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A Role for Parasites in Stabilising the Fig-Pollinator Mutualism

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Mutualisms are interspecific interactions in which both players benefit. Explaining their maintenance is problematic, because cheaters should outcompete cooperative conspecifics, leading to mutualism instability. Monoecious figs (*Ficus*) are pollinated by host-specific wasps (Agaonidae), whose larvae gall ovules in their 'fruits' (syconia). Fenale pollinating wasps oviposit directly into *Ficus* ovules from inside the receptive syconium. Across *Ficus* species, there is a widely documents segregation of pollinator galls in inner ovules and seeds in outer ovules. This pattern suggests that wasps avoid, or are prevented from ovipositing into, outer ovules, and this results in mutualism stability. However, the mechanisms preventing wasps from exploiting outer ovules remain unknown. We report that in *Ficus rubiginosa*, offspring in outer ovules are vulnerable to attack by parasitic wasps that oviposit from outside the syconium. Parasitism risk decreases towards the centre of the syconium, where inner ovules provide enemy-free space for pollinator offspring. We suggest that the resulting gradient in offspring valsafility is likely to contribute to selection on pollinators to avoid outer ovules, and by forcing wasps to focus on a subset of ovules, reduces their galling rates. This previously unidentified mechanism may therefore contribute to mutualism persistence independent of additional factors that invoke plant defences against pollinator oviposition, or physiological constraints on pollinators that prevent oviposition in all available ovules

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Introduction

In a biosphere driven by selection at the level of the individual gene [1], explaining the existence of cooperation, such as mutualism, is a major scientific challenge. Mutualisms are interspecific ecological interactions characterised by reciprocal benefits to both partners [2] that usually involve costly investments by each. What factors thus prevent one partner from imposing unsustainable costs onto the other to enable mutualism stability (9-79) In some mutualisms, the larger, more sessile partner, manipulates the other by directing benefits to cooperative individuals and costs to cheaters [4-7]. However, a general consensus on mutualism persistence has only recently been formulated, and this clearly shows that a high benefit-to-cost ratio of cooperating is one important factor [8,9].

Fig trees (Ficus) and their host-specific agaonid pollinator wasps are a classic example of an obligate mutualism [10,11]. The wasps pollinate the trees, and the trees provide resources for wasp offspring. In monoecious *Ficus*, female wasps push their way through a specialised entrance into receptive syconia (colloquially, "figs"), which are enclosed inflorescences. The wasns then pollinate the tree while depositing their eggs individually into ovules. Thus, each egg laid costs the tree one seed, but upon emergence, the female wasp offspring Received September 14, 2007; Accepted January 22, 2008; Published March 11, 2008 disperse that tree's pollen. Trees need to produce both waps and seeds for the mutualism to persist, but natural selection should favour wasps that exploit the maximum number of fig ovules in the short term, resulting in a conflict of interest between wasp and tree. However, the mutualism has persisted Abbreviation: s.e., standard error 750 species pairs [12]. The mechanisms preventing wasps + To whom correspondence should be addressed. Email: jame

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from overexploiting figs remain unknown, despite intensive study over four decades. Within receptive syconia, the lengths of floral styles are highly variable [13,14], and ovipositing pollinators (foun-dresses) favour flowers with shorter styles for their offspring [15-18]. Style and pedicel lengths of flowers are negatively correlated. Short-styled ovules develop into seeds or galls (when a wasp is present) near the syconium inner cavity, whil most long-styled oxules develop into seeds near the outer wall [19,20] (Figure 1). These patterns have been shown to refle the oviposition preferences of foundresses, and are unlikely to be the result of greater elongation of pedicels containing eggs during syconial maturation, because in receptive syconia, pollinators' eggs are mainly present in short-styled inner ovules [16]. These widespread observations have been tied to four, not necessarily mutually exclusive, mechanisms that have been proposed to stabilise the fig-pollinator mutualism: (1) Unbeatable seeds—outer ovules may be defended biochemically or physically against oviposition or larval development [21]. However, no mechanism has ver been identified. (2) Short ovipositors-pollinators' ovipo tors may be too short to fully penetrate the long styles of

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