Figs (*Ficus* spp.) and fig wasps (Chalcidoidea, Agaonidae): hypotheses for an ancient symbiosis

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Figs and their pollinating fig wasps are dependent on one another for propagation of their own kinds. The wasps reproduce by ovipositing through the styles of female flowers within the closed fig receptacles (syconia). About half of the female flowers within the syconia of monoecious figs have styles which are longer than the ovipositors of the wasp, and they will therefore produce seeds rather than wasp larvae. Since a longer ovipositor would enable a wasp to reach more ovules and deposit more eggs, the question arises at to why longer ovipositors have not evolved.

In an attempt to answer this question, four seemingly plausible hypotheses are examined but each is shown to be problematical in some way. Consideration is then given to a fifth hypothesis which proposes that ovipositor length is constrained by abortion of syconia with relatively few seed embryos and many agaonid larvae. It is argued first that this pattern of abortion will be selected during a sustained period of heavy wasp infestation because seeds will then become scarce relative to pollen-carrying wasps. Increased expenditure by the fig on seed production would therefore be favoured by natural selection. A greater expenditure on seeds would occur if young syconia with exceptionally heavy wasp infestations were dropped and the saved nutrients invested in syconia of a subsequent crop containing average levels of wasp larvae and seeds. Provided that the energy and nutrient cost of dropping young syconia is small, the selective advantage to the wasp of longer ovipositors is eliminated in this way. A stable coexistence of figs and wasps is therefore possible. The paper concludes by discussing two general predictions of the abortion hypothesis, and how these may be tested.

KEY WORDS:—Symbiosis – pollination – sex ratio – abortion – fig wasp – *Ficus* – Agaonidae.

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INTRODUCTION

The ancestral pre-*Ficus* is thought to have had an open head of flowers with projecting styles (Ramírez, 1976; Corner, 1978) but during the Cretaceous

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period, more than 100 million years ago, the flowers became completely encapsulated, creating the classical urn-shaped receptacles (syconia) of the modern species of *Ficus* (Galil, 1977). In the modern fig species, pollen is carried into the receptacles by minute wasps of the family Agaonidae. The pollinating fig wasps (agaonids) have therefore become indispensable for the reproduction of figs. The figs too have become indispensable for the reproduction of the agaonids, since they provide the flower ovaries within which the agaonid larvae develop. Today, there are approximately 900 species of fig, each with its own species of pollinating fig wasp (Wiebes, 1979a). The great age of this symbiosis, and the large diversities of the two sets of species (Corner, 1958), show that the reproduction of both wasps and seeds in each generation must be highly stable.

During egg laying, which takes place within the syconium, the agaonid female inserts her ovipositor through the styles of female flowers and deposits her eggs in the flower ovules. She probably requires the stimulus of the flower's ovary on the tip of her ovipositor before she will release an egg (Galil, 1973a). Generally, about half the styles are longer than the female's ovipositor. These do not allow egg laying and therefore produce seed (Johri & Konar, 1956; Hill, 1967a; Galil & Eisikowitch, 1971; Ramírez, 1974; Janzen, 1979a). The ovaries of short-styled flowers develop into galls containing wasp larvae. However, both short- and long-styled flowers are potentially capable of producing seed or galls (Johri & Konar, 1956; Galil & Eisikowitch, 1971; Neeman & Galil, 1978). Since an agaonid with a longer ovipositor would be able to reach more ovaries and lay more eggs, why have longer ovipositors not evolved? In fact, the length of styles in *Ficus* has probably been shortening over the course of evolution (Corner, 1978; pers. comm.), so the further question can be asked: Why have shorter ovipositors evolved over the same period?

In this paper, four hypotheses are examined which purport to explain the evolutionary stability of the symbiosis between figs and their wasp pollinators. It is concluded that these hypotheses are not well supported by available evidence. A new hypothesis (the 'abortion hypothesis') is then proposed and ways of testing it are suggested. All the hypotheses refer to the monoecious species of fig, which bear syconia that individually contain both long- and short-styled female flowers and male flowers.

