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Fighting strategies in two species of fig wasp

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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

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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 strategy coupled with an incidental association between loser RHP and RHP difference (Taylor & Elwood 2003). Hence, opposing relations of roughly equal slope between duration and loser RHP (positive) and winner RHP (negative) should be tested for. The same is predicted in no-assessment CAM strategies, as is the prediction of the SAM that behaviour intensity will be higher in contest winners than losers. These two strategies can be distinguished though, by how behaviour intensities change over contests: with the SAM, intensities will not change during a phase to maximize information transmission, but will escalate in successive phases. If this strategy is used in a prefight phase in our study species, we predicted that differences in body size and mandible length between fighting males will be smaller than those between randomly chosen pairs from figs. The average trait values of fighting males will be similar to average trait values of males in figs.

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

In these, behaviour depends on the individual's phenotype compared to its estimate of its opponent's RHP. Theory is limited and testable predictions few (Colegrave 1994; Rheinhold 2003), but, as future fitness is at stake, individuals will often contest at times other than when specific resources are disputed. Individuals will also be more likely to attack an opponent when the RHP advantage is large. Hence, if this strategy is used in our study species, we predicted that differences in body size/mandible length between fighting males will be greater than those between randomly chosen pairs from figs. If there is no variation in the propensity to fight, the average trait values of fighting males will be similar to the average trait values of males in figs.

Study Species

We made our observations during January–May 2004 and November 2005–March 2006, using wasps from *F. rubiginosa* figs collected from trees situated in and around the city of Brisbane, Queensland, Australia (27°24′S, 153°09′E). We found two *Sycoscapter* female morphospecies in figs: one with a longer ovipositor for a given body size than the other (J. M. Cook, unpublished data). However, we did not find morphological characteristics that allowed us to distinguish male morphospecies, so we developed molecular techniques to type them (see Supplementary Material). Analysis conducted during this period indicated three separate species: one with long-ovipositor females (sp. A), and two with short-ovipositor females (sp. B and sp. C). We also found two *Philotrypesis* female morphospecies, one black bodied and one brown bodied. Again, we did not find morphological characteristics that allowed us to distinguish males, so we developed molecular techniques to type them (see Supplementary Material for details). Analysis conducted during this period supported the treatment of the black-bodied (sp. A) and brown-bodied females (sp. B) and their males as separate species. This meant that, in our observations, we did not know the *Sycoscapter* or *Philotrypesis* species involved until after the individual(s) was typed. We do not report on *Sycoscapter* sp. B and *Sycoscapter* sp. C here because low densities meant we obtained too few observations. We mention *Philotrypesis* sp. A behaviour in the Discussion.

Male Behaviour

We cut open figs and observed male behaviour under a dissecting microscope, counting any female wasps eclosing. Males spent time either in the lumen or among the fig galls (when they sometimes disappeared from view), but rarely left the opened fig. They searched for females still in their galls, and, when they located one, attempted to cut a hole in the gall with their mandibles. When the hole was complete, the female eclosed and mated with the male. Physical interactions between males occurred at all of these times. When a fight (defined as a physical interaction lasting >2 s) occurred, we recorded whether it was over a definable mating opportunity (i.e. whether it resulted from a challenge to a male cutting an exit for, or mating with, a female), which male initiated it, who won (defined by the loser becoming moribund or retreating from the winner) and fight duration. We then collected the fighting males, measured their head widths (as an estimate of body size) at ×10 and mandible lengths at ×40, and scored them for injuries using Murray's (1987) index. In this, a damaged/lost antenna scores 0.5 points, a damaged/lost tarsus 1 point, a damaged/lost tibia 2 points, a damaged/lost femur 3 points, a damaged/lost coxa 4 points, a <half-severed abdomen/head 4 points, and a >half-severed abdomen/head 8 points. Points were summed to give a total score (Murray considered a score of ≥8 to constitute a serious, i.e. life-threatening injury). Then, we typed them. Following this, we placed the fig sections in a mesh-lidded pot. After 96 h we counted and noted the species of any females in the pot (we also counted females eclosing during the observations), and collected, measured and typed any males found in the pot or among the fig galls.

