection has favored a breakdown in synchrony" (91). Ramírez did not examine enough figs to know if the San Andres fig wasps are as rigidly fig-specific as mainland wasps are reputed to be.

The colonization of islands by figs and their wasps contains a relevant paradox. A single seed from a mainland cannot start a fig population because the single tree it produces cannot sustain a pollinating wasp population. Likewise, a pollinating wasp population cannot survive until there is a population of fig trees. A very unlikely solution is for a mutant with intra-crown asynchronous flowering to be the colonist seed, followed by wasp colonization (note that the colonizing wasp will bring mainland fig pollen with it). More likely is the extension of a mainland fig-seed shadow to an island by means of fruit pigeons or bats, followed by wasp colonization of the resultant island population of the mainland fig genome. This could then easily be followed by selection favoring individuals with asynchronous intra-crown fruiting (better to be self-pollinated than not at all). Once the population had begun to act like that described above on San Andres Island, it would be island-adapted and perhaps hop from island to island through even very rare seed dispersal events. In the unfolding of such a scenario, the presence of a second species of island fig could easily favor indiscriminate use of both fig species by one species of wasp and even pollination of both figs by that one wasp with attendant convergence of fig flower and fruit traits.

Very harsh mainland environments should be similar to islands: Unpredictable weather events, as well as predictable extreme ones, could occasionally reduce severely the population either of wasps or of fig trees bearing receptive figs. Florida is such a place, being the northern limit for two fig species. Without supporting data, it has been stated that "the Florida fig wasp [*Secundeisenia mexicana*] occurs abundantly in the fruits of our two native fig trees, *Ficus aurea* and *F. laevigata.* It has not been observed in the fruits of other common [introduced] *Ficus* species, including *F. altissima, benjamina, glomerata, religiosa,* and *retusa* (=*nitida*)" (10). Assuming that *S. mexicanus* in Florida is really only one species, it can pollinate both figs. It is likely that each time a new crop of pollinating agaonids is produced in a fig tree the wasps spread out over the habitat. Those that find a fig tree of the species that did not produced them complete their life cycle but do not pollinate their fig, though they will carry pollen when they leave. Ramírez's Venezuelan case mentioned above is probably a potential intermediate step in the evolution of wasp survival without pollination, and the evolution of *S. sycomorus* in Israel (47) is another. A one-wasp-two-figs system should be facilitated by three environmental traits. First, Florida is frequently subject to weather severe enough to reduce greatly the crop of receptive figs for one of the species. This should select strongly for latitude in fig choice by wasps, latitide in ability to develop in a fig for which no conspecific pollen has been brought, latitude of retention of figs pollinated by the wrong pollen (mixed sets of wasps in single fruits may facilitate this), and intra-crown asynchrony of fig flowering. Even if the wrong pollen is brought into the fig, the next generation of wasps may carry pollen off to conspecific trees and therefore render the fruit at least a pollen donor. Second, the wasp is not endemic to Florida; it occurs in *Ficus laevigata* figs in Puerto Rico (117) and probably elsewhere in the Caribbean. Florida is therefore constantly bombarded with new agaonid colonists. If the local agaonid population were eliminated, the hosts would soon be reinvaded. The opportunity for founder effects is obvious. The colonists themselves, coming from islands, may behave as they do in Florida. Third, both of these species of *Ficus* occur on Caribbean islands and undoubtedly continually bombard Florida with seed (and vice versa). If these island populations have the same pollinator overlap as do the Florida populations, then the system did not even have to evolve in Florida since it should be functional on small islands as well as at the margins of *Ficus* distributions.

Severe conditions for figs do not occur only at the margins of *Ficus* distributions. Tropical sites with severe dry seasons may select for the use of incorrect hosts by agaonids during drought-induced loss of fig crops, especially with those species that live on dry hillsides adjacent to riparian populations that are less likely to lose their fig crops during the long dry season or during rainy season droughts. No systematic search for such an example has been initiated, but there is at least one case where such circumstances seem to have led to selection for asynchrony in the fig crown (see the following section).

There is still room for skepticism about the one-on-one relationship in some cases. In Hill's (57) discussion of the situation he presents the curious anomalous definition that

> in many cases the host species of *Ficus* occur as well-defined, and genetically distinct varieties, and in some cases also subspecies; the varieties of some species may be allopatric although it is more usual for them to be more or less sympatric. As the varieties are genetically distinct, it follows that the agaonids which pollinate these varieties must either be distinct species (or sometimes subspecies) themselves or else quite separate populations of the same species, in view of the absence of natural hybridization in *Ficus* species. Clearly, it is to be expected that the agaonids inhabiting different varieties of the same fig species will be different species themselves. The present work has shown, what has been suspected for some while, namely that the agaonids inhabiting the different varieties of the same fig species are often morphologically indistinguishable, although it is felt that usually they must be biologically distinct species.

If Hill is correct about the wasps, what a fig taxonomist calls a variety of subspecies of fig would be called a species by any contemporary zoologist. Second, it is not at all obvious how one is to know that the "varieties are genetically distinct" when no artificial crosses have been made with any of these *Ficus* species.

As an example of how these taxonomic concepts can confuse the issue, Hill's (58) revision of the agaonid genus *Liporrhopalum* contains the following case. A wasp was described as *L. rutherfordi* from a single specimen from an unknown host in Sri Lanka (Peradeniya). Hill found a wasp that was morphologically similar to this one to be common in *Ficus tinctoria gibbosa* on Hong Kong, but described it as a new species, *L. gibbosae* (which has 5 or 6 lamellae on the mandibular appendage, as opposed to 4 in the one specimen of *L. rutherfordi*). Since *F. tinctoria gibbosae* occurs only as far west as Malaysia, and since *F. tinctoria parasitica* occurs all over India and Sri Lanka, Hill concludes that *L. rutherfordi* and *L. gibbosae* are separate species because they are on different varieties of host!

The most vexing problem encountered by Hill (56) was that the Hong Kong native figs *F. pyriformis, F. variolosa,* and *F. erecta* var. *beecheyana* were pollinated by morphologically indistinguishable agaonids. In his taxonomic treatment of the Hong Kong wasps (57) he rationalized the situation by concluding that they must be three species that cannot be distinguished morphologically.

PARENTAGE OF FIG SEEDS

The prevailing opinion that mainland fig seeds are obligatorily outcrossed owning to the behavior of the wasps and the intra-crown flowering synchrony is probably reasonable. The exceptions would occur when adult fig wasps survive for 3–6 months between successive crops on one tree (doubtful) and in habitats where there is some intra-crown asynchrony. A *Ficus ovalis* tree in the deciduous forest of Santa Rosa National Park, Costa Rica, bears receptive figs at the same time it is releasing pollen-bearing wasps and therefore may self-pollinate, providing that the wasps do not have a long pre-fig-entry flight requirement (72).

Figs differ from other plants in the location of the plants they mate with. While in most plant species it is likely that plants mate most often with their nearest conspecifics in space (barring incompatability of neighbors owing to excessive genetic relatedness), figs should mate most often with plants that are their nearest neighbors in past (pollen reception) or future (pollen donation) time. The longer the wasps live, the less true this generalization. This mating pattern means that if each fig tree waits a very regular time between flowerings, each would repeatedly mate with the same individuals in the population (W. Hallwachs, personal communication) and the pollen flow would never be reciprocal. Selection should thus cause figs to wait a varying number of months between flowerings, which is what Morrison (86) found to be the case with the two commonest species of rainforest figs on Barro Colorado Island (BCI). Incidentally, the greater the asynchrony of fig-wasp reception and production within a crown, the greater the number of other fig trees with which a given tree is likely to mate.

