



Fig wasps from the centre of figs have more chances to mate, more offspring and more female-biased offspring sex ratios



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Pollinator fig wasps serve as useful empirical models for studies of sex ratio evolution because females adjust their offspring sex ratios in relation to the number of foundresses that share a fig. Placement of pollinator offspring within figs is not random and more centrally located flowers are more likely to support pollinator development. We compared components of fitness of female fig wasps developing in central and peripheral flowers and whether this influenced the sex ratios of their offspring. We used *Ceratosolen solmsi marchali*, a pollinator of the Asian dioecious fig tree, *Ficus hispida*. Mating frequency was determined from the number of mating holes in females' flowers. Most females mated once, but some had the opportunity to mate up to four times and multiple mating opportunities were more frequent among centrally located galls. Body size was not linked to flower location, although the females that mated most were significantly larger than others, and came from significantly larger galls. Females that had multiple mating opportunities produced more daughters but similar numbers of sons, resulting in more female-biased broods. These females are likely to have produced more offspring because of their larger size but may have also benefited from mating with more males. The results demonstrate that differences in the natal locations of foundresses can modify offspring sex ratios and obscure sex ratio adjustment in response to the number of foundresses sharing a fig.

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Sex allocation strategies are a productive field of study in evolutionary biology because they allow empirical, quantitative tests of theory based on optimality predictions (Flanagan, West, & Godfray, 1998; Moore, Zavodna, Compton, & Gilmartin, 2005; Orzack, 1990). Since Hamilton (1967), the proportion of male offspring in spatially structured mating populations has received particular attention. Under these local mate competition (LMC) conditions foundress females are predicted to produce a female-biased offspring sex ratio because it reduces competition between sibling males for mates, but as foundress numbers increase a less female-biased offspring sex ratio becomes optimal. Numerous empirical studies are in broad agreement with this expectation (Hardy, 2002; West, Reece, & Sheldon, 2002).

The unusual biology of the fig wasps (Hymenoptera, Agaonidae) that pollinate fig trees (*Ficus* spp., Moraceae) has led to their widespread use in studies of sex ratio selection (Hamilton, 1967; Herre, 1985, 1987; Kathuria, Greeff, Compton, & Ganeshiah,

1999; Moore, Compton, Hatcher, & Dunn, 2002). In haplodiploid organisms such as fig wasps and most other hymenopterans, fertilization of the eggs results in the production of diploid females, whereas unfertilized eggs result in haploid males (King, 1987; Werren, 1987). Mated female fig wasps produce highly female-biased broods but, in line with theory, the extent of this bias is often found to vary between figs according to the numbers of foundress females that entered to lay their eggs. Foundress numbers determine the extent of LMC within individual figs and also, more generally, determine average levels of inbreeding for each species. Qualitative agreement has regularly been achieved between empirical data and model predictions that incorporate these factors, although some of the biological assumptions of simpler models have been questioned and the quantitative fit is often poor (Greeff, 2002; Herre, 1985, 1987; Kathuria et al., 1999; Molbo, Machado, Herre, & Keller, 2004; Moore et al., 2002; Nelson & Greeff, 2009; West, Murray, Machado, Griffin, & Herre, 2001).

Sex ratio adjustment in insects is often achieved by a 'male eggs first' strategy, whereby male eggs are laid at the start of an oviposition sequence, after which mostly female eggs are laid (Hokyo,

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Shiga, & Nakasuji, 1966; Strand, 1988; Waage, 1982; Waage & Lane, 1984). This produces sufficient males for all the females to be inseminated and results in progressively more female-biased sex ratios as the clutch size increases. An increasing number of fig wasps are now known to lay mostly male eggs first, including species of *Kradibia* (= *Liporrhopalum*) (Raja, Suleman, Compton, & Moore, 2008), *Ceratosolen* (Sun, Wang, & Hu, 2009) and *Pegoscapus* (Ramírez, Monge-Nájera, & Chavarría, 2009). This produces changes in offspring sex ratio in response to an increase in foundress number because the average number of offspring produced per foundress declines, and most of these later offspring would have been females (Moore et al., 2005; Raja et al., 2008; Yu & Compton, 2012). In species in which male eggs are laid mainly at the start of an oviposition sequence, any factors that influence clutch size, in addition to the number of foundresses sharing a patch, will also modify offspring sex ratios, and additional more direct responses to the presence of other females have been detected (Greeff & Newman, 2011). The number of eggs a fig wasp carries when emerging from a fig correlates with her body size (Ghara & Borges, 2010; Moore & Greeff, 2003) suggesting that in the absence of oviposition site limitation, larger females should produce more female-biased sex ratios. Body size can be influenced by the location of the wasp's (galled) natal flower, with smaller wasps produced from more peripheral ovules (Dunn, Yu, Ridley, & Cook, 2008).

