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# Fighting strategies in two species of fig wasp

**JAMIE C. MOORE*, DARREN J. OBBARD*, CAROLINE REUTER†‡,**
**STUART A. WEST* & JAMES M. COOK†‡**
*Institute of Evolutionary Biology, University of Edinburgh
†Division of Biology, Imperial College London
‡School of Biological Sciences, University of Reading

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Although theory exists concerning the types of strategies that should be used in contests over resources, empirical work explicitly testing its predictions is relatively rare. We investigated male fighting strategies in two nonpollinating fig wasp species associated with *Ficus rubiginosa* figs. In *Sycoscapter* sp. A, males did not assess each other before or during fights over mating opportunities. Instead, fights continued until the loser reached an energetic cost threshold that was positively correlated with its body size (fighting ability) and retreated. In *Philotrypesis* sp. B, prefight assessment was indicated, with males attacking competitively inferior rivals to remove them from the competitor pool (they then continued to do so until they reached a cost threshold that was again positively correlated with body size). Using data on species ecology, we discuss our findings with respect to theory on when different fighting strategies should evolve. We argue that the type of strategy used by a fig wasp species is determined by its relative benefits in terms of inclusive fitness.

*Keywords*: *Ficus*; fig wasp; fighting strategy; opponent assessment; *Philotrypesis*; *Sycoscapter*

Contests over resources are common in nature (Huntingford & Turner 1987). Resources contested for include food (Blanckenhorn 1991), mates (West et al. 2001), oviposition sites (Moore & Greeff 2003) and territories (Kemp & Alcock 2003). Behaviour varies from nonviolent ritualized displays (e.g. Davies 1978) to fatal fighting (e.g. Hamilton 1979). There may be distinct phases in which different behaviours are used (e.g. Clutton-Brock & Albon 1979), and behaviour may be modified in the light of information acquired about the opponent (e.g. Pratt et al. 2003). A challenge to evolutionary biologists is to explain why this diversity occurs. Theory indicates that the costs individuals should risk to obtain resources (the likely severity of contests) will increase with resource value in terms of future expected fitness (Enquist & Leimar 1990), a prediction receiving empirical support (West et al. 2001). Indirect fitness benefits through relatives can also be important, with, depending on population structure, individuals potentially selected to be altruistic (Hamilton 1964) or spiteful (Gardner & West 2004) to rivals. In addition, theory predicts different types of strategy. In extended contests, these may be divided into three categories.

(1) Strategies not involving opponent assessment: such strategies are predicted to evolve when individuals risk high costs to obtain resources that have high future expected fitness value (Enquist & Leimar 1990). The propensity to contest resources may be independent of the individual's own phenotype, or may increase with fighting ability (e.g. McNamara & Houston 2005). The fighting ability of an individual is generally termed its resource-holding potential, or RHP (Maynard Smith & Parker 1976).

(2) Strategies involving opponent assessment in which the most costly contests are between evenly matched rivals: in these, individuals use cues associated with RHP to assess opponents and retreat if it becomes apparent

*Correspondence and present address: J. C. Moore, Institute of Evolutionary Biology, School of Biological Sciences, University of Edinburgh, Ashworth Laboratories, Kings Buildings, West Mains Road, Edinburgh EH9 3JT, U.K. (email: jamie.moore@ed.ac.uk). C. Reuter and J. M. Cook are at the School of Biological Sciences, University of Reading, Whiteknights, Reading RG6 6AS, U.K.*

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they are unlikely to win an all-out fight. This reduces the cost of contests, so if reliable cues exist (information may be obtained with or without physical contact) the strategy is predicted to evolve at lower resource values than no-assessment strategies (Enquist & Leimar 1990).

(3) Strategies involving opponent assessment in which the most costly contests are between unevenly matched rivals: in these, individuals attack lower-RHP rivals to remove them from the competitor pool (Colegrave 1994; Rheinhold 2003). They are predicted to evolve when there is little or no population replacement, particularly if the competitor pool is small and/or if relatedness levels favour spiteful behaviour towards less than averagely (negatively) related rivals (Gardner et al. 2007).