The number of pollen-donors represented by the cloud of fig wasps arriving at a receptive tree will depend very strongly on the longevity of the wasps, the density of fig trees within their flight range, and their flight behavior. If they are mixed by air over a large area and then settle out on a fig tree in response to an attractant, a fig population would be the most panmictic of any tree species in a tropical forest, yet have the most feeble of pollinators. The large and diverse nature of the seed-dispersing coterie for many fig trees will render this panmixis even more thorough. The parent fig can strongly influence the number of parents it has for its seed crop by modifying the amount of time it bears receptive figs and then aborting figs pollinated by wasps that bore pollen that was "wrong" in some sense. An increase in the period of fig receptivity to wasps would increase the number of crops to which pollen is contributed, since it would increase the period over which pollen-bearing wasps are released from the tree.

The parent fig can also increase the number of crops to which it contributes pollen through evolution of traits that lead to a larger number of smaller wasps per fruit and an increase in the amount of pollen per fruit. For example, figs of *F. religiosa* and *F. sycomorus* produce 9–19 and 60–80 anthers per fig, respectively, while the summer caprifigs of *Ficus carica* may contain 200 male florets, each with several anthers (41). With the exception of *Ficus pumila,* which may have as many as 1000 male florets to 5000–6000 female florets in a caprifig, Hill (56) found the Hong Kong figs to have ratios of about 20–170 male florets to 150–600 female florets. In commercial varieties of *Ficus carica* caprifigs, the proportion of male to female florets varies from 2 : 1 to 10 : 1, with 7 or 8 : 1 as the normal [for 39–1350 female florets per fig (11)]. However, these ratios mean little in the absence of information on variation in numbers of pollen grains per wasp, anther or male floret. It is of interest that the agaonid that pollinates *F. pumila* is also one of the largest of its family (56).

The seed parentage within a fig fruit is somewhat problematical. With *Ficus sycomorus* in Kenya, the number of adult agaonids gaining entry to a fig ranged from 0–13, with averages of 1–4 for different small samples. In 88 figs from a single Costa Rican tree, Ramírez (92) found that a range of 1–4 and a mean of 2 agaonids had gained entry per fig. Despite large numbers of *Pleistodontes imperialis* arriving at the fig, Froggatt (33) states that only 2 or 3 females gained entry and the remainder died stuck in the ostiole. I found (73) in 3 Costa Rican deciduous forest fig crops (3 species) that 93, 53, and 52% of the figs had only one mother for the contained wasps (average of 1.07, 2.97, and 1.72 wasps per fig, respectively). A fourth crop (*Ficus insipida*) had a mean of 7.2 wasps per fig. This crop had some figs with 20–30 wasps that had gotten past the ostiole. In general, however, the number of parents available to sire the hundreds of seeds in a fig fruit may be only 1 and usually less than 4. Furthermore, I suspect that the first and second wasps to enter do most if not all of the pollinating, and therefore seed parentage is even more monotonous than a mean of, for example, 4 wasps per fig suggests. The low number of parents for the seeds in a fig means that the decision to keep or reject a given fruit after pollination may involve very few choices of parentage. If any seeds have the wrong parentage, then likely a large number do. However, there are no records of abortion frequencies in wild figs. In doing such a study, care must be taken to distinguish between fruits aborted because no agaonids arrived and fruits aborted because the wrong species of pollen-bearers arrived. Since the wasp has made an irreversible decision when it enters the fruit, there should be strong selection for the ability to choose trees that will not reject it or its pollen load. No information is available on abortion rates of fertilized fig florets within the developing fig, but aborted (unpollinated?) florets within ripe figs certainly exist.

No data have been gathered that would allow a guess about how much inter-specific gene flow occurs in figs. Ramírez (91) agrees with Corner (20) that hybrids are rare, but that statement needs quantification. Experimental crosses are needed, as are attempts to introduce wasps into the "wrong" receptive figs. Wild agaonids do make mistakes, as mentioned in the section on Fig Wasp Specificity. The presence of the wrong agaonid wasp in a fig not only labels that fig as containing potentially hybrid seed, but should also identify the putative male parent. An extensive (and laborious) examination of the specific indentity of the remains of the fig wasps in wild developing figs (before the next generation has emerged) would be of great interest.

Ira Condit (e.g. 13, 15–17) noted that "perusal of the literature relating to the genus *Ficus* reveals few if any records of natural hybridization among the various species" (14). He then puffed the pollen of *Ficus carica* into female *Ficus pumila* syconia and got viable F_1 seeds that produced two saplings large enough to make figs. "Syconia of various common figs [*Ficus carica*] pollinated with the pollen produced by the hybrid appear to be producing fertile seeds." Before we can hope to understand the importance of intra-generic pollen flow in *Ficus,* a large number of such experiments should be attempted. When matched against the flimsy data on the frequency of mistakes by agaonids, a possible cause of the apparent lack of *Ficus* hybrids becomes more obvious. It may simply be that frequent hybridization makes little impact on the phenotype represented on herbarium sheets. Fig trees are extremely similar with respect to more than fig macromorphology. I doubt that interspecific hybrids would be noticed in most cases.

LONGEVITY AND MOVEMENTS OF AGAONIDS

The assumption that female fig wasps are "short-lived" [unquantified—e.g. (91)] is based on the observation that they live only a few days in captivity. However, no biological law dictates that a small insect must have a short adult life span. The females of one of the fig-wasp parasitoids, *Philotrypesis caricae,* have a longevity of 30–35 days (79). There is no reason that pollinating fig wasps should not live as long between figs (and see the section on Phenology of Flower and Fruit Production). However, Condit (11) says that in hot, dry, and windy California fig orchards, female *Blastophaga* live only 4 or 5 hours. If fed nectar or other liquid nutrients, parasitic Hymenoptera of similar size have much longer life spans than if not fed.

If pollinating fig wasps can live for many weeks before finally locating a receptive fig, not only will their selection for maximum sexual asynchrony among individual fig trees be somewhat relaxed, but also the chances for self-pollination by a somewhat asynchronous crown should arise. Further, the longer fig wasps live, the larger becomes the breeding population of fig trees at any given moment. At the limit, if fig wasps could live the average duration of the inter-crop period for a tree, the entire population would be in flower simultaneously.

Free-flying fig wasps must be subject to the same sorts of predation and other mortalities experienced by other small flying insects. I have seen hundreds of large dragonflies (Odonata) darting in and out of the leaves of a large Costa Rican *Ficus* just as the wasps were emerging from the figs (Playa Coco, Guanacaste Province, 1969). They were presumably preying on the wasps just as they normally prey on mosquitoes.

As indicated earlier in describing Hill's work at Hong Kong, fig wasps must move long distances at times to re-colonize areas vacated by natural catastrophes. Their apparently indigenous presence on Pacific oceanic islands [e.g. Okinawa (62)] suggests that winds may on occasion carry them very great distances. Ramírez (91) gives some indirect evidence that agaonids may sometimes move distances of many kilometers between individual trees. Condit (11) feels that a wind in a California fig orchard may carry females for several miles.

While it seems that fig wasps would easily be dispersed passively by wind, the rarity of fig trees bearing receptive figs at any given moment suggests that if wasps were dispersed only passively most would die without finding such a tree. I hypothesize that the fig tree releases a species-specific allomone at the time the fig crop comes of receptive age, and I assume that the parasitoids respond to it as do the pollinating agaonids.

SEED PREDATION BY FIG WASPS

The literature contains no information on the intensity of seed predation by pollinating agaonids and the various parasites, yet this intensity is a rather direct measure of one of the prices the fig pays for pollination (the amount of resources moved into the wasp-containing floret is one of the other direct prices). Galil & Eisikowitch (37) noted that Israeli *Ficus religiosa* had *Blastophaga quadraticeps* in 94% of the short-styled fruitlets in July; in November the figure was 92%. Of the long-styled fruitlets, 5% contained the agaonid in July, and by November this number had increased to 25% (probably more wasps enter the fig as the population builds up during the summer). The Israeli *F. religiosa* figs were losing about half of their seeds to agaonids. Indian *F. religiosa* figs contain 105–113 long-styled florets amd 81–107 short-styled florets (78). However, my unpublished records for Costa Rican figs show clearly that many long-styled as well as short-styled florets produce wasps, and therefore this ratio does not aid in determining percent seed mortality. In 5 species of Costa Rican deciduous forest figs, I found the average seed mortality due to pollinators and parasites to be 41–77% (72). In one tree of *Ficus ovalis,* the percent mortality rose from 44 to 61% per fig from the beginning to the end of two presumably overlapping generations of fig wasps on the same tree with relatively overlapping asynchronous flowering.