Data Analysis

To investigate who won fights we used generalized linear models (GLMs) with binomial error structures. We randomly assigned one male in each fighting pair as the focal male, and used whether they lost (0) or won (1) the fight as the response variable. As explanatory variables we fitted relative head width (focal/other) and relative mandible length as covariates and whether the focal male initiated the fight as a fixed factor. We then found the minimum adequate model (MAM), containing only significant variables, by stepwise deletion, evaluating significance with chi-square tests. Given the potential for relative head width and relative mandible length to have collinear effects on the probability of winning, when neither variable was significant in the full model we also evaluated their significance with the other variable removed from the model. In the analyses in this paper, we report variable significance after removal from the MAM. To save space and improve readability, in cases where variables have collinear effects we report the variable explaining the most variation/deviance in the data, and also only report non-significant ($P > 0.05$) effects of contestant physical traits and injuries (see below). All analyses were conducted with S-Plus 7.0.4 Professional Edition (2005, Insightful Corp., Seattle, WA, U.S.A.).

We compared head width and mandible length differences between fighting pairs to differences between randomly chosen pairs from the population, using paired *t* tests. In *Sycoscapter* sp. A, we estimated the latter value as the average of the differences between all possible pairings in the fig. In *Philotrypesis* sp. B, given the existence of a morph that avoids the lumen and therefore rarely fights, we estimated the value as the average of the differences between all possible pairings of fighting males (head width > 0.365 mm) in the fig (J. C. Moore, D. J. Obbard, J. M. Cook & S. A. West, unpublished data). We also used paired *t* tests to compare the average trait values of fighting pairs to the average values of their rivals.

To investigate factors affecting fight duration, we used linear models (LMs). We log-transformed duration to normalize its distribution, and as explanatory covariates fitted loser and winner head widths and mandible lengths, and the injuries incurred by each male during the fight. Following theoretical work indicating they should affect strategies (Murray & Gerrard 1985; Murray 1987; Enquist & Leimar 1990; Rheinhold 2003), we also fitted competitor number (total males – 1), female number and the female:competitor ratio (females/competitors). In addition, we fitted whether the male initiating the fight won and whether the fight was over a definable mating opportunity as fixed factors. We then found the MAM using the same techniques as previously, evaluating variable significance with *F* tests. Also here, we investigated factors affecting contestant injury scores. We used GLMs with negative binomial error structures because the high number of zeros meant the data were too overdispersed to analyse with Poisson errors. We fitted the same explanatory variables as in the fight duration analyses, and found the MAM as before using chi-square tests to evaluate variable significance.

RESULTS

Who Wins Fights?

Sycoscapter *sp. A*

We observed 18 fights. Five (27%) were over a definable mating opportunity; 14 (78%) were won by the male with the wider head (estimated body size) and 14 (78%) by the male with longer mandibles (in one a male with a wider head but shorter mandibles won, and in another the reverse occurred). The probability of a focal male winning increased with either relative head width or relative mandible length: the two variables were collinear (GLM: relative mandible length $\beta \pm \mathrm{SE} = 6.57 \pm 3.62$, $\chi^2_1 = 8.95$, $P = 0.003$; Fig. 1a).