FOUR HYPOTHESES

Hypothesis 1. *There is selection in the fig for longer style lengths to maintain seed production which prevents the evolution of longer ovipositors.*

This hypothesis was suggested to me by Professor J. Galil (pers. comm.). It may be expanded in two ways. It could be argued that, despite the much greater generation time of the figs as compared with the wasp, styles somehow lengthen more quickly under selection than ovipositors, and so a favourable production of seeds can be maintained. An immediate problem with this interpretation is that no reason has been given as to why an inequality in the effect of selection might occur. In any case, even if ovipositors were so constrained as to lengthen slowly under selection, over evolutionary time one should expect competition for oviposition sites to cause a gradual lengthening in ovipositors followed closely by a lengthening of styles. However, the length of

styles has apparently been shortening during the history of *Ficus* (Corner, 1978): this argues strongly against the first explanation.

A second aspect of this hypothesis concerns the possibility that a fig population may become extinct if seed production is seriously impaired (Galil, 1973b). It might then be argued that only those agaonids with short ovipositors would avoid such a catastrophe. In the short term, an individual which inherited a long ovipositor would leave more offspring than her less well-endowed sisters, but, in the long term such strains would tend to die out because of local extinctions of the host figs. Applying Maynard Smith's (1964, 1976) analysis of selection occurring at different levels, this argument is seen to be less plausible because individual selection could act rapidly on the naturally occurring variation in ovipositor length within any population (see hypothesis 2). Also, group selection would only maintain an 'altruistic' gene which was responsible for a reduced length of ovipositor under stringent conditions of population structure. Records of long-distance dispersal by agaonid wasps (Corner, 1958; Ramírez, 1970b) and the lack of evidence for rapid extinction rates of fig tree populations provide no support for this possibility. Thus, the available evidence runs contrary to hypothesis 1.

Hypothesis 2. *The absence of intermediate length styles in the syconia of figs eliminates any selective advantage to fig wasps with slightly longer ovipositors.*

Style lengths are often described as either short or long, and may vary by 0.6–0.7 mm in length (e.g. Galil & Eisikowitch, 1968a, b). However, close examination of two Old World fig species (*F. religiosa* and *F. sycomorus*) has revealed a continuous range of styles of intermediate length, through which oviposition sometimes occurs (Johri & Konar, 1956; Galil & Eisikowitch, 1968a, 1969). There is no reason to believe *a priori* that other figs could not have intermediate length styles. It is, therefore, possible that a small increase in ovipositor length would increase the number of sites available for oviposition by any species of agaonid. Hill (1967b, 1969) noted a range in ovipositor length of 0.1 mm in several species of agaonid, which would seem to provide sufficient variation for selection of longer ovipositors through exploitation of intermediate-sized styles. I believe these data offer sufficient reason to reject the second hypothesis.

Hypothesis 3. *The ovipositor length of agaonids is closely correlated to their body size. (a) Figs which reduce the nutrient supply to agaonid larvae thereby reduce the length of ovipositor in the adult wasp. (b) Alternatively, figs may develop a narrow passage in the ostiole, so restricting entry to agaonids of small size and short ovipositors.*

The third hypothesis makes the assumption that the upper limit to ovipositor length is constrained by the body size of the wasp. Thus, should natural selection exert pressure to lengthen ovipositors, some constraint associated with body size will act as an effective ceiling on length. If this were so, one would predict that larger species of agaonid wasp in any given genus, would have longer ovipositors.