Over a two year period, percent seed mortality per fig per crop in four crops on this tree has ranged from 44 to 77% (D. Janzen, unpublished), which suggests that percent seed mortality in mature figs may not show much variation. There are two reasons to expect this narrow range of mortality, as well as only minor inter-specific variation in intensity of seed predation by wasps. First, figs that do not receive any wasps are aborted by the parent. Those that get at least one wasp will have 200–400 of the florets pollinated, and many of these florets will receive an egg. This means that there will be few if any figs with less than 20–25% seed predation. In the survey of deciduous forest fig-seed predation mentioned above, I counted seeds in many hundreds of figs froms tens of crops; well over 95% of the figs have greater than 25% seed predation by wasps. Second, the percent seed mortality optimal for the mutualism will be a value that generates (*a*) at least enough wasp males to cut an exit hole out of the fig and (*b*) some optimum number of pollen-laden females leaving that exit. This number is unknown but likely to be large. To keep this number high while lowering the percent seed mortality would require both a strong restriction of the number of entering pollinating wasps and an increase in the number of florets. But the increased number of florets would require an increased number of wasps for pollination. It is difficult to postulate the survival of a mutant wasp that pollinates many flowers but produces few offspring. Entrapment of pollen-carrying wasps by gynodioecious figs with purely long-styled florets is probably the only possible solution, and here the gynodioecious figs parasitize the monoecious figs (i.e. their frequency probably has the usual upper limits found in parasite-host relationships).

Within a single fig, control of intensity of seed predation is achieved in part by the ostiole. I suspect it has traits that control the average number of females entering. If the wasp were purely a seed predator, I would expect the tree to abort figs with seed predation above a certain level. However, even a fig in which all seeds are killed is of value for pollen production. In fact, depending on the relative value of seed flow versus pollen donation, it may be more valuable than one with many viable seeds. The often-noted floret dimorphism is clearly a mechanism that holds the percent seed predation in a general area. Most short-styled florets produce wasps. However, as the number of female wasps per fig rises, the unoviposited floret becomes a resource in short supply and the wasps oviposit in many of the long-styled florets. This is especially conspicuous in fig species bearing very small figs. Here, the absolute difference in style length between short-styled and long-styled florets is less than in large figs and it is likely that, with effort, more of the ovaries of long-styled florets can be reached. Furthermore, many seed and wasp parasitoids can oviposit in ovaries with styles of any length, and therefore the ratio of long- to short-styled florets is again not useful in determining percent seed predation.

SEED PREDATION BY OTHER ANIMALS

In addition to the fig wasps, some other insects prey on the fig seeds. There are at least 17 species of weevils in the neotropical genus *Ceratopus* (D. Whitehead, personal communication) whose larvae feed in nearly mature figs. In Costa Rica I have found these weevils only in rainforest species with large figs. They appear to be absent from fig species with small figs and fig species in deciduous forest or riparian habitats. The larvae mine through the fig, consuming seeds, fruit wall, intact florets, and florets from which the wasps have emerged. In some samples they occupy nearly 100% of the newly fallen figs, but since I do not know whether trees abort attacked fruits I cannot determine whether this is a high percent fig attack. The larvae pupate in the soil and adults emerge within 2–3 weeks, presumably flying off in search of new crops of ripe figs. Occasional moth larvae are encountered in maturing figs. *Boetarcha stigmosalis* (Pyralidae), for example, grazes florets and seeds and may destroy as much as 30% of a crop of *Ficus ovalis* fruits in Santa Rosa National Park, Costa Rica (D. Janzen, unpublished).

Lygaeid bugs appear to be the major nonwasp seed predators of mature and maturing fig seeds. They are small and cryptic species and have been studied best in South Africa and the West Indies. From Slater's (104, 105) study of a complex of some 46 species I have extracted a list of their traits most relevant to fig biology.

1. The fig-seed lygaeids are divisible into four groups—arboreal seed predators (mostly Heterogastrinae: *Dinomachus, Eranchiellus, Trinithignus*), obligatory terrestrial seed predators, facultative terrestrial seed predators, and accidental terrestrial seed predators. That there are four groups rather than simply a set of species that forage in the fig tree and its environment suggests specialization to different stages of development of the seed crop, driven at least in part by interspecific competition.
2. The arboreal species have exceptionally long mouth parts (as long as the abdomen or longer), presumably for penetration through the fruit wall. They may be found clustered on the fruit or, when not feeding, clustered under loose slabs of bark. These are very active insects; they fly or run

quickly when disturbed. Apparently they do not go to the ground to feed on fallen figs. Not only is this fraction of the fig seed-predator guild made up largely of one lygaeid subfamily, but the tropical Heterogastrinae are almost exclusively fig seed predators [the extra-tropical species feed on mint and nettle seed (104)]. Heterogastrinae do not occur in the neotropics, but Slater (105) suspects that the widespread rhyparochromine genus *Cholula* may act in the same manner.

3. Obligatory terrestrial seed predators "appear to feed only on the fallen seeds of figs. Several of the species swarm in great numbers under fig trees [(in Jamaica, there were estimated to be over a quarter of a million *Ozophora* under a single tree)] but have never been taken elsewhere. Generally they are found directly under the tree, and their numbers decrease drastically with increased distance from the trunk. Most are extremely active insects and when disturbed, fly readily. This latter habit is very uncommon in terrestrial Lygaeidae, but in the fig fauna it occurs in members of quite distinct tribes" (105). I suspect that this skittishness prevents the bugs from being stepped on by large mammals foraging for fallen figs.

One of the most prominent obligatory terrestrial seed predators in Africa is *Stilbicoris,* a bug that not only offers a seed to a female bug as copulatory bait, but also can fly off carrying a seed, which makes it a potential seed disperser.

A second set of obligatory terrestrial seed predators are small (seldom over 2–3 mm long), do not fly readily, and appear to prey on seeds deep in the litter. They may still be present long after the fig crop is finished and the above-mentioned species have moved on. While less abundant than the above-mentioned species, they may be especially important in eliminating the remnants of the seed crop left by the bugs that concentrate at sites where seeds are very abundant.

4. Facultative terrestrial seed predators "tend to be present in relatively small numbers and to be distributed near the periphery of the seed crop" (105). They also can develop and produce eggs while feeding on other species of seeds.

5. Accidental terrestrial seed predators are rarely taken in the litter below fig trees but are found in large numbers elsewhere. They are not taken as nymphs below fig trees and probably do not breed there. Their presence is probably due to the ability of the adults to feed on seeds that are inadequate for nymphal development or facultatively to take the fig seeds while in search of seeds of higher quality for themselves or their nymphs.

6. It is common for litter-inhabiting lygaeids to be polymorphic for brachypterous/macropterous morphs. Sweet (105a) stressed that brachyptery is most strongly correlated with permanence of the habitat. "The entire fig fauna of Lygaeidae is totally macropterous" (104). The reason seems

straightforward. Fig trees produce enormous numbers of seeds in a very short time; it may then be many months before more are available at that tree. For the arboreal species, the seeds will be present for the shortest period; for species that can find seeds deep in the litter, food will be present for the longest time. By flying readily, having well-developed wings, and being ovoviparous (*Stilbicoris* does this, presumably as a way of shortening the development time), the fig-lygaeids appear well adapted to seeking out new fig crops and rapidly migrating to them in large numbers.