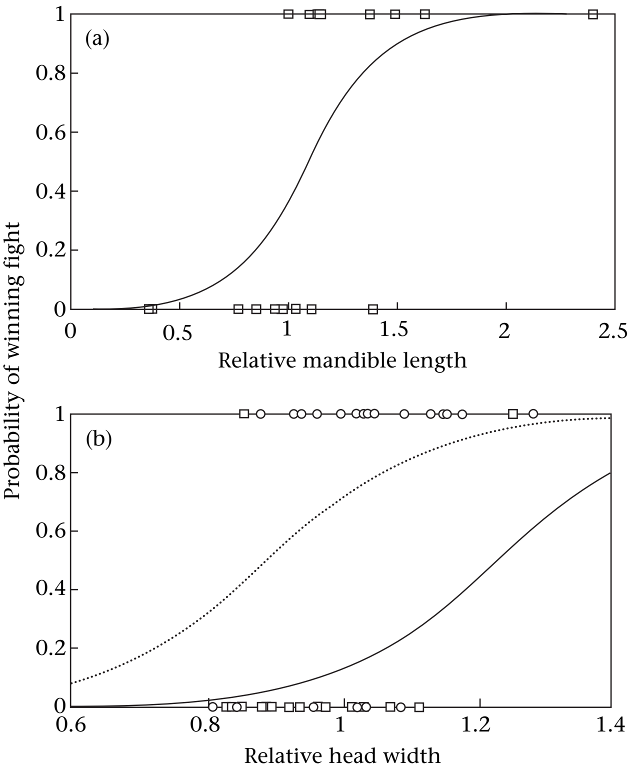

Figure 1. Relations between relative mandible length and the probability of focal males winning fights in (a) *Sycoscapter* sp. A, and (b) *Philotrypesis* sp. B. In (b) squares denote focal males that did not attack their opponents (predicted relation indicated by solid line), circles focal males that did (predicted relation indicated by dotted line).

Philotrypesis *sp. B*

We observed 36 fights. Six (17%) were over a definable mating opportunity; 21 (58%) were won by the male with the wider head and 23 (64%) by the male with the longer mandibles (in one a male with a wider head and shorter mandibles won, and in two others the reverse occurred). The probability of a focal male winning increased with either relative head width or relative mandible length: the two variables were collinear (GLM: relative mandible length $\beta \pm \mathrm{SE} = 3.31 \pm 0.69$; $\chi^2_1 = 4.80$, $P = 0.03$). The probability increased if the focal male initiated the fight ($\beta = 1.55 \pm 0.14$; $\chi^2_1 = 11.30$, $P < 0.001$; Fig. 1b).

Who Fights?

Sycoscapter *sp. A*

Of the 18 fights 12 were in figs with other males. Fighting males were no more or less evenly matched than randomly chosen pairs: head width (paired *t* test: $t_{11} = -0.39$, $P = 0.71$) and mandible length ($t_{11} = -0.51$, $P = 0.62$) differences between fighting pairs did not differ from average differences between males in figs (Fig. 2a). However, they were larger: average trait values were greater than those of rivals in figs (head width: fighting pair mean ± SE = 0.385 ± 0.015 mm, range 0.312–0.477 mm; fig mean = 0.363 ± 0.014 mm, range 0.297–0.443 mm; $t_{11} = 3.36$, $P < 0.001$; mandible length: fighting pair mean ± SE = 0.126 ± 0.009 mm, range

