Are Mating and Mate Competition by the Fig Wasp *Pegoscapus assuetus* (Agaonidae) Random within a Fig?[1]

Female-biased sex ratios are often observed in parasitic Hymenoptera that mate within small, isolated groups before dispersing to colonize new hosts (Hamilton 1967, Charnov 1982). In these groups there is both mating between sibs and competition among brothers for mates. Much theoretical attention has been devoted to predicting the sex ratio within the groups for the population structure that occurs in these parasitic wasps (reviewed by Charnov 1982, Frank 1983a). Recent theoretical studies indicate that the proportion of males is negatively correlated with the relatedness among males competing for mates and with the relatedness between mates (Borgia 1982, Colwell 1982). The predicted sex ratio (males : females) for diploid organisms is $1 - \alpha : 1 + \beta$, where α is the proportion of competitive interactions between brothers, and β is the proportion of matings between sibs (Frank, unpub. ms.). An untested assumption of previous quantitative models (e.g., Hamilton 1967, Taylor and Bulmer 1980, Colwell 1981) is that mate competition among males and mating occur randomly within a local group. Random mate competition and mating within a group means that if the proportion of sibs in the group is ρ, then sib mating is expected with probability ρ, and ρ of the interactions among males will be between brothers. If a group is founded by n egg-laying females, each producing the same number of eggs, then $\rho = 1/n$, and the predicted sex ratio is $1 - 1/n : 1 + 1/n$, or, given as males/total, $(n - 1)/2n$. This is Hamilton's (1967) widely cited result for diploid organisms. The predicted sex ratio for haplodiploid organisms such as fig wasps is slightly more female-biased than for diploids (Hamilton 1979, Taylor and Bulmer 1980, Frank 1983a).

Two empirical studies have been published that report female-biased sex ratios in fig wasps correlated with mate competition and inbreeding (Hamilton 1979, Frank 1983b). Neither study concerned itself with the assumptions of random mate competition and mating in local groups. In this note I report the results of an experiment that yielded correlative evidence inconsistent with these two assumptions.

A monoecious fig (*Ficus* spp.) is a globular inflorescence containing hundreds of staminate and pistillate florets lining a nearly sealed cavity. A few female fig wasps (Agaonidae) enter the fig through a narrow passage (ostiole), and once inside, never leave. They pollinate many of the pistillate florets with pollen carried from the fig from which they emerged, lay an egg in the single-seeded ovary of some of the pistillate florets, and then die. Each larva develops by eating the tissues associated with the developing seed or the seed itself. About one month later the next generation of wingless males emerges and mates with the eclosed females while the females are still in the individual florets. A male gains access to a female within a floret by chewing a hole through the wall of the ovary and inserting his telescoping abdomen. Usually 1–4 females enter each fig (97% of the figs of *Ficus citrifolia*, Frank 1983a; 98% of the figs of *F. cotinifolia, F. morazaniana,* and *F. ovalis,* and 29% of the figs of *F. insipida,* Janzen 1979a), and one-quarter or more of the progeny within a fig are likely to be sibs. After mating, the males chew an exit tunnel through the wall of the fig. The females leave their florets, collect pollen, then depart through the exit tunnel to find other figs and begin the cycle again. See Janzen (1979b), Wiebes (1979), and Frank (in press) for further details of the natural history.

The assumptions of random mate competition and mating within figs are difficult to test directly for fig wasps. (Here 'random' means uncorrelated with respect to genetic relatedness.) The fig, which contains the local mating group, must remain sealed until the males emerge and begin to mate. During mating, the movement of the males may be observed by cutting open a fig; however, no method has been developed to determine which wasps are sibs. In order to test for a possible searching pattern used by the males, a simple experiment was performed. The null hypothesis tested was that male movement while searching for mates is uncorrelated with the location of (i) related females, (ii) related males, and (iii) any other cues that allow a male to discriminate between a fig in which he was born and a foreign fig.