If one compares the average ovipositor length with body length across 61 species of agaonid (see Fig. 1) there is a positive correlation ($r = 0.615$, $P < 0.001$), although only 37.8% of variation in ovipositor length can be explained by variation in body length. However, within genera there are no
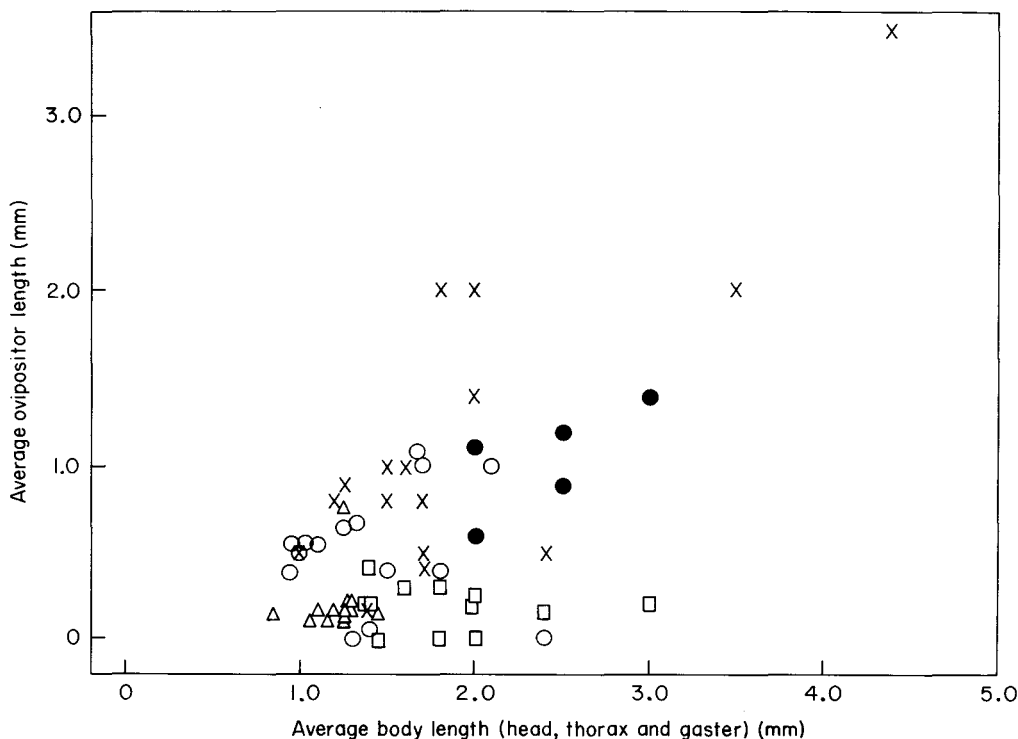
Figure 1. Ovipositor length plotted against total body length (mm) for different genera of agaonid. ○, *Blastophaga;* □, *Ceratosolen;* △, *Liporrhopalum;* ●, *Agaon;* X, miscellaneous genera. Sources of data: Hill, 1967b, 1969; Wiebes, 1968, 1974a, b, 1976, 1977a, b, 1978, 1979b, 1980, 1981; Ramírez, 1970a.

significant correlations between these two variables (*Blastophaga* $r = 0.051$, $P = 0.428$, $N = 15$; *Liporrhopalum* $r = 0.180$, $P = 0.278$, $N = 13$; *Ceratosolen* $r = -0.125$, $P = 0.349$, $N = 12$; *Agaon* $r = 0.725$, $P = 0.083$, $N = 5$). The absence of a significant association between ovipositor length and body length, at the species level of comparison, indicates that one variable is not actively constraining the other. As it is unlikely that a morphological constraint acting strongly on individuals would fail to show up in a species comparison, these results contradict the third hypothesis.

Part (a) of the third hypothesis faces another difficulty which relates to the proposed mechanism for controlling size, by restriction of the nutrients available to larvae. Such a mechanism might evolve, should small (starved) agaonids subsequently enter (1) young syconia on the parental tree, or (2) a related tree which had inherited the same system of restricting availability of nutrients. However, the former event is unlikely because of the extreme protogyny of figs and the synchrony of their fruiting. The second event, though possible, is less likely in the banyans which are widely scattered (Corner, 1958), and therefore probably not so strongly clustered in family groups.

Hypothesis 4. *A trend towards longer ovipositors is generated when several female agaonids compete for oviposition sites within one syconium. Competition is prevented by restricting the*

number of agaonids entering the ostiole and increasing the number of oviposition sites within the syconium.