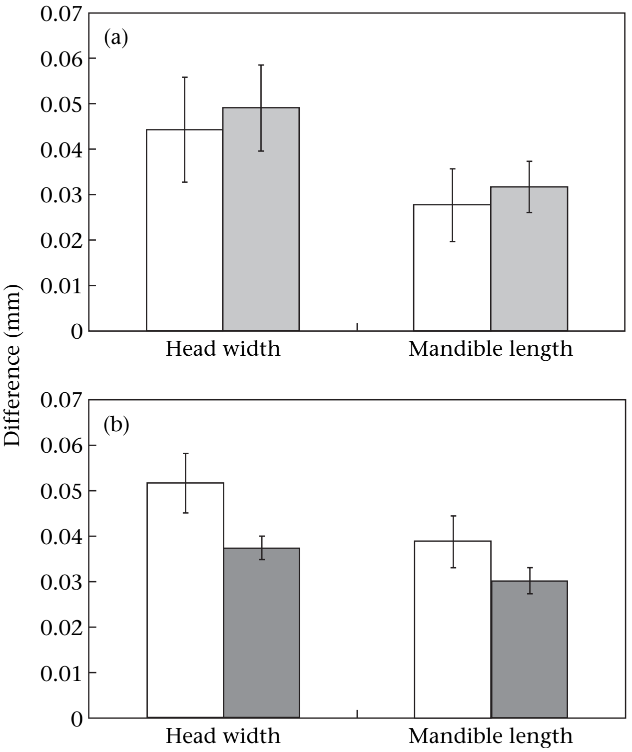

Figure 2. Head width and mandible length differences between pairs of fighting males (white bars) compared to average differences between rivals in figs (grey bars) in: (a) *Sycoscapter* sp. A, and (b) *Philotrypesis* sp. B. All measurements in mm. Error bars indicate SEs.

0.076–0.174 mm; fig mean = 0.111 ± 0.008 mm, range 0.074–0.172 mm; $t_{11} = 2.94$, $P = 0.01$).

Philotrypesis *sp. B*

Of the 36 fights 27 were in figs with other males. Fighting males were less evenly matched than randomly chosen pairs: head width (paired *t* test: $t_{26} = 2.73$, $P = 0.01$) and mandible length ($t_{26} = 2.04$, $P = 0.05$) differences between fighting pairs were larger than average differences between (fighter) males in figs (Fig. 2b). They were also larger: average trait values were greater than those of rivals in figs (head width: fighting pair mean ± SE = 0.483 ± 0.007 mm, range 0.421–0.568 mm; fig mean = 0.474 ± 0.007 mm, range 0.423–0.557 mm; $t_{26} = 2.65$, $P = 0.01$; mandible length: fighting pair mean ± SE = 0.205 ± 0.004 mm, range 0.176–0.258 mm; fig mean = 0.197 ± 0.003 mm, range 0.168–0.234 mm; $t_{26} = 3.23$, $P = 0.003$).

Behaviour in Fights

Sycoscapter *sp. A*

Mean ± SD fight duration was 27.05 ± 19.52 s (range 2–75 s). No winning males were injured, but 13 (72%) losing males were, eight (44%) seriously (score ≥ 8: mean loser score = 5.44, range 0–16). Fight duration increased with either the loser's head width or mandible length (the two variables were collinear; LM: loser mandible length $\beta \pm SE = 13.39 \pm 5.84$; $F_{1,16} = 5.26$, $P = 0.04$; Fig. 3a). It was independent of the winner's head width ($F_{1,15} = 0.53$, $P = 0.48$) and mandible length ($F_{1,15} = 0.29$, $P = 0.62$). However, the loser's head width/mandible length relation could be better explained by an increase with the loser's injuries ($\beta = 0.16 \pm 0.04$; $F_{1,16} = 16.59$, $P < 0.001$; loser mandible length term: $F_{1,15} = 2.39$, $P = 0.20$). This reflected a correlation between duration and the loser's injuries. The loser's injuries increased with either the loser's head width or mandible length (the two variables were collinear; GLM: loser mandible length $\beta \pm SE = 14.86 \pm 6.56$; $\chi^2_1 = 5.13$, $P = 0.02$; Fig. 3b), were independent of the winner's head width ($\chi^2_1 = 0.49$, $P = 0.48$) and mandible length ($\chi^2_1 = 0.18$, $P = 0.67$), and increased with the female:competitor ratio ($\beta = 0.21 \pm 0.10$; $\chi^2_1 = 4.35$, $P = 0.04$) and if the winner initiated the fight ($\beta = 0.91 \pm 0.40$; $\chi^2_1 = 4.77$, $P = 0.03$). However, the effect of these terms could equally be explained by an increase in injuries with fight duration ($\beta = 0.03 \pm 0.01$; $\chi^2_1 = 5.59$, $P = 0.02$; terms all NS when in same model: our unpublished data).

