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Intersexual sibling interactions and male benevolence in a fig wasp

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We studied interactions between males and females of the Australian pollinating fig wasp, *Pleistodontes imperialis* (Chalcidoidea, Agaonidae), in *Ficus platypoda* (Moraceae). As for many other fig wasps, all mating occurs within the confines of a syconium before females depart. We show that initially there is scramble competition between males for access to virgin females. During this time males excavated a small hole into a female's gall to mate through. These holes were just large enough for insemination, but not large enough for females to exit their galls. Males ignored mated females, and as virgin females became scarce males switched strategies and began to enlarge insemination holes until they were large enough for females to escape, showing that males enhance female fitness by means other than just mating. Syconia with experimentally reduced numbers of males had fewer liberated females, suggesting that female fitness is strongly affected by the number of males present. Females may be unable to escape their galls unassisted because of morphological adaptations to syconium founding. We argue that sex allocation should be affected not only by competition among males but also by intersexual interactions between siblings. This could potentially offset the strong female bias predicted by local mate competition.

The vast majority of animal species allocate equal resources to male and female offspring and the selective factors underlying this phenomenon are well understood (Fisher 1930; Shaw & Mohler 1953). Consequently, animals with a population-wide sex allocation bias attract added attention because of their relative rarity and, more importantly, because they tend to flag unusual life history or behavioural traits. Deviations from equal sex allocation have been attributed to a variety of factors, mostly involving competitive or cooperative interactions among close relatives of one sex or the other (e.g. Hamilton 1967; Clark 1978; Frank 1987, 1990; Clutton-Brock et al. 1982; Seger & Charnov 1988; Crozier & Pamilo 1996). Although mechanisms leading to such biases are behaviourally and ecologically diverse, Taylor (1981) elegantly showed that such phenomena can be understood as special cases of four fitness interaction types, involving interactions between sisters or between brothers (intrasexual siblings), and the reciprocal interactions between sisters and brothers (intersexual siblings). The most familiar phenomena involve intrasexual competition, namely local mate competition (LMC; Hamilton 1967) and local resource competition (LRC; Clark 1978).

Intrasexual sibling interactions are expected under diverse situations since members of the same sex often have similar life history strategies. However, intersexual sibling interactions are comparatively uncommon because reproductive strategies and ecological requirements often differ between males and females. Indeed, fitness interactions between brothers and sisters that could bias sex allocation remain speculative, but have been suggested in some cooperatively breeding birds where adult males act as helpers-at-the-nest (Emlen et al. 1986). Allocation bias from such interactions could arise if investment in males affects mean fitness returns through daughters, and vice versa (Toro 1982).

Fig wasps are haplodiploid and arrhenotokous, and mothers control their offspring's sex by regulating sperm access to eggs during oviposition (Charnov 1982). In the fig/fig wasp system, one or a few gravid, pollen-bearing female pollinator wasps enter the fruit-like syconia of figs and pollinate the flowers while laying eggs within some of them. A single egg is deposited per flower, and the larvae consume the seed and develop within the seed coat. After adult eclosion, the wingless males burrow out of their galls and search for galled females to mate with, after which females disperse. Since foundress numbers are

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