The fourth hypothesis was proposed by Janzen (1979b: 16) as a possible counter to the tendency for pollinating agaonids to evolve longer ovipositors. The main problem with this hypothesis is that while it could arguably apply to figs with large syconia containing many hundreds or even thousands of flowers, it can hardly be applied to the smaller figs. Many species of *Ficus* have fewer than 200 female flowers per syconium, but newly emerged female agaonids have been variously reported with up to 149 eggs (Pemberton, 1921) and 300–400 eggs (Grandi, 1961). Fig species with small syconia are often pollinated by small agaonids (pers. obs.) which may carry fewer ova. However, in one pair of species for which data on both ova and ova sites are reported, there is evidence that the number of well-developed eggs carried by a single newly hatched female agaonid can even exceed the number of sites suitable for oviposition (Pemberton, 1921). As frequently more than one and sometimes many agaonids are found ovipositing in a single syconium (Pemberton, 1921; Galil & Eisikowitch, 1968c; Ramírez, 1970a; Janzen, 1979c), it would seem inevitable that the possession of a longer ovipositor would sometimes provide a competitive advantage. The behaviour of female agaonids when several are laying eggs in the same syconium does suggest that sites for oviposition are in short supply. Individual females may be confined to clearly delineated areas (Galil & Eisikowitch, 1969; see also Bouček, Watsham & Wiebes, 1981) or be overtly aggressive to one another (Ramírez, 1970a). The potential advantage of a long ovipositor is supported by the observation of oviposition in more long-styled flowers when several agaonids have entered a syconium (Janzen, 1979b: 29). Thus, several lines of evidence show that competition does occur among female agaonids for oviposition sites; considered together, they argue strongly against the fourth hypothesis.

THE ABORTION HYPOTHESIS

The evolution of longer ovipositors in agaonids is constrained by selective abortion of syconia with relatively few seeds and many agaonid larvae.

The idea that figs might abort syconia with excessive numbers of agaonid larvae has been mentioned previously by Janzen (1979b) and by Axelrod & Hamilton (1981). Janzen pointed out that abortion of syconia would be an adaptive response to seed predation by agaonids if the wasps were purely seed predators. However, he implies that abortion is unlikely because the wasps are valuable as vectors of pollen. In a general discussion of the evolution of co-operation, Axelrod & Hamilton (1981) state that developing fig syconia are aborted at an early stage if insufficient flowers are pollinated and too many are infested by agaonid larvae. Their idea is that fig wasps cannot 'defect' from an evolutionary co-operation with fig plants if there is effective 'retaliation'. I wish to expand on these basic ideas by considering a fifth hypothesis, the abortion hypothesis, from three different perspectives: (a) from the point of view of the fig and the selective pressure causing retention or abortion of fruit; (b) from the point of view of the female agaonids and the adaptations likely to increase their reproductive success; and (c) by examination of factors bearing on long-term stability of the symbiosis.

Economics of abortion

According to Fisher's (1958) theory of sex ratios, the expenditures of figs on their female and male gametes should be equal (an assumption being that pollen grains from different plants compete equally for stylar growth). Expenditure on female gametes includes formation of long-styled pistils and supply of nutrients to seed; expenditure on male gametes includes the formation of stamens, short-styled pistils which will contain pollen-carrying agaonids, and the nutrient supply to agaonid larvae. By Fisher's theory, if seeds become scarce in the neighbourhood of a tree because of heavy infestations by agaonids, then each seed produced by the parent plant takes on a higher reproductive value than its equivalent wasp-pollen propagule. (Most seeds will be fertilized, but most of the pollen is in excess and will be wasted.) Therefore, even though a heavily infested syconium might contribute pollen to gametes forming the next generation, a lightly infested syconium with many seeds will make a greater contribution to fitness of the fig. This inequality could lead to early abortion of syconia with the heaviest infestations if, by aborting early, energy and nutrients are conserved which may be used to produce syconia in a subsequent crop. Energy and nutrients conserved could be invested in the next crop either by increasing the number of syconia or by decreasing the interval between crops. The investment would then contribute to production of all the new syconia with their usual spread of wasp infestations. The benefit of aborting heavily infested syconia in a current crop depends on two factors: the relative scarcity of seeds to pollen-bearing wasps as determined by the productions of neighbouring fig trees; and the average ratio of seeds to wasps produced in the subsequent crop. Figs would be expected to adapt to predictable seasonal or other variation in either factor.

When agaonids are locally abundant, pollination of nearly all syconia on a plant can occur within a few days. Uninhabited syconia are then aborted while still small (Condit, 1947; Galil & Eisikowitch, 1968c; Ramírez, 1970a). I predict that abortion of heavily infested fruits occurs at about the same time. The cost to the fig in nutrient and energy losses is therefore a small fraction of that required to fully develop and ripen these fruits. Occasionally energy and nutrients which could have been used to ripen aborted figs in the current crop will be lost altogether because the plant dies before producing the next crop.