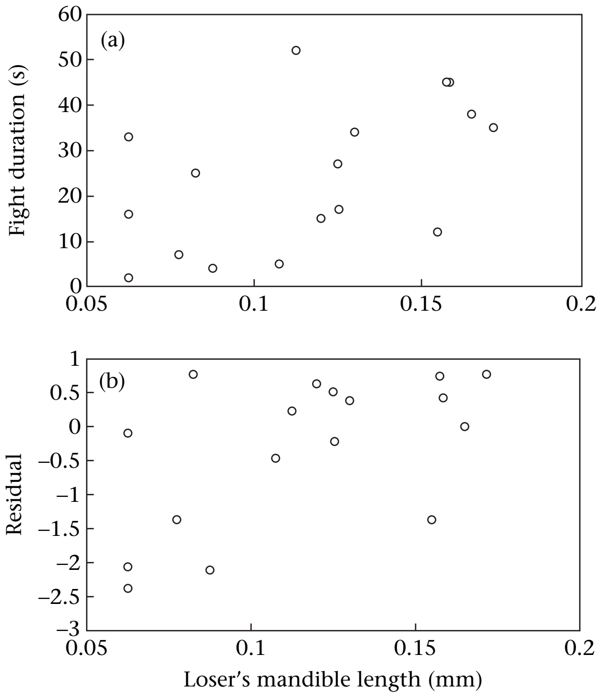

Figure 3. Relations between the loser's mandible length and (a) fight duration and (b) the loser's injury score in *Sycoscapter* sp A. In (b) the data are presented as a residual plot after we fitted a negative binomial GLM with whether the winner initiated the fight and the female: competitor ratio in the fig as explanatory variables.

Philotrypesis *sp. B*

Mean ± SD fight duration was 38.22 ± 41.28 s (range 3–170 s). Only one winning male was injured, whereas eight (22%) losers were, four (11%) seriously (mean loser score = 1.59, range 0–16). Fight duration increased with the winner's head width (LM: $\beta \pm SE = 7.85 \pm 3.76$; $F_{1,33} = 4.35$, $P = 0.04$; Fig. 4), and decreased with competitor number ($\beta = -0.10 \pm 0.04$, $F_{1,33} = 7.22$, $P = 0.01$). It was unaffected by the winner's mandible length

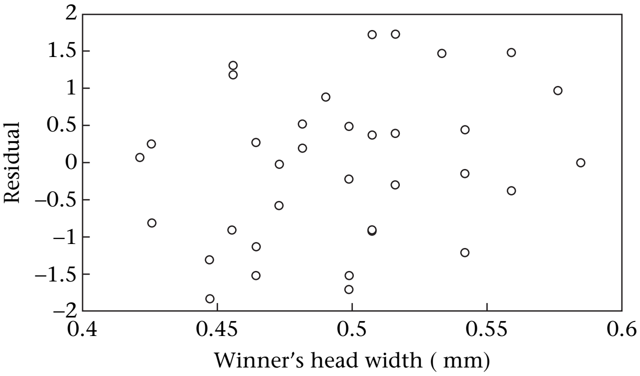

Figure 4. The relation between the winner's head width and fight duration in *Philotrypesis* sp. B. Data are presented as a residual plot after we fitted a linear model with competitor number in the fig as the explanatory variable.

($F_{1,32} = 0.21$, $P = 0.65$), the loser's head width ($F_{1,32} = 0.32$, $P = 0.57$) or the loser's mandible length ($F_{1,32} = 0.01$, $P = 0.91$). The winner's head width effect, though, was better explained by an increase with the loser's injuries ($\beta = 0.12 \pm 0.04$; $F_{1,33} = 6.93$, $P = 0.01$; loser mandible length term: $F_{1,32} = 2.15$, $P = 0.15$). Full analysis of the factors affecting injuries was precluded by the low number observed. However, the loser's injuries were positively correlated with fight duration (GLM: $\beta \pm SE = 0.03 \pm 0.01$; $\chi^2_1 = 4.42$, $P = 0.04$).