7. Slater (105) has noted in Africa and I have noticed in Costa Rica that *Ficus* seedlings are extremely scarce below and near the parent, despite the very heavy seed flow into the litter below fig trees.

> The absence of juvenile plants below the trees may be due, of course, to many factors (shade, toxicity, etc.) but may be largely related to the seed predation of lygaeid bugs. To judge by the size and ubiquity of the lygaeid populations, it seems possible that they are capable of destroying nearly 100% of the seed crop that falls beneath the trees.... The predominance of *Ficus sycomorus* along [East African] water courses is presumably largely due to this habitat being optimum for establishment and growth of this species. It must also be realized that seeds which fall in flowing water will escape the heavy seed predation that occurs below the trees.... When it is realized that many birds and monkeys are concentrated along water courses, and that these vertebrates are presumably an important means of seed dispersal, it is probable that the concentration of sycomore figs along such water courses is due at least as much to greater survival of seeds in such areas as to a more favorable physiological habitat (105).

I should add, however, that no one has ever recorded what fraction of the seeds in a fig seed crop are already dead owing to fig wasps and lygaeids by the time they enter a vertebrate or fall to the ground.

In addition to direct seed predators there are insects that attack ripe and nearly ripe figs to feed on some combination of seeds and fruit wall. These have been studied only in commercial situations (4, 5, 60, 84, 110).[1] In the wild, such animals probably cause the death of many seeds by rendering the fruit unattractive to dispersal agents (and see 69). *Ficus carica* figs are attacked by the dried-fruit beetle *Carpophilus hemipterus* (Nitidulidae) in the field and in storage in California and the Mediterranean region. The adults lay their eggs in breaks in the fig epidermis or enter through the opening ostiole, and both adults and larvae feed on the mixture of figs and microbes (28, 51). The adults can be trapped with baits of ripe fig mash innoculated with a variety of spoilage fungi and yeasts (114) and are probably coevolved with these microorganisms as are figs and other fruit eaters. An anthicid beetle, *Formicomus ionicus,* treats Turkish figs in the same manner (51). The larvae of moths of the genera *Ephestia* and *Plodia* attack dry figs (as well as other fruits) in storage and after they have fallen from

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[1] See (79a), encountered while this article was in press.

the tree (25, 51, 103). In Israel the Mediterranean fruit fly *Ceratitis capitata* (Tephritidae) oviposits in *F. carica* figs on the tree (50, 100). Of apple, pear, peach, and fig fruit, the fly has the shortest development time in figs (100). The larvae of the fly *Lonchaea aristella* (Lonchaeidae) also develop in Old World fig fruits (6, 50). There is a South African weevil, *Cyllophorus rubrosignatus* (Curculionidae) whose larvae apparently develop in fig fruits (81).

Ripe figs are also attacked directly by adult frugivorous insects. *Allorhina mutablis,* the large diurnal cetoniine scarab called the "green June beetle" in the southwestern United States, chews directly into ripe figs on the tree (85). The adults of the cotton leaf worm, *Alabama agrillacea* (Noctuidae), puncture Texas ripe figs with their proboscis to feed and indirectly cause premature souring of figs (61).

PHENOLOGY OF FLOWER AND FRUIT PRODUCTION

By now it should be obvious that *Ficus* sexual phenology is very different from that of other tropical trees. "Species of the genus *Ficus,* as a result of dependence for pollination on specific, short-lived symbionts (the agaonid wasps), have evolved several features to favor the continuous development of these symbionts the year around in the tropics. . . . [There is] year-around production of figs, so that in any particular area fig trees of the same species may usually be found with syconia in all phases of development, although any one tree has all syconia in the same stage. . . . Synchronization of development of all the syconia of a tree [occurs] so that usually every syconium of a particular tree is pollinated on the same day" (91). This description is probably accurate except for the population-level–selection flavor of the beginning of the first sentence. However, no detailed study of the sexual phenology of even one individual native wild fig tree, of a population of fig trees, or of an array of fig species in one habitat has been published. Furthermore, I would explain it differently: If the goal of a flowering fig is to attract a maximum number of pollen-bearing wasps that did not originate from its own figs, it should be receptive (produce new young figs) well after its wasps have left the tree, it should flower in one burst so as to maximize the amount of attractant cue while minimizing its cost per fig, and it should flower at random in the yearly cycle so as to minimize the chance of flowering at the same time as other fig trees (it cannot flower uniformly out of phase because it cannot know when other fig trees are not flowering). In addition, one cannot use ripe-fruit phenology to explain flowering phenology, or vice-versa. There is no physiological reason why the intra-crop timing of ripe fruit production has to mirror the intra-crop timing of flowering, and indeed it does not in a number of tropical tree species.

By far the best information on fig sexual phenology is contained in Hill's (56) taxonomically oriented 3 year study of Hong Kong *Ficus* and Morrison's (86, 87) 2 year study on Barro Colorado Island of wild figs as bat food. In the somewhat seasonal rainforest on BCI, Canal Zone, Morrison carefully located all the 142 *Ficus* individuals large enough to bear fruit in a 25 ha area (*F. yoponensis,* 71; *F. insipida,* 48; *F. tonduzii,* 15; *F. obtusifolia,* 5; *F. turbinata,* 1; *F. trigonata,* 1; *F.* sp. 1), counted their fruit weekly from March to November 1973, and then had them counted every other week through February 1975. Since the majority of the fig individuals were *F. yoponensis* and *F. insipida,* his generalizations were derived mainly from observations of these two species. While the published part of the study was largely based on ripe figs produced by the tree (and thus does not tell us the pattern of figs available to wasps), numerous relevant traits of the system are evident.

1. For both *F. yoponensis* and *F. insipida* a frequency distribution of the distance to the nearest conspecific neighbor of reproductive size has a peak at 20–29 m (*F. yoponensis,* n=56; *F. insipida,* n=36) with a range of 0 to 50–70 m [Figure 5 in (86)]. If the conspecific members of either of these two fig populations were in synchrony, or if a tree fruited continuously within its crown, the wasps would have to move only a short distance from their parent tree to find new receptive figs. I should add, however, that researchers on BCI regard Morrison's study area as having an exceptionally high density of fig trees.

However, "synchrony in fruiting either within or between species was not apparent. There is some suggestion of peak times for the initiation of fruiting by *F. yoponensis* in June and December. Local synchronies in the fruiting times of trees in the same area were not detected." Considering that the study area is only 25 ha in area, that for *F. insipida* there was at least one tree in ripe fruit in 22 of the 23 months of data collection, and that for *F. yoponensis* there was at least one tree in ripe fruit in 22 of the 22 months of data collection, it is evident that in some absolute sense the wasps need not live more than a month nor travel more than 700 m even when there is extreme intra-crown synchrony of new fig production.

2. The time from first appearance of the receptive figs to that of the ripe figs was about 5 weeks, and thus the generation time of the wasps is probably about 4 weeks. Ramírez (93) reports that this period for different fig species is 15–100 days but does not give the source of the information (and see 48).

3. "As many as 50 live, winged females [of agaonids?] per fig were found in several fallen, sixth week figs in 40% of the 76 fruitings from which there

were ground samples taken (86)." Where wasps are still present in a fallen fig it is likely that the fig has many fewer pollinating agaonids than normal since their presence suggests that there were not enough males to cut an exit hole. This estimate of the number of wasps produced per fig is therefore very low. Until we have a numerical study of the number of female pollinating wasps produced per fig by a wild monoecious fig species, a reasonable round number is probably about 250 per fig (based on J. T. Wiebes, personal communication, and my own unpublished observations of Costa Rican figs).