Ficus citrifolia figs containing *Pegoscapus assuetus* wasps searching for mates were selected haphazardly from trees in the Everglades Park, Florida, and brought into the laboratory during June, 1982. Two figs were chosen, and only one-half of each of the two figs was used in each trial. From one-half of each of the two figs a male was chosen and marked with Testors enamel paint. Each marked male was then returned to the fig-half from which it was taken (designated 'own fig,' or 'O'), or was placed in the fig-half from which the other marked male was obtained (designated 'not own fig,' or 'N'). The two fig-halves, each containing one marked male and many unmarked males, were then joined with insect pins for 60 minutes. After this time elapsed, the location of each marked male was determined as either 'own fig-half' (O) or 'not own fig-half' (N).

TABLE 1. *Mating area preference for male fig wasps. See text for details.*

Start		No switches	One switch	Two switches
	O,O	15	9	3
	N,N	5	15	4

The data are reported in Table 1. The rows designate whether both experimental males began a trial in their own fig-half (O,O) or in the fig-half that is not their own (N,N). The columns are defined as follows: (i) if both males finished the trial in the same fig-half in which they began the trial, 'no switches' was recorded for that trial; (ii) if one male finished the trial in the same fig-half in which it began the trial and the other male finished in the opposite half from which it began, 'one switch' was recorded; and (iii) if both males finished the trial in the opposite fig-half from which they began, 'two switches' was recorded. For example, if a trial started (O,O) and no switches occurred, then the finish was (O,O); if one switch occurred, the finish was (O,N); and if two switches occurred, the finish was (N,N). The standard contingency table χ^2 test yields $\chi^2_{(2)} = 6.4889$ ($P = 0.039$) when testing the null hypothesis that the location of a male at the end of the trial was independent of the fig from which that male was reared versus the two-sided alternative that either a positive or negative correlation exists between final location and the fig from which a male was reared. The data suggest that males spend significantly more time in the fig-half from which they were reared than in a fig-half from which they were not reared.

A control was performed to test the efficacy of the design. First, it was noted that the observed probability of switching fig-halves during the experiment, when both types of starts (N,N or O,O) are counted, is 38/102, or 37 percent (Table 1). The experiment was repeated, except that the two marked males were returned to randomly selected fig-halves that belonged to neither male. The prediction was that a male would change fig-halves 37 percent of the time, the average rate of exchange over both types of switches (N to O and O to N) in the first experiment. Switches were observed in 14 of 32 trials, or 43 percent. These two rates of exchange are not significantly different ($P = 0.52$, using a test for the equality of two percentages given by Sokal and Rohlf 1969, p. 607). This is independent evidence that the observed trend in male movement is real, and not an artifact of the experimental design.

The results show that a male prefers his own fig-half over a foreign one. Exactly what attracts the male is not clear. If males are attracted to cues within their natal figs independent of relatedness to other wasps, then there is no effect on the predicted sex ratio. If, however, the cue is positively correlated with the males' tendency to mate with sibs, then the predicted sex ratio becomes even more female biased, since β increases (see first paragraph). Inbreeding biases the sex ratio towards females because, to a parent, the reproductive value of a totally inbred daughter is twice the value of an outbred one; an inbred daughter carries twice as many of a parent's genes as an outbred daughter. This is the much discussed two-fold cost of sexual reproduction (reviewed by Maynard Smith 1978). This inbreeding effect assumes that a male's only investment in offspring is sperm, and that a single male can potentially mate with many females. Both of these assumptions appear to be true for fig wasps. For haplodiploids, increased inbreeding further increases the predicted proportion of females (Hamilton 1979, Frank 1983a). The observed sex ratios in both empirical studies (Hamilton 1979, Frank 1983a) were more female-biased than predicted under the random mating assumption. Finally if the males try to remain with groups of their male sibs, then implications for the sex ratio are unclear. The proportion of competitive interactions among brothers, α (see first paragraph) would increase; to a parent, increased competition among sons reduces the reproductive value of each son and thus reduces the predicted proportion of males. However, one can easily imagine possible benefits to individual males that move in brother-mating groups. For example, in a cooperative brother group little time may be wasted on jostling with nearby males, so an individual's reproductive success might be increased.

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