We now examine the abortion hypothesis more critically by asking what minimum ratio of seeds to agaonids is required within a syconium in order for it to be retained. To answer this question, it is helpful to introduce a simple model. Firstly, several quantities require definition:

$S =$ reproductive value of a seed as viewed by the fig

$W =$ reproductive value of a wasp as viewed by the fig (S and W will differ when either seeds or wasps become scarce)

$p =$ proportion of flower ovaries which contain seed within an unspecified syconium of the current crop

$(1-p) =$ proportion of flower ovaries containing wasps within an unspecified syconium of the current crop

$\bar{p} =$ proportion of flower ovaries which contain seed, averaged across all inhabited syconia of the next crop of that tree (it is assumed initially that all syconia will be occupied by agaonids)

$l =$ fraction of energy and nutrient investment remaining for use in the next crop after abortion of a syconium.

l is given by

$$\frac{\text{cost of mature syconium} - \text{cost of young syconium}}{\text{cost of mature syconium}}$$

$\times$ probability that tree survives between crops.

A syconium of the current crop could be aborted and replaced without loss or gain of fitness if

$$p^*S + (1-p^*)W = l(\bar{p}S + (1-\bar{p})W).$$

In this equation p^* is that critical minimal value of p for which a syconium is just retained (p^* will also have a critical maximal value, see Fig. 2). Rearranging we obtain

$$p^* = l\bar{p} - \frac{(1-l)}{\alpha - l}. \tag{1}$$

where $\alpha = S/W$, a measure of the value of a seed relative to that of a wasp. Values of p^* calculated from equation (1) reveal the range of seed to agaonid ratios which will cause a syconium to be aborted.

For example, suppose that $(1-l) = 0.2$, indicating a moderate cost of abortion, and that agaonids have evolved such long ovipositors that in the next crop they can implant ova in all but 10% of flower ovaries ($\bar{p} = 0.1$). Over time, seeds will soon become scarce and α therefore increases. For an approximate estimation, I shall assume that $\alpha = (1-\bar{p})/\bar{p}$, so that $\alpha \simeq 9.0$ in the present example. By reference to equation (1) or Fig. 2, we can then predict that any syconium with less than 5.5% seeds ($p^* = 0.055$) is likely to be aborted. It will be argued that abortion of heavily infested syconia can cause the evolution of shorter ovipositors. Assuming this to be true, then after a few agaonid generations the proportional seed content of syconia in a local population of figs will rise in response (i.e. $\bar{p}$ will rise). As seeds become more plentiful, their value to the fig relative to that of wasps declines (so α decreases). Provided that abortions still occur, it is assumed that ovipositors continue to decrease in length. Eventually a stable equilibrium is reached (at $\bar{p} = 0.37$, $\alpha = 1.7$) at which abortion is no longer profitable, even for those syconia producing no seeds at all. Two factors affect the location of this equilibrium. If the cost of abortion is high, then the equilibrium point is reached with the trees producing a lower ratio of seeds to wasps i.e. $\bar{p}$ is lower). Also, if a fig tree is isolated it is common for many syconia to remain uninhabited. There is then a greater cost to aborting figs as energy and nutrients expended in the next crop will often be wasted. As a result, p^* is lowered such that the equilibrium point is again reached with a low production of seeds to wasps.