DISCUSSION

We investigated male fighting strategies in two species of nonpollinating fig wasps. In *Sycoscapter* sp. A, larger males, both in head width (body size) and mandible length, tended to win fights, indicating potential for the two traits to be used as cues to assess the opponent's fighting ability (RHP) in encounters. However, assessment appeared not to occur before fights: differences in the traits between fighting male pairs were similar to those between randomly chosen pairs, rather than being smaller or larger (fighting males were, though, larger than the average size of males in the fig: possibly this indicates that males use a strategy in which the propensity to fight in encounters increases with their own RHP: see McNamara & Houston 2005 for theory). Assessment also appeared not to occur during fights: 44% of fights resulted in life-threatening injuries to losers (winners were not injured), indicating that not all were to the death. Fight duration increased with the loser's body size/mandible length, but was unaffected by the winner's physical traits or the injuries inflicted on losers. If males assess opponents and retreat if they are unlikely to win, a negative relation between fight duration and the winner's RHP is predicted (the SAM: Enquist & Leimar 1983). In addition, the results are contrary to those predicted if males use a no-assessment strategy in which fights continue until the loser retreats having reached an RHP-dependent cost threshold that includes the cost of the opponent's actions (the CAM: Payne 1998): a negative relation should occur between fight duration and the loser's injuries (and with the winner's RHP if it is correlated with the ability to inflict costs, although this did not occur either). Instead, the positive relation between the loser's body size and fight duration, coupled with the correlation between fight duration and the loser's injuries, is consistent with males continuing until the loser retreats having reached a similar threshold that includes only energetic and time costs (a WOA: e.g. Payne & Pagel 1996). Having argued this though, we note that only 27% of fights were over a definable mating opportunity. In WOAs and the other strategies mentioned above, to reduce costs individuals should only contest the ownership of specific resources. We suggest this indicates that males often fight over more than just single matings. Specifically, they probably also fight over dominance of the fig lumen: from there they can quickly reach other parts of the fig if a rival locates a female, and also females will often pass through as they attempt to exit the fig.

Fights that were not over specific resources were also a characteristic of behaviour in *Philotrypesis* sp. B. Only 17% were over a definable mating opportunity. Given the fighting strategy used though, this is for different reasons than in *Sycoscapter* sp. A. Males with larger bodies and longer mandibles tended to win fights, again indicating potential for the traits to be used to assess the opponent's RHP, with the probability of winning also increasing if the male initiated the fight, implying an additional position or surprise effect (see Hansen 1986 and Taylor et al. 2001 for similar in raptors and arachnids, respectively). This time though, there was evidence that assessment did occur before fighting: body size and mandible length differences between fighting male pairs were larger than those between randomly chosen pairs from figs (fighting males were also larger than average, again implying that larger males were more likely to fight). These inequalities are consistent with males assessing and attacking lower-RHP rivals to remove them from the competitor pool, a strategy in which fights are over future fitness returns and need not be over the ownership of specific resources (see Rheinhold 2003 for theory; males using the strategy would also be expected to attack rivals when they have a positional or surprise advantage). This is the first time this strategy has been documented in nature. Work is now needed to investigate the traits males use to assess rivals. Pereira & Prado (2005; see also below) presented observations on three *Idarnes* fig wasp species suggesting that males compare mandible gape widths (perhaps using chemical cues: the closed fig is probably too dark for visual assessment, and the antennae are aligned along the mandibles) in a prefight phase, retreating if the assessment indicates they are unlikely to win a fight. However, our data do not allow us to determine whether similar assessment (even if the behaviour that follows differs) occurs in *Philotrypesis* sp. B. Regarding behaviour in fights, fight duration increased with the winner's body size. Fights were less injurious than in *Sycoscapter* sp. A (11% of losing males incurred life-threatening injuries). Too few males were injured to analyse in-depth, but again losers incurred more injuries than winners and the loser's injuries were positively correlated with fight duration. No predictions exist for the fight phase when lower-RHP rivals are attacked, but intuitively the winner's body size–fight