4. "The number of trees in the study area bearing prime, fifth week fruit varied from 0 to 8 per week, averaging 2.4 ± 2.0 per week. The total number of trees which came into prime fruit in any given month varies from month to month, but there is a significant correlation between the two sample years in the number of trees in fruit in any given month (Spearman rank correlation coefficient, $r_s = .675$, $p < .05$). There appears to be a particularly invariable low in figs in the months of August, September and October of both years" (86). M. Estribi (86) offers the following highly reasonable hypothesis for this seasonal low. His hypothesis is based on the assumption that the seasonal low in ripe fig production is the result of an increase in abortion of young figs owing to a failure of pollination, rather than simple nonproduction. "The incidence of aborted fruitings is correlated with the presence of insects other than fig wasps whose larvae develop inside the figs. These larvae are primarily those of two species of snout beetles (Coleoptera; Curculionidae) and several different species of Diptera. At some times of the year, these larvae become so numerous that it is possible to open fig after fig and find it eaten hollow and filled to capacity with larvae. Light trap data by N. Smythe shows that the adults of these fig parasites are most numerous from June through September. The high density of fig parasites causes a substantial reduction in the number of fig wasps available for pollinating, which in turn accounts for the abortive fig production in these months." It is not obvious why the density of nonhymenopterous fig parasites should decline after September. Fig wasps may be short-lived, but adult weevils generally are not.

5. "There was no correlation between the month an individual tree was in fruit in the two sample years ($r_s = 0.165$, $p > .05$). Further, there does not appear to be any consistent endogenous periodicity in fruiting of individual trees. The interval between fruiting varies both among individuals and within individuals. The interval between first and second fruiting is not significantly correlated with the interval between second and third fruiting for either *F. yoponensis* (Pearson correlation coefficient, $r = .057$, F-test, $p > .25$) or *F. insipida* ($r = .114$, F-test, $.05 < p < .10$). The number of crops borne by a tree per year was greater for *F. yoponensis* (1.13 ± .61) than for

F. insipida (.93 ± .46) (t-test, $p < .005$)" (86). For most *F. yoponensis* trees the interval between the first and second fruiting is 20–50 weeks; for most *F. insipida* it is 25–60 weeks. These figures are probably much closer to the real inter-fruit periods for wild figs (and see 83) than are statements such as "most species of figs yield 3 or 4 crops per year" (49); they reflect a situation quite different from the orderly progression of synchronized crops produced by *Ficus carica* and *Ficus sycomorus* in the Mediterranean region. The reader must also be careful to distinguish between statements about the population as a whole and statements about individual trees (i.e. the word "figs" is ambiguous in much of the literature).

6. "The number of figs in a full crop of figs varied from 5,000 to over 50,000 per tree, depending on crown size." It was estimated that this amounted to 114,000 and 78,000 figs per ha per year for *F. yoponensis* and *F. insipida,* respectively. If a figure of 250 female agaonids per fig is representative (see #3 above), the airspace for a hectare of this forest should contain about 20 million pollinating agaonid females per month or about 62,500 per day of the species specific to each of these two fig species. This is about 8 wasps per m^3 of the approximately 0.5 ha^3 occupied by 1 ha of forest. If a fig tree needs about 2 wasps per fig for normal pollination, and has 5000–50,000 figs in a crop, the degree of superfluity of wasp production (and competition among wasps) will depend on the unknown life span of the wasps. It would be of great interest to match these figures with the arrival rate of pollinating agaonids at each fig (to say nothing of their parasites).

While Morrison (86, 87) was interested in figs as bat food, Hill (56) tried (*a*) to document the phenology of the 17 species of indigenous figs and 4 species of introduced ones in Hong Kong from 1962 to 1964, (*b*) to collect their contained wasps for taxonomic purposes, and (*c*) to determine the wasps' host-specificity. Since Hong Kong experiences a cool winter and is on the edge of the tropics, *Ficus* sexual phenology there should be quite different from that in lowland tropical BCI. Hill checked his plants every two weeks; wherever possible he had a sample size of 10 individuals (20 if gynodioecious). Several of his findings are relevant:

1. "The female agaonids leave their respective figs and fly in search of young figs of the same species in which to oviposit; sometimes they will be able to find such figs on the same tree that bore their figs, but more often they will have to find other trees" (56). Allusions to a few figs being out of phase with the main crop on a single *Ficus* appear in places besides Hill's (56) monograph (e.g. 82). It would be very nice to have both a quantification of this phenomenon and information on the entrance rate of the wasps to these out-of-phase figs. Such figs could be extremely important for self-pollination and for wasp survival in seasonal habitats or in habitats where

the main crop is heavily damaged by other animals. On the other hand, newly emerged fig wasps may have the behavioral trait of having to fly or otherwise delay before they can (will) attempt to enter a receptive fig (much as some newly molted alate aphids refuse to feed until they have flown a certain length of time).

2. "All the banyans except *F. superba* v. *japonica* bear their fruit in the summer (including spring and autumn) and the trees are either bare, or have only small retarded crops, during the winter. *F. superba* v. *japonica,* however, has the main crop of figs during the winter, although some fruit (sufficient for insect propagation) is borne during the summer. Even in this case, during the coldest period of winter development is very retarded. *F. pyriformis* also bears the vast majority of its figs over the winter (from November to April) as does *F. pumila* and probably also *F. sarmentosa* v. *impressa.* Some species (*F. variolosa* and *F. hederacea*) tend to have a very large crop of figs in the spring, but for the remainder of the year only odd plants have fruit. And then usually quite small crops. The other species of *Ficus* bear their figs during the warmer months (from May to October) and just have sufficient fruit production over the winter to allow insect propagation" (56).

Hill's sexual phenological records imply that one can speak of successive synchronized crops within a mono-specific population of figs, and indeed he often says things like "The species had five crops per year [(*Ficus superba* v. *japonica*)], although no individual tree had more than three of these per year (16 trees observed), and even then one crop was small. More than 60% of the trees under observation had only one or two crops of figs per year; but then each tree always had crop 5 [(the winter crop)]." However, only 30% had the March-April crop, 10% had the June-July crop, 20% had the July-September crop, and 10% had the September-November crop. Whether these should be called "crops", with the ensuing implication of population-level synchrony, is not at all clear to me.

3. It is clear from Hill's data, albeit derived from small sample sizes, that most species have periods of 1–2 months of each year when there are no figs on the trees. Either the fig wasps live longer than is generally thought or they are repeatedly extinguished locally and have to reinvade from outside the study area.

> During the years of observation it was frequently found that certain species were without agaonid wasps at some times of the year, and successive crops of figs fell prematurely after only partial development. This happened twice with trees of *F. variegata* v. *chlorocarpa* and *F. hispida* on Hong Kong Island in the spring, when the last major crop ripening had coincided with a strong typhoon the previous autumn; in 1964 a group of trees under observation in the University Compound did not get any figs infested until the third crop was well developed, and then less than 5% of this crop became lightly

> infested. In the case of *F. pyriformis* so few figs were produced during the summer that when the first large crops developed in November, the vast majority of the figs fell uninfested. After continuous fig production during November and December eventually some of the figs on the observed bushes began to become infested, and after further continuous production, by March most of the bushes were carrying ripe infested figs. This pattern of events was observed over a two year period (56).

Hill also notes that the figs seem to remain receptive to agaonids for several weeks.

Hill's comments suggest that the biomass of fig production by an individual tree in a particular crop is likely to be determined by the degree of pollination of previous crops. It seems reasonable that a tree that aborts its figs at an early age will have expended many fewer resources (especially of the kind needed for maturing seeds) than a tree that carries a crop through to maturity. This may even explain why unpollinated commercial figs (*Ficus carica* and *F. sycomorus*) can have numerous successive large crops of parthenocarpic figs during the year. If they are not making seeds, they have many more resources for the production of later figs.

