



How Many Babies Do Figs Pay for Babies?

Daniel H. Janzen

Biotropica, Vol. 11, No. 1. (Mar., 1979), pp. 48-50.

Stable URL:

<http://links.jstor.org/sici?sici=0006-3606%28197903%2911%3A1%3C48%3AHMBDFP%3E2.0.CO%3B2-K>

Biotropica is currently published by The Association for Tropical Biology and Conservation.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/tropbio.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is an independent not-for-profit organization dedicated to and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact support@jstor.org.

How Many Babies Do Figs Pay for Babies?

Daniel H. Janzen

Department of Biology, University of Pennsylvania, Philadelphia, Pennsylvania 19104, U.S.A.

ABSTRACT

The percent seeds killed by pollinating agaonid wasps and their associated parasitic Hymenoptera in four species of Costa Rican deciduous forest fig trees averaged 41 to 77 percent in nine samples. No fig fruits lost less than about 25 percent of their seeds to predation, and it was commonplace for more than 80 percent of the seeds to have been preyed on in a fruit. One tree's crop was found to be sufficiently asynchronous that wasps leaving the early-maturing figs could have entered much younger figs receptive at that time; in this case, the later-maturing, and perhaps in part self-pollinated, fig crop had fewer seeds per fig and a higher percent seed predation.

THE FLORETS OF FIG INFLORESCENCES (= syconia) are pollinated only by minute wasps (Agaonidae). An agaonid also oviposits in the ovary of some of the florets it pollinates. The floret has a single-seeded ovary, and only one larva develops in each, killing the seed in the process. Additionally, various species of other parasitic Hymenoptera develop in the ovaries and then exit through the exit hole cut through the wall of the infructescence (= ripe fig) by the male agaonid wasps. Having recently reviewed the literature on the details of this interaction (Janzen 1979a), I can state with assurance that no one has asked the central question of how much does the parent fig pay for its pollination? There are at least three distinct ways to answer this question. (1) How much would the fitness of the parent fig be reduced if it were to rely on wind or some more conventional animate type of pollen movement? This question cannot be answered as the hypothetical tree in question would not be a fig. (2) How much in resources and options does it cost the tree to produce those parts of the fig associated with such specialized pollination (ostiole, floret timing, florets whose seeds are eaten by wasps, etc.)? With sophisticated ecological microenergetics and more knowledge of fig trees, this question might be approachable. (3) How many and what fraction of the offspring are paid for the pollination of their sibs? Here, I address this question.

METHODS

In many populations of *Ficus*, the fruiting individuals do not fruit synchronously with each other or in a particular season; thus a tree may be found in fruit for several short periods at almost any time of year but most of the population is not in fruit at any given time. Whenever one of these sporadically fruiting individuals was encountered, a sample of several hun-

dred ripe figs was collected from the branches or the ground beneath. A subsample of eight to 21 fruits was randomly chosen from this. Each fig was split in half through the poles and the seeds in one of the halves examined under a dissecting microscope. Intact seeds were conspicuous; they are clear ivory-yellow, hard, and often surrounded by a sticky jelly. Damaged seeds usually had wasp exit holes; seeds with exit holes or with dead wasps inside were discolored and the thin seed coat broke easily when squeezed. Less than 5 percent of the seeds were empty yet had intact seed coats; these may have been aborted, or killed by early wasp larva activity. These were counted as killed by the wasps.

All the trees whose samples are described in table 1 are in Santa Rosa National Park, northwestern Guanacaste Province, Costa Rica, except for 10899 which grows on the banks of the Rio Estanque near Bagaces (about 65 km southwest of the Park). All are in deciduous forest, riparian evergreen forest within deciduous forest, or agricultural remnants of these forests. All are large adult trees that produced crops of many thousands of figs.

All species names used in this paper are suspect, which is why the collection numbers are included in table 1. Despite Burger's monograph of Costa Rica figs (1977), they are still so poorly collected that few determinations can be made without risk of misidentification at this stage (Burger, pers. comm.).