Table 1. Average female and male numbers in figs and fighting strategies of the six species of fig wasps for which information is available

	Females	Males	Strategy
Sycoscapter sp. A[1]	3.85	1.58	No assessment
Philotrypesis sp. A[2]	4.14	2.93	Assess and retreat without fighting if unlikely to win
Philotrypesis sp. B[1,2]	6.95	3.17	Assess and attack lower-RHP rivals
Idarnes sp. 1[3]	16.3	5.2	Assess and retreat without fighting if unlikely to win
Idarnes sp. 2[3]	14.3	6.9	Assess and retreat without fighting if unlikely to win
Idarnes sp. 3[3]	14.0	14.5	Assess and retreat without fighting if unlikely to win

Sycoscapter and *Philotrypesis* spp. are from *Ficus rubiginosa*, *Idarnes* spp. from *Ficus citrifolia*. Sources: (1) this study; (2) J. C. Moore, D. J. Obbard, J. M. Cook & S. A. West, unpublished data; (3) Pereira & Prado (2005). We note here that Pereira & Prado's (2005) behavioural observations were qualitative rather than quantitative.

duration relation is consistent with fights continuing until the winner reaches an RHP-dependent cost threshold and allows the loser to retreat. Theoretical work is now needed to investigate whether this strategy would be expected in these conditions.

Our work represents a rare empirical test of competing hypotheses concerning the fighting strategies used by various species. Other studies have often not completely excluded alternative explanations (Gammell & Hardy 2003; Taylor & Elwood 2003) and/or present data that may not capture the full extent of interactions in the wild (Pratt et al. 2003). Also notable is that the two species use different strategies. These also differ from the strategy used by *Philotrypesis* sp. A, another species associated with *F. rubiginosa* (J. C. Moore, D. J. Obbard, J. M. Cook & S. A. West, unpublished data), in which males assess the opponent's RHP before fighting and retreat if they are unlikely to win, as in the *Idarnes* species mentioned above. Fights themselves are WOAs: relations between the contestants' physical traits and fight duration/injuries are similar to those in *Sycoscapter* sp. A. This raises the question of why strategies differ between species. Theory indicates that the strategy used should depend on several population parameters (see Introduction). In particular, Enquist & Leimar (1990) predicted that when contested resource value is high in terms of future expected fitness, noassessment strategies will evolve, but when resource value is lower, strategies in which individuals assess each other and retreat if they are unlikely to win will occur. Table 1 presents population data from the six fig wasp species for which information about fighting strategy is available. Consistent with predictions, the average number of females in figs (the number of mating opportunities) is lower in *Sycoscapter* sp. A, in which there is no opponent assessment, than in *Philotrypesis* sp. A or the *Idarnes* species, in which males retreat if prefight assessment indicates they are unlikely to win. Regarding *Philotrypesis* sp. B, lower-RHP rivals are more likely to be attacked when the competitor pool is small (Rheinhold 2003). However, the average number of males in figs is higher than in *Sycoscapter* sp. A or *Philotrypesis* sp. A. Another factor favouring this strategy is a population structure that results in selection for spiteful behaviour towards less than averagely (negatively) related rivals. Rheinhold (2003) found that when nonkin can be distinguished they should sometimes be selectively attacked. This occurs at intermediate levels of average relatedness, when the potential for negative relatedness is highest (see also Gardner & West 2004). We are currently developing molecular methods to estimate wasp relatedness, which will allow us to test whether *Philotrypesis* sp. B males do attack negatively related rivals, and also whether population structure differs between our (three) study species.

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Supplementary Material

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.anbehav.2008.01.018.

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