The combination of preferential oviposition into shorter-styled flowers and the laying of mostly male eggs first leads to the relatively small numbers of male offspring tending to be concentrated towards the centre of a fig, with female offspring distributed in progressively longer-styled flowers as foundress number increases (Compton, Rasplus, & Ware, 1994). In dioecious figs, style length variation is not pronounced, but a concentration of male offspring towards the centre of the figs is achieved through the elongation of gall pedicels containing male offspring, probably because these were the first flowers to be galled (Yu & Compton, 2012). The major natural enemies of pollinator fig wasps are nonpollinating fig wasps, which either destroy pollinator larvae or compete with them for oviposition sites (Al-Beidh, Dunn, Power, & Cook, 2012; Dunn, Segar, et al., 2008; Yu & Compton, 2012). Nonpollinating fig wasps mainly oviposit from the outside of the figs, making more peripheral flowers more vulnerable to attack. As a consequence of the different distributions of pollinator offspring this can result in differential mortalities and changes in their realized sex ratio, because female offspring are more likely to be killed (Pereira & Prado, 2005).

Male fig wasps emerge from their galls before the females and mate with them while the females are still in their natal galls. Matings are often between siblings because few foundresses contribute offspring to each fig. Female fig wasps have less scope for precopulatory mate choice because they are still in the galls. They have generally been assumed to mate only once (Frank, 1985; Hamilton, 1967, 1979; Herre, 1985, 1987; West & Herre, 1998), an assumption supported by some paternity analyses (Zavodna, Compton, Raja, Gilmartin, & Van Damme, 2005). Although multiple mating has been reported in pollinating fig wasps, its influence on offspring sex ratios has not been considered (Kinoshita, Kasuya, & Yahara, 2002; Murray, 1990). Not all pollinator females succeed in mating with even one male (West, Herre, Compton, Godfray, & Cook, 1997), and those from inner galls can be more likely to mate (Dunn, Segar, et al., 2008; Dunn, Yu, et al., 2008). Body size can also be correlated with gall position and thereby fig wasp fecundity (Anstett, 2001). In this study, we examined the relationship between the location of natal flowers within figs and the fig wasps that emerged from them, and asked the following. (1) How many *Ceratosolen solmsi marchali* females only have an opportunity to

mate with one male? (2) Do female fig wasps that develop in more central locations benefit in terms of having a higher frequency of mating opportunities and a larger body size? (3) Do such benefits translate into greater fecundity and changes in their offspring sex ratios? And (4) does multiple mating modify sex ratio changes in response to foundress numbers inside shared figs?

METHODS

Study System

Ceratosolen solmsi marchali Mayr is the pollinator of *Ficus hispida* L. in the Xishuangbanna area of southwestern China. *Ficus hispida* is a small to medium-sized free-standing dioecious fig tree that produces figs on leafless branchlets hanging down from the trunk and major branches. Figs are present on different trees all year round, but there are seasonal peaks in production (Patel & McKey, 1998). Mature male figs have a diameter of about 28 mm and contain 1774.33 ± 48.79 (mean \pm SE, $N = 92$) female flowers.

Foundress females actively pollinate the fig flowers and are unable to leave a fig once they have entered it. The ovipositor of *C. solmsi marchali* is long enough to reach almost all the ovules in male figs of *F. hispida*. Locally, mean foundress number per male fig is 2.08 ± 0.12 (SE, $N = 182$, range 1–9), with about 53% of the figs pollinated by a lone foundress. Three species of nonpollinating fig wasps, *Philotrypesis pilosa* Mayr, *Philotrypesis* sp. and *Apocrypta bakeri* Joseph are also present. They oviposit from the outside of the figs into ovaries containing pollinator eggs or larvae. Reflecting the locations from which the fig wasps oviposit, pollinator offspring are concentrated in more central locations (mean pedicel length of occupied flowers = 0.76 ± 0.02 mm, $N = 154$), and the three species of nonpollinating fig wasps are located more towards the periphery of the figs (pedicel lengths of occupied flowers = 0.16 ± 0.01 mm, based on measurements from 134 flowers). All three nonpollinating fig wasps are parasitoids/inquilines, so pollinator larvae developing towards the periphery are more liable to be attacked.

Observations of Mating Behaviour

The behaviour of male pollinators was observed under a dissecting microscope during the period from when they first emerged from their galls until the first females emerged. The figs were broken into pieces to allow observation. Along with general observations, focal galls were marked and followed for several hours to record the numbers of visits by males, or individual males were similarly followed to record sequences of behaviour. The observation was performed during 4–5 h periods each day and continued for 1 week.

Mating Opportunities for Females

Mating frequency estimates were generated by counting the mating holes present in galls that contained female pollinators (Murray, 1990). Observations confirmed that the chewing of mating holes was almost always followed by the male inserting its abdomen into the female's gall, but direct confirmation of mating and insemination was not possible. The mating holes therefore provide a measure of the number of times that females had an opportunity to mate, rather than their number of matings per se. Figs were opened at the stage when the first females were starting to emerge from their galls and the male fig wasps were starting to produce a communal exit hole through the fig walls. Two male trees were used as sources of male-phase figs (the wasps emerged from the figs), with 15 figs collected from each. The figs were split into quarters through the ostiole and the numbers of mating holes

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