RESULTS

It is evident that the average percent seed destruction by wasps in these wild figs (41 to 77 percent) was substantial (table 1); a round figure of 55 percent is probably reasonable for generalizations. The low standard deviation of percent seeds killed per fig is because no fig had less than 25 percent dead seeds,

and in 98 percent of the figs, greater than 30 percent of the seeds were killed.

TABLE 1. Intensity of seed predation on fig seeds by agaonid wasps and associated Hymenoptera in deciduous forest (Santa Rosa National Park, Guanacaste Province, Costa Rica).

<i>Ficus</i> species	n	\bar{X} seeds per fig	s.d. seeds per fig	\bar{X} % seeds killed per fig	s.d. % seeds killed per fig
<i>obtusifolia</i> H.B.K. 15 December 1977, 10899	20	937	113	41	6
<i>cotinifolia</i> H.B.K. 5 December 1977, 10663	20	68	18	77	16
<i>hondurensis</i> Standley 11 December 1977, 10776	20	250	67	74	14
<i>hondurensis</i> Standley 12 December 1977, 10788	20	226	55	67	15
<i>ovalis</i> (Liebm.) Miq. 6 December 1977, 10775	10	314	78	65	15
<i>ovalis</i> (Liebm.) Miq. 28 June 1977, 10551	21	279	49	54	11
<i>ovalis</i> (Liebm.) Miq. 23 June 1977, 10561	21	251	50	44	12
<i>ovalis</i> (Liebm.) Miq. 9 August 1977, 10561	20	215	37	61	18
near <i>cotinifolia</i> H.B.K. 15 August 1977, 10569	8	248	76	48	21

DISCUSSION

In a very crude sense, outcrossing (pollen donation and pollen reception) is worth 55 percent of a fig tree's offspring. No one knows what the loss of 55 percent of a fig tree's seed crop is worth in reduced fitness. However, the relationship between fig-tree fitness and seed-crop size is probably not linear (if the number of fig seeds offered to the dispersers is doubled, it need not double the fitness of the doubly fecund parent). It is, however, tempting to suggest that the seed-crop size associated with about 55 percent mortality is in the vicinity of the curve where fitness takes a severe downward dip if seed mortality is increased.

It is usual for some fruits of a species with multi-seeded fruits to be free of seed-predator damage while others lose nearly all their seeds. Fig seed predation is exceptional since there are almost no figs encountered with less than 25 percent of their seeds destroyed (2 of the 160 figs in table 1 had 19-24 percent pre-

dition). The cause is probably very straightforward. If no fig wasp gets into the fig, no pollination occurs, the fig is aborted (dehiscid), and it would not be encountered in my samples of ripe figs. If only one wasp gets in, it not only pollinates many florets but it also oviposits in many, making a low percent seed predation unlikely. The Old World dioecious figs are an exception to this generalization. In this case, the wasp is unable to reach the ovary with her ovipositor in those figs that bear only long-styled female florets, and therefore all of the fertilized florets produce undamaged seed and the fig generates no wasps.

Seed predation by agaonids differs from that of ordinary multi-seeded fruits in a second way. Given that seeds are the only items that the plant can feed the wasps (i.e., barring galls in the fig wall as an evolutionary possibility), selection will not necessarily reduce the number of seeds killed to that minimum that would be tolerated by the wasp. Some greater number of seeds killed, and therefore wasps generated, may be selected for because this will increase the amount of pollen carried away from the fig tree and because some optimal, rather than minimal, number of wasps will generate a pollen shadow with maximum fitness for the pollen donor. This optimal number of wasps leaving the fig may well be greater than the minimum number of seeds that the wasp has to kill to maximize its fitness (W. D. Hamilton, pers. comm.). In short, when offspring are part of the bill paid for a mutualistic relationship, predation intensity need not be minimized for maximum fitness of either partner.