Agaonid reproductive success

The reproductive success of a female agaonid will depend upon the number of ova deposited in flower ovaries and on a series of mortality factors affecting the larval and adult stages of her brood. External agents influencing survival
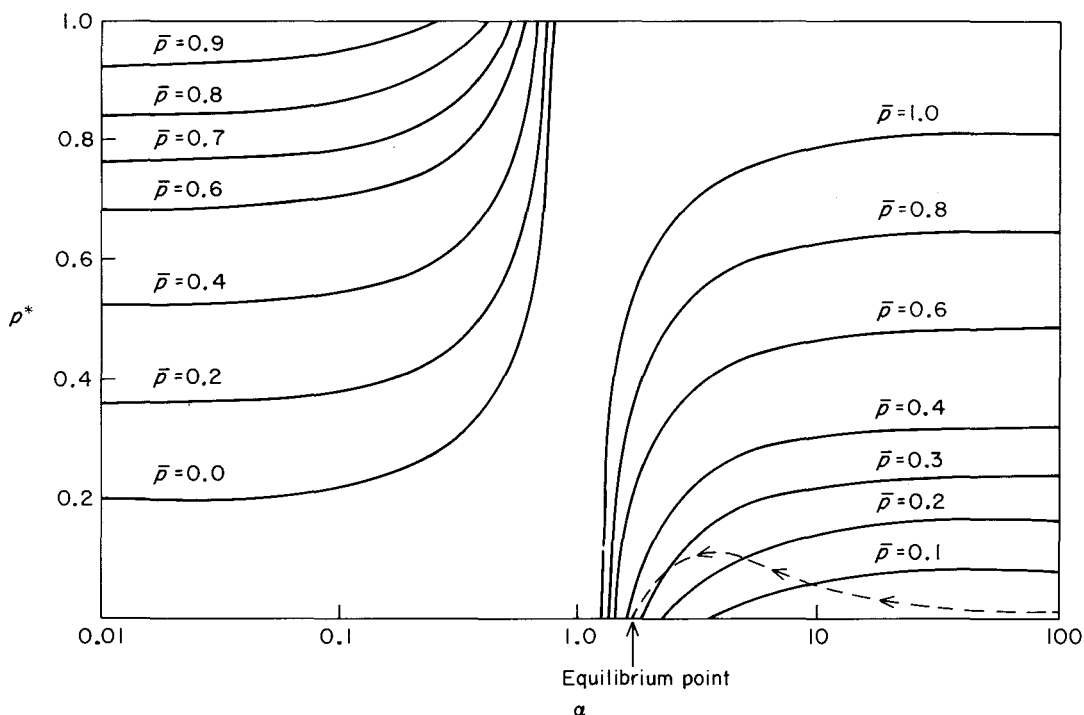
Figure 2. Curves indicating the conditions under which abortion of syconia is predicted. Continuous lines show the relationships between p^* and α for particular values of $\bar{p}$ (the average proportion of ovaries producing seed in the next crop). If a particular syconium has a proportion of seeds less than that indicated by the curves of p^* on the right-hand side of the figure, it will be dropped because of the lack of seeds. This response could therefore be caused by an agaonid foundress with a long ovipositor. If the syconium has a proportion of seeds greater than that indicated by the curves of p^* on the left-hand side of the figure, it will be dropped because of the lack of wasps. The dashed line indicates the course of evolution expected starting from a point where seeds are in short supply because of very high infestations of flower ovaries and moving towards an equilibrium point (see text for further details). The cost of abortion $(1 - l)$ is arbitrarily chosen to be 0.2 in all cases.

include larval parasites, whole fruit predators, predators of dispersing female agaonids such as insect-eating birds, and extreme climatic conditions. I suggest that the abortion of young syconia with high ratios of agaonid larvae to seeds can also be a major mortality factor when agaonids are abundant and most young receptive syconia are quickly inhabited. Furthermore, I suggest that agaonids have responded with adaptations which reduce the risk of their syconia being aborted. Before discussing these adaptations, I shall digress briefly in order to consider the possible physiological mechanism underlying abortion in *Ficus*.

In the common fig (*F. carica*), abortion is easily prevented by application of hormonal sprays to fruit or foliage (Crane & Blondeau, 1950), and it is generally implied that retention of fruit is naturally controlled by local production of hormones in individual syconia. In dioecious figs, where individual plants produce either seed-syconia (with long-styled female flowers) or wasp-syconia (with short-styled female flowers and male flowers) it is probable that both developing plant embryos and growing agaonid larvae play

a role in the production of hormones. In the monoecious *F. sycomorus*, parasitic fig wasps are capable of preventing abortion when present in syconia without seeds or the legitimate agaonid pollinator (Galil & Eisikowitch, 1968a, b, 1969; Galil, Dulberger & Rosen, 1970). As Janzen (1979b) points out, evolution of the ability to cause fig retention is not unexpected in parasitic species which never pollinate; but if it were shown that agaonids can cause retention of monoecious figs, then the abortion hypothesis would founder since the tree would be unable to abort unwanted, inhabited figs. Professor J. Galil (pers. comm.) has suggested that some results of experimental studies on the symbiosis between syconia and agaonids of *F. religiosa* point to just such an ability. Seedless syconia of *F. religiosa* (whether caused artificially by entry of pollenless wasps or naturally in the case of exceptionally small syconia) did not abort but produced mature viable wasps in both instances (Galil & Eisikowitch, 1971). However, it was noted in the same study that bagged, uninhabited syconia persisted on the tree for a long time, "ripening only shortly before the ripening of normally inhabited controls". This being so, it is not possible to deduce from the results of the study whether or not the agaonid larvae actively inhibited abortion of their syconia.

