How Many Parents Do the Wasps from a Fig Have?

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ABSTRACT

In three fruit crops of Costa Rican lowland deciduous forest figs, the mean number of pollinating agaonid female wasps which entered the figs was 1.07, 2.97, and 1.72 (93, 53, and 52 percent, respectively, of the figs received only 1 wasp). In these crops, the males would be quite likely to mate with their sisters since mating occurs in the fig before the newly emerged females leave. In one crop, there was a mean of 7.2 potential mothers per fig (maximum of 32 wasps per fig), and it would appear that the offspring within one of these figs would be of much more heterogeneous parentage. However, since the first wasps to enter the fig probably do most of the pollinating and ovipositing, I suspect that these figs also have only a few mothers for most of the offspring that they contain.

THE FLORETS OF FIG (*Ficus* spp.) inflorescences (= syconia) are pollinated by minute wasps (Agaonidae). Access to the florets is restricted by a series of overlapping scales blocking the entrance hole (=ostiole) to the spheroidal cavity containing the florets. The female wasps do not leave this cavity after entering. Once inside they pollinate the florets and oviposit in some of them. If the fig interior is examined before the developing florets expand and crush the remains of the wasp, it is possible to know the maximum number of female agaonids that are the parents of the set of agaonid wasps that will emerge from the florets and mate within itself inside the ripening fig. Having just completed a review of the fig-fig wasp interaction (Janzen 1979b), I can state with certainty that there is only one record (Hamilton 1979) of this interesting variable as an approach to understanding the degree of relatedness among fig females and their mates. Here I report the frequency of pollinating female fig wasps among the figs they have recently entered, for four fig crops growing in the deciduous forest lowlands of Guanacaste Province, Costa Rica.

METHODS

Several hundred immature figs were picked from the highly synchronized crop in a tree's crown. No collection bias is possible for the number of wasps inside the fig at the time of selection; all figs from a chosen branch were collected. The age of the figs was such that most of the wasps had died within the past 2-6 days and the cavity in the fig was often moist from (antibiotic?) fluid secreted into it; about 20 percent of the wasps were still alive in each sample. No further wasps would have entered the figs, but there had not yet been time for abortion of figs that had not received wasps. Substantiation of the latter statement is based on the absence of many aborted figs below the tree.

Each fig was split open and the wasps inside counted. On rare occasions, wasps were stuck between the ostiolar scales; these were almost always dead and were not counted. Only agaonids were present in the figs in these four crops.

Since the alpha-taxonomy of these fig species is still in question (K. Wiebes, pers. comm.), collection numbers, as well as the names supplied by the Field Museum of Natural History, Chicago (W. Burger, pers. comm.), are used for identification (see Janzen 1979a for another study of the same species).

RESULTS

The distribution of female wasps among the figs is recorded in table 1. In the first three crops, the distribution of wasps among the figs is significantly different from a random distribution generated by a Poisson distribution. Had the female wasps been distributed at random among the figs within each of these three crops, there would have been many more figs with zero wasps in them, and many more figs containing more than one wasp. In the fourth crop, that from *Ficus insipida*, there were too many figs in the zero category. Further, the curve is badly truncated in the area of the mean number of wasps per fig (7.2) and severely skewed to the right. An inordinate number of figs contained more than 13 female wasps.

DISCUSSION

I interpret the departure from random in the first three crops in table 1 as due to active selection of un-

