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Sex ratio and foundress number in the parasitoid wasp *Bracon hebetor*

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Abstract. As predicted by the theory of local mate competition, the offspring sex ratios of many parasitoid wasps become increasingly male biased as the number of conspecific females ovipositing in a patch rises. The braconid wasp *Bracon hebetor* appears to be an exception. Recent experiments have suggested that wasps ovipositing in the presence of a conspecific female produce more daughters than solitary wasps. Larval competition is more intense when two females oviposit together and it has been suggested that females lay fewer sons in these circumstances because the resultant small males have poor mating success. Experiments are reported that (1) compare the sex ratio of solitary and paired *B. hebetor*; (2) investigate the importance of differential mortality and (3) explore the relative mating success of small and large wasps. Paired and solitary wasps produced the same sex ratio and there was no evidence of differential mortality. Small males were able to mate both large and small females and, at least in the laboratory, appeared to suffer no disadvantage in competition with larger males. There are statistical problems with some previous analyses of sex ratio and foundress number in *B. hebetor*, and there are also problems in making inference about adaptation from inbred strains of a naturally outbred species.

Much of the empirical support for the theory of sex allocation has been obtained through experiments with parasitoid wasps. Like other Hymenoptera, female parasitoid wasps are able to control the sex of their offspring at oviposition by fertilizing or not fertilizing the egg. The ability of the mother to determine the sex of her offspring allows natural selection to influence female behaviour to produce sex ratios adapted to local conditions. Biased sex allocation patterns are common among parasitoid wasps and, in large part, are successfully explained by sex allocation theory (Charnov 1982; Waage 1986; King 1987; Werren 1987; Godfray 1993).

One of the most important factors influencing parasitoid sex ratios is local mate competition (Hamilton 1967). Mating frequently takes place between siblings, and sons often compete together for mates. In these circumstances, the mother obtains diminishing fitness returns from the production of sons and the evolutionarily stable strategy (ESS) is for the sex ratio to be biased towards females. The extent of the female bias depends on the severity of competition between siblings. Hamilton (1967) showed that if mating occurred randomly between the progeny of n females (called foundresses), each of whom produce the same number of offspring, the ESS sex ratio is $(n-1)/2n$. When $n=1$, this expression predicts a sex ratio of zero which is interpreted as only enough sons to fertilize the female's daughters; for $n>1$ the sex ratio becomes progressively less female biased, approaching 0·5 as n becomes large. This result applies exactly to diploids. In haplodiploid species, mating between siblings causes the mother to share more genes with daughters than with sons; the increased coefficient of relatedness of daughters to mothers selects for a small extra female bias in the ESS sex ratio (Hamilton 1979; Taylor & Bulmer 1980). Hamilton's (1967) original model has been extended in many directions (e.g. Taylor 1981; Frank 1985, 1986; Nunney & Luck 1988) and has been tested both experimentally and using comparative data (for reviews see King 1987; Godfray 1993). For example, a number of workers have manipulated or observed natural variation in foundress number and found that progeny sex ratio varies in line with theoretical predictions (Werren 1983; Waage & Lane 1984; Frank 1985; Herre 1985, 1987; King & Skinner 1991; though see Orzack 1986 for a dissenting view of the explanatory power of theory).

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