The issue which needs to be resolved is whether agaonids can cause retention of syconia which would otherwise be aborted. When a fig tree or shrub with receptive syconia is visited by a large number of agaonids, most fruit are quickly inhabited; the few uninhabited syconia drop to the ground a few days later (Condit, 1947; Galil & Eisikowitch, 1968c; Ramírez, 1970a). If the agaonids are less abundant and a majority of syconia remain uninhabited, the unpollinated fruit of many fig species persists for a long time without dropping (Condit, 1969; Ramírez, 1970b; Galil & Eisikowitch, 1971; Janzen, 1979b). It would not be surprising to find that inhabited syconia were retained in these latter conditions even if unpollinated through experimental means or if heavily infested. In the spring crop (the *profichi*) of the common fig, no naturally occuring seeds have been found, since viable pollen is lacking in the preceding winter crop (the *mamme*) (Neeman & Galil, 1978). Thus, here too is a special case where it is not surprising to find that inhabited but unpollinated syconia of the spring crop are retained. I predict that agaonids, when at moderate or high density and inhabiting syconia of wild, tropical monoecious figs, will experience losses because of abortion. I propose that the risk of abortion is minimized by natural selection of agaonids that allow production of seeds from a proportion of the flower ovaries. One way of achieving this end would be through purposeful pollination of the long-styled flowers in which successful oviposition is barred. 'Ethodynamic pollination' of long-styled flowers has been systematically observed in dioecious species of fig (Galil, 1973a), and can be inferred for monoecious species from the presence of fertile seed and the direct observation of agaonid behaviour during the oviposition and pollination phase (Galil & Eisikowitch, 1969; Galil, Ramírez & Eisikowitch, 1973).

Female agaonids could further minimize the risk of abortion by withholding oviposition after some threshold proportion of flower ovaries has been infested. However, this behaviour would require quite a sophisticated assessment to be effective, and it seems more likely that the female will follow the simple policy of ovipositing in any flower within reach of her ovipositor. Given this policy, the likelihood of abortion will rise depending on the length of the ovipositor relative

to the distribution of style lengths. The optimum length of ovipositor would then be the best compromise possible which both maximizes the number of flower ovaries in reach but minimizes the probability of abortion. Consider the case where wasps in a population have evolved long ovipositors relative to the length of styles. Seed production in the neighbourhood will soon decline leading to an increase in abortions. Under these conditions, it is easy to show that the optimum length of ovipositor is below the average length in this agaonid population. Conversely, if in another population larval production is reduced relative to that of seeds (for instance because agaonids have evolved short ovipositors), the optimium length of ovipositor is above the average length. Thus, abortion of syconia can easily reverse selection pressure on ovipositor length, but the question still remains whether this mortality factor can account for the long-term stability of the symbiosis between fig and wasp.

Long-term stability of the symbiosis

One problem in using the abortion hypothesis to explain long-term stability of the symbiosis would occur if, for example, nutrient costs of abortion were high. Then, selection would allow the retention of syconia with a comparatively high ratio of larvae to seed. In consequence, the infestation level of agaonids would be likely to rise such that the fig's expenditure on production of seeds and wasp-pollen propagules would no longer be equal. This inequality would give rise to a selective advantage for figs which produce slightly longer styles, enabling them to achieve a more favourable ratio of seeds to wasps. The conditions are now set for an evolutionary chase in which styles lengthen followed by ovipositors. The generation time of the Agaonidae is approximately two orders of magnitude shorter than that of *Ficus*. One would therefore expect the evolution of longer ovipositors to follow closely any increase in style length, as the process of selection can potentially operate 100 times more quickly in agaonids*. We can conclude that a high cost of abortion will potentially destabilize the symbiosis between fig and wasp.