Aside from the multiple-species studies mentioned above, one can extract a few interesting data on fig sexual phenology from studies of individual species. However, generalized comments such as "most species of figs yield 3 or 4 crops per year" (49) are not useful here because of their ambiguity. Apropos *Ficus sycomorus* as a native tree in East Africa, Galil & Eisikowitch (39) report that a single developmental cycle lasts 6–7 weeks, but did not tell how often a single tree fruits. They imply, as do many authors, that there are plants in fruit somewhere in the population throughout the year. McClure (82) found an individual of *Ficus glabella* (Ulu Gombak, West Malaysia) to fruit once in 1960, twice in 1961, once in 1962, 1963, and 1964, and not at all in 1965. Nearby, two individuals of *Ficus ruginerva* pooled produced 2 fruit crops each year for 4 consecutive years. Another nearby tree of *Ficus sumatrana* produced 3 fruit crops per year for 5 consecutive years. Considering that each mature fruit crop lasted 2 months, the latter tree had figs on it for 50% of the year. Medway (83) gives further data on these individual trees. From 1966–1969, *F. glabella* had only 2 fruit crops, one plant of *F. ruginerva* produced 2 crops per year from 1963–1969 (except for 1968 when it had one), and the *F. sumatrana* tree continued to fruit 3 times a year until 1969.

As was discussed under "Pollinator specificity", fig trees on islands (91) and in extremely seasonal warm climates may have intra-crown asynchrony of flowering.

As an introduced plant in the Egypt-Israel region, *Ficus sycomorus* seems to be synchronized by the winter. In Egypt, the first fig crop is in April, the next in May, and the third in the first half of June. "After this there is more or less continuous production of new syconia until autumn and even throughout the winter" (8). *F. sycomorus* can have up to 6 generations of figs per year in Israel (38, 44). Does this mean that each tree fruits 6 times (as is probably possible since no seeds are produced) or that the population has 6 peaks?

DIOECIOUS FIGS

The subgenus *Ficus* contains what have commonly been called dioecious species of figs (e.g. 56). Described more accurately they are gynodioecious trees-to-shrubs and creepers. While there are trees in a gynodioecious species that bear figs with no male florets (e.g. the commercial fig of *Ficus carica*), the other morph has figs containing both male and female florets (e.g. the caprifig of *F. carica*). Apparently all caprifig florets are short-styled (11, 15, 56, 101). They may have very high levels of seed predation and may even become effectively male plants if all the seeds are destroyed.

In short, the pollinating agaonids have a normal life cycle in the figs of the trees containing both male and female florets. However, the pollen-bearing wasps also enter the figs containing nothing but female florets. They pollinate them and probe them with the ovipositor. They lay no eggs, apparently because the styles are all too long. They then die in the fig. While this process has been studied best in *F. carica* (11), it occurs in a number of wild species of *Ficus* and is thus not the result of selection by humans. Also, the large difference in edibility between Smyrna and caprifigs applies to wild gynodioecious species as well (e.g. 19). Since monoecious figs of gynodioecious species in nature commonly lose all their seeds to pollinating wasps, I expect them not to attract animals. Galil (35) gives the best account of pollination of a wild gynodioecious fig.

I expect strong selection for agaonids that are able to distinguish between the female figs and the monoecious ones. On the other hand, there should be strong selection for chemical mimicry between the two fig morphs. It seems to me that this situation is most likely to evolve where it is commonplace for many more female wasps to arrive at a receptive monoecious fig than that fig needs and where the plants are at their peak of production of figs. A mutant plant that deleted its male florets and had only long styles could take advantage of such a wasp surplus by avoiding both the male floret costs and the loss of seeds to pollinating agaonids. However, such a cheater has the disadvantage that it is reproducing only by seed and not by pollen. As the proportion of such plants rises in the population, the possibility of pollination failure for both morphs arises. Just as with ordinary sex ratios then, there should be some ideal ratio of female and monoecious plants (or figs) from the viewpoint of the fitness of the parent producing them. This ratio has never been recorded for any wild population of *Ficus*. In a planting of seed of *F. carica* in California, of 139 seedlings, 74 were caprifigs (i.e. monoecious) and 65 were Smyrna figs (female) (11). In commercial orchards, it is recommended that 3–5 caprifigs be planted for each 100 Smyrna figs (11), but here the caprifigs are harvested and hung in the Smyrna fig tree, so the wasp's search problem is eliminated. Condit also noted that in *F. carica* caprifigs it is the spring fruit crop that has the high number of male florets; in later crops there are fewer florets, and even some (short-styled) florets set seed. There is also inter-variety variation in the amount of pollen produced per fig.

DISPERSAL OF FIG SEEDS

Who eats figs? Everybody. Wild figs are famous for being consumed by a very large number of species of vertebrates. They constitute a large part of the diet for more species of animals than any other genus of wild tropical perennial fruit. Ridley (99) records 44 tropical species of birds, bats, and nonvolant mammals feeding on figs. McClure (82) lists 32 species of vertebrates feeding on the figs of a single tree of *Ficus sumatrana* in West Malaysia. Freeland (32) found that mangabey monkeys (*Cercocebus albigena*) eat the figs of five species of *Ficus* in the Ngogo Reserve, Uganda. Figs comprised 16–17% of their diet; they ate the fruit of an average of 2.4 fig species each month for 8 months of the year. In a mainland lowland tropical forest with a normal complement of 5–10 *Ficus* species, all terrestrial species of herbivorous, frugivorous, and omnivorous vertebrates eat some species of fig at some time during the year. As a working generalization, nearly all of these animals (except small parrots) disperse fig seeds rather than intensely preying on them or spitting them out directly beneath the parent tree. They therefore probably generate the most thorough and extensive seed shadows found in any vertebrate-dispersed tropical perennial. This is not to say that fig seed shadows lack high intensity peaks (see e.g. 71, 86, 87), but rather that a fig seed probably lands occasionally on every square meter of the habitat. On the other hand, the user of this generalization must keep the following qualifiers in mind: Some molars and gizzards (as in *Treron* fruit pigeons) may grind up seeds as small and hard as fig seeds. Small parrots and very small rodents extract seeds directly from the fig and crack them. I found approximately 5000 cracked *Ficus ovalis* seeds inside an adult *Brotogeris gularis* in Costa Rican deciduous forest (D. Janzen, unpublished). Some primates eat immature figs [e.g. howler monkeys (86, 87)] and therefore act as seed predators. Finally, since figs are generically easy to identify and to lump into one ecological category, and since they often grow in gardens near forest, many naturalists have not had the time or inclination to record what visits different species of figs in different parts of the forest, or even to keep the observations separate for different species of wild figs. A *fig* is not a FIG is not a **fig.**

There are several different but not evolutionarily independent reasons why figs are eaten by so many kinds of animals. They have a high nutrient value per fruit fresh weight, and much of their weight is edible flesh. The seeds are apparently not toxic even if ground up during consumption. Figs occur in very large numbers and total weights when a crop ripens. In most tropical habitats ripe figs are available at any time of year. Most species of ripe figs do not appear to contain secondary compounds that would make them available only to very specialized frugivores (dispersal agents). They occur in a variety of sizes. Given these traits, it is not surprising that certain vertebrates seem to be heavily specialized at feeding on figs—bats being the most conspicuous of these.

Nutrient Value

Figs are no exception to the general rule that it is almost impossible to find relevant analyses of nutrient content of wild fruits (e.g. 33, 102). There are three indirect measures of their high nutrient value (and see 97). First, Mediterranean fruit fly larvae develop roughly twice as fast in fresh figs as in apples, pears, and peaches (100). Second, their obvious popularity among a very wide variety of frugivores suggests that they are either exceptionally free of secondary compounds, very rich in nutrients, or both. I suspect the latter to be the case. Third, if it is really true that a number of species of bats eat a diet of almost pure figs (7, 86, 87), then they must provide a moderately balanced diet.