These strategies are empirically distinguishable, differing in their predictions about: (1) whether contests are over specific resources; (2) relations between contestant RHP and contest duration; (3) whether the per unit time energetic costs (intensities) of contestant behaviours differ; and (4) how behaviour intensities change during contests (see Theoretical Predictions). However, conclusive empirical tests are rare. Many previous studies do not exclude alternative explanations for their conclusions, owing to statistical limitations and/or a lack of data on relevant aspects of behaviour (see Gammell & Hardy 2003; Taylor & Elwood 2003; see also Theoretical Predictions). Also, they have frequently used staged contests (see Pratt et al. 2003), so may not capture the full extent of interactions in natural conditions (for example, early-phase opponent assessment may be missed). We note that this paucity, coupled with pertinent information about the species' population ecology often being unavailable even if behaviour is known, has in addition meant that predictions concerning when the different fighting strategies evolve have not been evaluated.

We investigated fighting strategies in male nonpollinating fig wasps. Females of these species oviposit in figs (*Ficus* spp. inflorescences), and their larvae mature in galls before mating in the fig (although in some species males may be winged and disperse). Males often use their mandibles in fights over females, frequently incurring injury (Hamilton 1979; Cook 2005). This natural history allows the aspects of species' population ecology predicted to determine fighting strategy to be quantified. We also note that in some species males appear to use mandible length to assess the opponent's RHP during a prefight phase, and retreat without fighting if they are unlikely to win (Pereira & Prado 2005; see also Discussion). We studied two species with wingless fighting males associated with *Ficus rubiginosa*: *Sycoscapter* sp. A and *Philotrypesis* sp. B. We began by investigating the possibility of prefight opponent assessment. We tested (1) whether male body size and/or mandible length predict RHP, by quantifying relations with the probability of winning fights, and (2) whether assessment occurs, by comparing the two traits in fighting male pairs with those of rivals in the fig (see also Theoretical Predictions). Next, we investigated behaviour in fights. We identified the strategies used in each species by quantifying whether fights are over specific resources (mating opportunities) and how physical traits of contestants and injury costs affect fight duration (in this case, data on behaviour intensities are not needed). Then, given data on species' population ecology, we considered the causes of differences found in the strategies, both between the two study species and between them and other fig wasps for which information exists.

## METHODS

### Theoretical Predictions

*Strategies not involving opponent assessment*

In these, behaviour depends only on an individual's own phenotype. To reduce overall costs, individuals will contest only when the ownership of specific resources is disputed. Contests will either be to the death (if resource value is very high) or be tests of endurance evolved to indicate the likely outcome of such fighting. In the latter case, they will continue until the loser reaches an RHP-dependent cost threshold and retreats, with predictions about the factors determining how quickly this threshold is reached (contest duration) and contestant behaviour intensities depending on the sources of the costs. In wars of attrition (WOAs) the costs are energy expenditure and the time spent fighting, and contest duration will increase with loser RHP (e.g. Payne & Pagel 1996). Behaviour intensities will be matched to prevent cheats that delay their actions until later in contests. Intensities may escalate, stay the same or de-escalate over contests depending on whether time costs accumulate at an increasing, linear or decreasing rate. If costs are also due to opponent actions (e.g. injuries), contest duration will both increase with loser RHP and decrease with the costs inflicted by winners, that is, assuming a correlation with the ability to inflict costs, winner RHP (the cumulative assessment model, or CAM: Payne 1998). Behaviour intensity will be higher in contest winners than losers, and to maintain an optimal balance between cost types both will escalate over contests (within and in successive phases). Regarding the physical traits of fighting males in our study species (assuming they are correlated with fighting ability), we predicted that differences in body size and mandible length between pairs of fighting males using this type of strategy will be either similar to or, if the propensity of males to fight in such encounters increases sufficiently with RHP (see McNamara & Houston 2005 for theory), larger than those between randomly chosen pairs from figs (see also Cook & Bean 2006). If the latter is true though, average trait values of fighting male pairs will also be larger than (rather than similar to) average trait values of males in figs.

*Strategies involving opponent assessment in which the most costly contests are between evenly matched rivals*

In these, behaviour depends on the individual's phenotype compared to its estimate of its opponents. To reduce overall costs, individuals will contest only when specific resources are disputed. Assessment is a sampling problem, so longer is needed to determine fight outcome if RHP differences are small (the sequential assessment model, or SAM: Enquist & Leimar 1983). However, the negative relation between RHP difference and contest duration that this predicts can also arise from a no-assessment WOA