It may be that the size of abortion costs has been overemphasized, and that in reality they are quite minor (J. Corner, pers. comm.). Normally, aborted figs are relatively small, and the energy and nutrients expended in their growth may be partially recovered during a period of shrinkage just prior to abscission Ramírez, 1970a). Additional resources could be reclaimed from fallen fruit after a period of decomposition (T. Caro, pers. comm.). If the cost of dropping young syconia proves to be small, then an important theoretical problem will be removed. Abortion of syconia by the fig can eliminate the selective advantage for longer ovipositors in the pollinating agaonids. Thus a stable state is reached which allows long-term coexistence of figs and their wasps.

TESTS OF THE ABORTION HYPOTHESIS

I have suggested that a mechanism has arisen in figs which in evolutionary time enables then to adjust the average level of agaonid infestation to their own

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* Nevertheless, should ovipositor length lag behind in our evolutionary chase, selection for longer styles would slow to a halt as pollen-bearing agaonids become progessively more scarce (Janzen, pers. comm.).

reproductive advantage. Two general predictions will now be discussed which enable this abortion hypothesis to be tested directly.

Prediction 1. *Syconia which drop prematurely from monoecious figs will either contain no agaonids (neither adult foundresses nor larvae) or an excess of developing larvae.*

Only one reference could be found to prematurely dropped syconia which contained agaonids (Ramírez, 1970a) and on that occasion it was assumed the wasps entered at too late a stage to prevent abscission. Also, D. S. Hill (pers. comm.) has examined a 'large number' of fallen fruits under monoecious figs in Hong Kong and found no sign of heavy infestation. Thus, the available evidence is mostly contrary to the second part of the prediction. A greater degree of certainty is desirable and could be obtained from the results of a systematic search for agaonid foundresses and their larvae in aborted syconia of wild monoecious figs. Ideally, the figs should be growing at high density with continuous production of fruit.

Prediction 2. *Agaonids with abnormally long or short ovipositors will raise fewer offspring.*

One way to test this prediction is to measure the ovipositor length on agaonids arriving at a fig tree bearing young receptive syconia, then construct a frequency distribution of these lengths and compare this distribution with two others: one to be constructed from the ovipositor lengths of corpses of foundresses found within syconia that are picked from the tree a week or two later; and the other to be constructed from foundresses found within aborted syconia. Further desirable information would come from a comparison of ovipositor lengths of single foundresses, with the numbers of seeds and larvae developing within their syconia, and the distribution of style lengths in those syconia. Well-preserved corpses of foundresses can be found within young syconia at a time when seeds and larvae are easily distinguished.

It should also be possible to test this prediction by experiment. For instance, the style lengths of flowers in syconia of *F. religiosa* collected near Delhi, India, are in the range 0.65–2.3 mm (Johri & Konar, 1956) but the range for syconia collected from the same fig species in Israel is 0.6–1.2 mm in summer, and somewhat less in autumn (Galil & Eisikowitch, 1968b). The same agaonid species (*Platysapa quadraticeps*) is known to oviposit in the majority of short-styled and a proportion of long-styled flowers in both countries. It is likely that the Indian population of this agaonid therefore has a longer ovipositor. If this proves to be so, then an alternative test of the second general prediction would be to bag a number of autumn syconia on trees of *F. religiosa* in Israel and introduce Indian wasps to some, and Israeli wasps to others, leaving a portion uninhabited as a control. A daily check could then be made for abortion of inhabited or uninhabited fruits.

CONCLUSION

The abortion hypothesis provides a theoretical explanation for the long-term stability of the symbiosis between figs and pollinating fig wasps, but so far lacks any substantial supporting evidence. The alternative hypotheses examined here are all unsatisfactory in one way or another. Since the abortion

hypothesis gives rise to clear predictions which are not difficult to test, I hope it will receive a rigorous examination in future studies.

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Note added in proof

After this paper had been completed, it was recognized that values given for the length of ovipositor in published descriptions of agaonid species, and plotted in Fig. 1 of this paper, in fact refer to the length of the third valvulae and not to the true ovipositor. (J. T. Wiebes & D. S. Hill, pers. comm.). Since the lengths of the two structures are probably closely associated in the Agaonidae, the misnomer is unlikely to affect the conclusions drawn from the correlation analysis.