Of a more direct but not necessarily more biologically meaningful nature, Hladik et al (59) found that *F. yoponensis* and *F. insipida* figs were, respectively, 4.5% and 6.1% (dry weight) protein, a percentage 2–3 times higher than that of the fleshy fruit pulp of *Spondias mombin,* an anacardiaceous fruit commonly eaten by bats. However, these protein percentages are difficult to interpret. Part of the protein is derived from wasp and seed fragments still in the fig. What fraction of this protein is obtained by the bat or other animal depends on the stage of ripening at which the animal eats the fig as compared with when the investigator harvests the fruit; it also depends upon whether the animal eats the trash in the pseudolocule. The wasps may be viewed as a legitimate part of the fig, since whatever nitrogen they contain came largely from the seeds they ate and thus from the parent plant. A second and much more serious complication is that the protein analyses were done on the fig wall with the good seed included. By grinding and otherwise digesting the seeds to different degrees, different animals will get variable amounts of the total protein in the fig. I suspect that bats, for example, rarely if ever actually chew up fig seeds, and thus 4.5% is much too high a measure of the protein they can get from the fruit. On the other hand, for an animal that thoroughly grinds its food much of the seed nitrogen might well be available.

While commercial figs (*F. carica*) have undoubtedly been bred for increased sugar content, and perhaps other nutrients, their nutrient content is at the high end of the range for commercial fruits. Winton & Winton (116) tried to summarize the literature on fig-nutrient analysis. The results are reported in too garbled a manner to be of use in a study of wild fig biology.

Seed Toxicity

I have found no suggestion that fig seeds contain any toxic secondary compounds. If this is the case, it is unusual for a tropical tree seed but not surprising for figs since many dispersal agents must grind some seeds. Seed toxicity need not be incompatible with the wasps, since many insects specialize on toxic seeds (e.g. 74). However, there is the problem that a mutant with a toxic seed would have to encounter simultaneously a resistant pollinating agaonid. Fig seeds are similar to the other tiny seeds embedded in tropical fruits eaten by tropical animals (e.g. *Cecropia, Piper, Miconia, Trema, Guazuma, Macaranga,* etc) and none of the seeds of these are known to be toxic.

Size of Fig Crops

When a fig tree comes into fruit, its branches are laden heavily with figs. No comparative data are available, but fig trees are certainly in the upper end of the frequency distribution of kilos of fruit per crop per tree for all tree species. Figs are generally spheres 1–4 cm in diameter. Many species of Hong Kong figs may have tens of thousands in a crop (56). On Barro Colorado Island, fresh ripe *F. insipida, F. obtusifolia,* and *F. yoponensis* figs weigh about 9, 17, and 3 g, respectively (7). [However, Morrison (86) gives the fresh weight of *F. insipida* figs as 5.6 g and that of *F. yoponensis* as 1.8 g.] This range is representative of the majority of tropical figs. Other trees may produce many large fruits in a crop, but figs are exceptional because most of the fruit is edible pulp. Among the Hong Kong figs an inverse relationship seems to exist between the number of figs in a crop and the size of the individual figs. For example, *F. microcarpa* var. *microcarpa* has one of the smallest figs (only 150 seeds per fig) and may have up to 100,000 figs in a large crop. *F. pumila* var. *pumila* has the largest fig (up to 6000 seeds in a fig), and a large crop is 200 figs (56). Morrison (86) presents the only data that can be used for a population estimate for wild-fig crop sizes. Calculating backwards from his figures for fig trees per hectare gives an average fruit crop size of 33,731 and 42,791 for *F. yoponensis* (n=71) and *F. insipida* (n=48), respectively. This works out to 61 and 240 kg of fresh figs (with seeds) per tree per crop. Morrison (86) calculated that all the species of figs (142 individuals of 7 species in 25 ha) in the BCI rainforest site were producing about 200,000 ± 75,000 figs per ha per year (low estimate is 650 kg fresh weight figs per ha per year, or 195 kg dry weight).

In determining the amount of food available to animals, it is not clear what measure is best, if any is. In theory dry weight is closer to the "nutrient" content. However, animals do not eat nutrients, they eat figs or fig parts. The water in the fig may be an important dietary item. Furthermore, the water-solid mix may be important for digestive processes and passage rates. Finally, the resources in the fig are not of some fixed and intrinsic value. Their particular value arises in the context of all the other foods that the animal eats. In order to substantiate the subjective impression that a fig tree in fruit represents a large, high-quality food resource one must compare the animals' use of or dependence on it with their use of or dependence on other fruit crops in the forest. The ideal measure of figs' importance is what happens to the animal population if figs are removed.

A. jamaicensis *as a Fig Specialist*

Bonaccorso (7) and Morrison (86) both did their Ph.D. dissertation research on the frugivorous bats of BCI. *Artibeus jamaicensis* was the most extensively studied and appears to be a specialist on fig fruits. Space is not available to discuss these studies, but they should be read by those dealing with fig biology (and see 27, 29–31, 53–55, 76, 77, 95, 106, 115).

Size and Other Traits of Ripe Figs

Different-sized bats on Barro Colorado Island appear to collect (carry away) different-sized fruits of *Ficus insipida* (presumably on occasion from the same tree) (7). This strongly suggests the possibility that not only may a tree choose its dispersers from among the total array of vertebrates through manipulation of the average size of its ripe figs, but it may do the same by the generation of array of fig sizes within its crop. In other words, variation in the sizes of ripe figs may be due to more than just the number of figs that happen to be produced on a branch, the number of florets fertilized in a fig, the amount of water the tree has, etc. Selection may lead to a given distribution of fruit sizes. Fruit-size distributions have never been recorded for any wild fruit tree.

Hill (56) noted a large variety of fig sizes, shapes, colors, and textures among 14 Hong Kong figs that bore fruit in his 1962–1964 study. I assume that this variety is adaptive in molding the disperser coterie and that it is a product of the forces generating intra-crown variation mentioned in the previous paragraph. Hill (56) noted that the subsection *Urostigma* of *Ficus* are all banyans, large monoecious trees "usually bearing large numbers of small figs." Banyans are generally strangler figs. Their disperser coterie should be molded to generate a seed shadow that spreads the seeds among the cracks and crevices of certain trees in the habitat. Perhaps one way to do this is to produce a very large number of very small figs that will be taken by the small vertebrates (small bats and small birds, since they should be the most arboreal frugivores). The big vertebrates can also eat many small figs. If the figs are large, the reverse is not necessarily true.

Ridley (99) has rather liberally interpreted the sizes, location, and color of figs. He interprets the Old World large subterranean and ground-level figs [e.g. *Ficus geocarpa, F. cunea, F. auriculata, F. capensis* (see 16)] as probably eaten by pheasants, pigs, rodents, and large mammals. He notes that fruits of smaller shrub species (e.g. *F. urophylla, F. diversifolia,* and *F. alba*) are small and yellow to red; on low climbers (e.g. *F. punctata, F. apiocarpa*) they are large and orange or red. Most large trees have brown, purple, or green figs. He feels these are usually taken by bats. Malaysian "fruit bats do not fly low; the smaller ones (*Cynopterus*) often feed on trees 15 to 20 feet tall, but not shorter; *Pteropus* only on trees 30 feet tall and higher. . . . The larger green or brownish inconspicuous figs borne on the trunks and boughs . . . of *F. polysyce* are eaten by bats only. In that species the figs are . . . about 1 inch long. . . . I watched for some time one fine tree in Singapore Gardens when the figs were ripe, but did not see a bird ever touch them. . . . A smaller tree . . . was regularly visited by *Cynopterus marginatus,* which flew up to the tree and carried off a fig to a distant point, ate it, and flew back for another till all were gone." McClure (82) noted that the mahogany-red, golf-ball-sized figs of *Ficus ruginervia* were ignored by birds but eaten by simiang whitehanded gibbons and 2 species of squirrel (one of which appeared to select them carefully by odor).