TABLE 1. *Distribution of pollinating agaonid wasps among young figs.*

Ficus sp. aff. *cotinifolia* HBK 10639 4 Dec 1977	wasps per syconium:	0	1	2	3	4	5	6	7	8	9
	Obs. no. figs:	50	257	17	1	0	0	0	0	0	0
	Exp. no. figs:	132	119	52	16						
	Chi square, 2 d.f.=249, p<.001										
Ficus morazaniana Burger 10889 12 Dec 1977	Obs. no. figs:	21	58	39	12	0	0	0	0	0	0
	Exp. no. figs:	35	46	31	14						
	Chi square, 2 d.f.=11.1, p<.001										
Ficus ovalis (Lieb.) Miq. 10561 23 June 1977	Obs. no. figs:	21	80	49	15	7	2	1	0	0	0
	Exp. no. figs:	39	58	44	22	8	3	1			
	Chi square, 5 d.f.=19.9, p<.001										
Ficus insipida Willd. 10568 12 Aug 1977	Obs. no. figs:	9	21	32	50	55	63	61	56	46	29
	Exp. no. figs:	.4	3	11	26	47	68	81	84	76	61
	Wasps per syconium:	10	11	12	13	14	15	16	17	18	19
	Obs. no. figs:	34	22	17	13	12	11	5	3	4	5
	Exp. no. figs:	44	29	18	10	5	3	1	1	0	0
	Wasps per syconium:	20	21	22	23	24	25	26	27	28	29
	Obs. no. figs:	1	1	0	1	1	3	0	2	1	0
	Exp. no. figs:	0	0	0	0	0	0	0	0	0	0
	Wasps per syconium:	30	31	32							
	Obs. no. figs:	1	0	1							
	Exp. no. figs:	0	0	0							
	Chi square, 30 d.f.=>479, p<.001										

occupied figs by newly arriving female wasps. The value of such behavior to the entering wasp is that she will have no competition for the florets within the fig. If in fact there is such an advantage, there should be strong selection for the ability to recognize chemical or physical signs that a wasp had entered previously, and thereby avoid occupied figs until there were no more unoccupied figs available. One might equally argue that there should be selection for the entering wasp to leave a chemical or physical signal that would "repel" wasps that arrive later. However, there should be strong selection for the arriving wasp to ignore such signals if there are no unoccupied figs yet to be located.

In the fourth crop in table 1 the same observations apply, but it is evident that figs with many wasps are being selectively chosen for entry by arriving females, with the result that there are too many figs in the upper end of the distribution. I suspect that the passage of several wasps through the ostiolar scales makes subsequent passage much easier, and therefore figs with moderate numbers of wasps become sinks for wasps.

In the first three crops, 93, 53, and 52 percent of the figs had only one mother for the agaonid wasps that each would have produced (the figs with no wasps would have been aborted and are therefore excluded from this calculation). In these three crops, there was an average of 1.07, 2.97, and 1.72 mothers per fig with at least one wasp, respectively. In short, a very substantial fraction of the female fig wasps emerging from these figs would have mated with their brothers. Furthermore, when the male wasps cut the exit hole through the side of the fig fruit, they commonly free not only their mates but their sisters. If there is more than one clutch of agaonids in a fig, I wonder if the males team up with their brothers, or with just any male to cut the exit hole. Sometimes, two or more exit holes are cut through the side of a fig, and these might have been cut by different groups of clutches of brothers working separately. However, Hamilton (1979) notes that males of pollinating agaonids are exceptional among the wasps in figs in not fighting among themselves, and it seems likely that they may cooperate even if not brothers. Cutting the exit hole has a fitness cost to the male even though it is not done until most or all of the mating has occurred; energy and structure that could have been used for mating must be used to cut the exit hole just before the male wasp dies.

The crop from *Ficus insipida* had a mean of 7.2 potential mothers per fig. The opportunities for outcrossing by the male wasps appear to be much higher in these figs than in the other three crops. However, all pollinating agaonids do not arrive simultaneously inside the fig. I suspect that the first couple of wasps to arrive do most of the pollinating and most of the ovipositing. If this is so, even figs with many potential mothers would still produce only 1-2 clutches of males (this figure applies to the fig crops with a lower mean number of mothers per fig as well). On the other hand, if late-arriving females can somehow displace their conspecifics, the resulting males from many clutches may actively avoid mating with their

sisters even when there is competition for mates within the fig, since many of the females will not be sisters. In the three crops with low numbers of potential mothers per fig, a male that avoided its sisters would be in danger of having no mates. Of course, as Hamilton (1979) has emphasized, the natural history of the system is such that there are probably selective pressures favoring strong inbreeding among fig wasps.

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LITERATURE CITED

HAMILTON, W. D. 1979. Wingless and fighting males in fig wasps and other insects. *In* M. S. Blum and N. A. Blum. (Eds.). Sexual selection and reproductive competition. Academic Press, New York.

JANZEN, D. H. 1979a. How many babies do figs pay for babies? Biotropica 10: 48-50.

———. 1979b. How to be a fig. Ann. Rev. Ecol. Syst. (in press).