At the moment I can neither give names nor detailed percentages, but it is clear that in many species of figs, as many as half of the wasps to emerge from the fig seeds may be parasites of the system, wasp species that do not pollinate the figs they enter or oviposit in. Therefore in calculating the cost of fig wasp seed predation, the out-going pollination service per seed killed must be substantially discounted.

Figs with better than 75 percent of their seeds destroyed were commonplace in the samples. Such high levels of predation per fig were most common in the species with small figs (1-2 cm in diameter when ripe). Presumably this circumstance is because the absolute difference in style length of short- and long-styled florets is less in small figs. Percent seed mortality is also likely to be related to the number of fig wasps that enter the fig. The mean number of female agaonid wasps gaining entry to a fig appears to vary from slightly more than 1 to about 7 among crops (Janzen 1979b, Hamilton 1979). However,

there may be behavioral barriers to ovipositing through a stigma that has already been pollinated by another wasp. This situation would prevent the percent seed predation per fig from rising past certain levels as the number of wasps to gain entry to the fig increases. Finally, the fig tree controls the upper limit of the number of seeds preyed on by controlling the number of florets with short styles (at least in the larger figs such as *Ficus obtusifolia*).

Fig seed predation by pollinators and associates generates two kinds of costs to the parent fig. First, there is the caloric cost of florets, ostiole, fruit wall, timing, et cetera. Given sufficient physiological and biochemical knowledge, this cost could be determined. Second, there is the loss of offspring. Seed predation should generate the same kinds of ecological and evolutionary consequences for fig trees as predation on young animals does for their parents. I find it very curious that the figs and wasps have not coevolved a system whereby the wasp pollinates only long-styled florets and oviposits in short-styled florets, with the fig maturing both kinds of florets.

Wild figs in general are believed to be outcrossed through the process of highly synchronized aging of fruit within the crown; at the time the fig wasps emerge from the figs, there are no receptive figs within the crown. However, I have predicted that there should be three places where figs may be self-pollinated as well as out-crossed: on islands, at the margins of the tropics (and thus the margin of the geographic

range of *Ficus*), and in areas with a long and severe dry season (Janzen 1979a). Tree 10561 (*Ficus ovalis*) provides an apparent example of the last case. At the time of the first sample, taken on 23 June 1977, there were large numbers of figs of all stages on the tree. The youngest-stage figs were receiving agaonid wasps at the same time that the ripe figs were producing them. These young figs were those that ripened for the 15 August collection of ripe fruit. Depending on the fig-finding behavior of agaonids (unknown), the young figs in June could well have been pollinated by agaonids coming from mature figs on the same tree. Whether such postulated self-pollination would also result in fertilization and production of viable zygotes is unknown. It is possible that that significantly lower number of seeds per fig in the August sample (215 as opposed to 251; $t=2.29$, 39 d.f., $p<0.05$) is due to lower seed set in self-pollinated figs. It is also possible that the higher percent and absolute number of seeds killed per fig in the August sample (table 1) was due to an exceptionally large number of agaonids entering the young figs in June from the nearby mature figs.

ACKNOWLEDGEMENTS

This study was supported by NSF DEB 77-94889 and by Earthwatch (Box 127, Belmont, Massachusetts 02178). P. DeVries aided in seed counting, G. Vega aided in fig capture. W. Burger aided in fig identification, and Horton and his friend gave psychological support. D. E. Gladstone and W. D. Hamilton offered constructive comments on the manuscript.

LITERATURE CITED

- BURGER, W. 1977. Flora Costaricensis. Family No. 52, Moraceae. Fieldiana, Bot. 40:94-215.
HAMILTON, W. D. 1979. Wingless and fighting males in fig wasps and other insects. In, Reproduction, competition and selection in insects. M. S. Blum and N. A. Blum. (Eds.). Academic Press, New York.
JANZEN, D. H. 1979a. How to be a fig. A. Rev. Ecol. Syst. (in press).
———. 1979b. How many parents have the wasps from a fig? Biotropica (in press).