While I have been unable to locate a detailed study of the array of animals that might visit a single fig tree and thus constitute its disperser coterie, there is ample field evidence to suggest that for some individuals and species the array of species may be quite broad. In Singapore, "When a tree of *Ficus benjamina* or *F. retusa* is covered with the small, inconspicuous, purple-black figs, myriads of bulbuls (*Pycnonotus*) and often glossy starlings (*Calornis chalybaea*) and green pigeons (*Treron vernans*) and many other fruit-eating birds appear and devour the fruit all day. . . . During the night these birds are replaced by fruit-bats (*Pteropus* and *Cynopterus*). . . ." (99).

As mentioned earlier, McClure (82) listed 24 birds ("and many others") and 7 mammals that took the figs of a single *Ficus sumatrana* at Ulu Gombak, West Malaysia. On the other hand, a nearby *Ficus ruginervia* had its larger figs taken by only 4 species of mammals and no birds.

While Morrison (86) and Bonaccorso (7) stressed the highly synchronized intra-crown ripening period for figs on Barro Colorado Island, McClure's (82) account of *Ficus sumatrana* suggests a more complex picture. He states that "all of the feeding by birds and mammals was selective, for the fruit were examined carefully and only the ripe ones eaten. Since ripening was progressive along the twigs, the tree provided a continuous food supply for almost two months during each fruiting period."

It is particularly interesting that the members of the subgenus *Ficus* (all Old World) are all dioecious "but with no external differences morphologically between gall [(monoecious figs)] and female plants, except for the differences in the shape and size of the figs, and sometimes in their colour and seasonal occurrence" (56). The gynodioecious habit might be related in some manner to subtle patterning of the dispersal coterie. What would be the consequences if the disperser coteries that visited the female trees and the monoecious ones were somewhat different? In this context it may be relevant that all species with only monoecious figs are trees. Shrubs (epiphytic) and climbers are largely restricted to the dioecious subgenus *Ficus.*

In closing this section, it should be noted that the "size" of a fig is particularly difficult to interpret. First, it is my impression that figs contain an exceptionally large pulp/seed volume ratio. The pulp nutrient/seed volume ratio is impossible to guess, but I suspect it is at the high end of the scale as well. Second, a 17 g *Ficus obtusifolia* fig may weigh the same as an *Astrocaryum standleyum* fruit (7), but chewing the thin pulp off an enormous, hard *Astrocaryum* nut may be a much more difficult (and slippery) operation than mushing up a fig containing many seeds. Third, it is possible that fig size may be evolutionarily altered by changing the size of the pseudolocule without changing the dry weight of the rest of the fig. This would be particularly important for volume-responsive dispersers.

SPECIES PACKING IN *FICUS*

When the plant genera of a mainland tropical habitat are ranked according to the number of species they contain, *Ficus* is almost always at or near the top of the list. For example, in the deciduous forest of Santa Rosa National Park, Costa Rica, there are at least 7 species of *Ficus* trees; only a couple of shrub genera (*Mimosa, Cassia*) surpass this in species richness (75). *Ficus* is one of the largest genera of woody plants in regional tropical floras. Yet in seeming contradiction to the concept of limiting similarity, *Ficus* is notorious for its similarity of flowers, fruits, seeds, leaves, and branching patterns. Once one has learned to recognize a few species of *Ficus,* one can recognize them all easily anywhere from fruit or foliage.

I hypothesize that *Ficus* has such high intra-habitat species richness because the species have no pollinators in common, can be pollinated at very low population density, fruit very asynchronously, have seeds dispersed by many vertebrates, and have many vegetative life forms.

Having no pollinator species in common, *Ficus* species can be stacked into a habitat without competing for pollinators just as can wind-pollinated plants such as grasses, conifers, oaks, etc that can also have many congeners in small areas. This should be especially important for trees that have flowering individuals at low density at the time of flowering. Because *Ficus* pollinators seek out particular *Ficus* and are not seduced by other trees as the density of a particular species of *Ficus* declines, pollination will occur at a very low density of individuals, thereby allowing both extreme intra-population asynchrony of flowering and great inter-individual distances between reproducers. The ability to be pollinated at a low density means that the tree can exist on a very scarce resource type or with a very low probability of seedling survival on a common resource type. Fig pollination differs from other pollination by animals in a way very important to successful pollination of scarce individuals in time or space. The wasp has to make only one trip between conspecifics and no trips to a nest site, to nectar hosts, or to pollen hosts. (However, fig wasps may well visit calorie-rich sources such as extra-floral nectaries or flowers.) The fig tree is therefore the most animal-like of all trees in the forest in that its mating is highly active.

By fruiting synchronously within the crown but asynchronously at the population level, and by being a relatively rare tree when in fruit, figs have a minimum chance of competitively excluding each other over the services of dispersal agents. When the fruits are edible to most of the vertebrates in the habitat, this affect is accentuated. Chances are that when one tree is in fruit, few others will be in fruit in the vicinity. The dispersal agents will therefore be divided among a minimum number of fruit-bearing trees (i.e. there will be a maximum number of dispersal agents per tree). At the opposite extreme, if all fig trees in the forest were to fruit simultaneously, the vast majority of the figs would rot beneath their parents. Incidentally, I am certain that the large crops of fruits produced by figs are at least in part possible because figs put no resources (*a*) into chemical protection of ripe seed, (*b*) into the fruit in the form of protective woody tissue, fibrous tissue, or chemicals designed to cause all but a certain small set of animals to ignore figs, and (*c*) into large flowers with nectar flow and pollen as pollinator food. To the degree that vertebrate populations are in fact maintained by fig crops, fig species even synergistically augment each other's densities. If a common species doubles the density of monkeys by its presence, for example, then several rare species may have their seeds much better dispersed if their individuals on average happen to fruit between local individuals of common species than if they were the only fig trees in the habitat. An upper limit to this process should occur when the density of any one fig species rises to a point that occasions strong competitive interactions between individual trees in fruit. The feedback should be direct. A fig tree not visited by aerial or arboreal dispersers will drop its figs directly below. If they are not eaten by terrestrial vertebrates the seeds will probably die, owing to lygaeid bug seed predation and the inadequacy of heavy shade as a site for seedling growth.

Figs are noted for many adult vegetative life forms. This implies that the seeds get dropped in many kinds of safe sites. This can be done in two ways in plants. The fruits of some plants have chemical or nutritional qualities that cause them to be dispersed by a specific part of the animal disperser guild—animals that will put the seeds in very specific places. Figs, on the other hand, appear to generate a thin sheet, with occasional peaks, of very small seeds over much of the habitat (a diffuse but thorough seed shadow). The peaks may not even be associated with particularly safe sites for a given species of *Ficus*. In this manner, fig seeds can hit very small safe sites—a resource type that may be likened to what a dandelion can hit when it subdivides apomictically each year into many small pieces (70). The locations of the small safe sites of the fig and the dandelion change from year to year, and their exact positions are unpredictable with respect to other major traits of the habitat such as the perches of certain kinds of birds.

Figs turn out to be very different from other plants. They deserve careful study for reasons besides the details of their peculiar pollination or their direct value as bat food. They are almost everywhere in the tropics and are often left standing even when the forest is cut. They should quickly provide that animal-plant interaction in the tropics about which we know the most.

CONCLUSION

A fig tree is a specialist at producing a large crop of highly edible fruits rich in small edible seeds that are dispersed into a large and thorough seed shadow. The large crops of outcrossed seeds are produced by massive pollination by minute wasps, for which there appears to be no competition among the sympatric fig species. This pollination is achieved at a very low density of flowering trees, probably by chemical attraction of the wasps. Substantial seed predation by the wasps is the price paid for the pollination service. Despite the large literature on the interactions of the wasp and fig, many major questions of natural history remain unapproached, and the system is long overdue for analyses at the level of the populations of wasps, figs, and the complex of their species to be found in any tropical habitat.

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