

ARTICLES

Recognition of competitive asymmetries reduces the severity of fighting in male *Idarnes* fig wasps

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Intense sexual selection leading to male fighting in fig wasps is extensively documented and has evolved independently in several lineages of nonpollinating and pollinating fig wasps. We studied wingless males of nonpollinating *Idarnes* fig wasps, and observed assessment display and defensive behaviour (mating inside the female galls and sheltering within empty galls) during the mating period, in opposition to reported indications that such behaviour does not play an important role in the avoidance of fatal combats in fig wasps. Compared to males of other species with similar morphology and future reproductive opportunities, males of these species generally showed lower scores of physical injuries due to aggressive confrontations. Our results are consistent with models of asymmetric contest competition, and suggest that defensive behaviour and particular internal features of figs may increase the importance of the recognition of competitive asymmetries in reducing the severity of fighting in closed systems.

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Sexual selection occurs when one sex competes for access to the other to obtain mating opportunities. Thus, characteristics that increase an individual's ability to compete for mates such as bearing elaborated ornaments or structures used as weapons are favoured by sexual selection (Alcock 1998). Sexual selection studies have largely focused on conflicts between males competing for mates (Brown et al. 1997). Enquist & Leimar (1990) predicted that fatal fighting should be expected to occur when the value of the contested resource is high relative to expected future fitness returns. Nevertheless, it is also known that there are mechanisms that limit the risk of severe injury during combats, such as the assessment of relative fighting ability, which could lead the weaker individual to give up prior to suffering injury (Enquist & Leimar 1983, 1990). The range of the conditions over which this conditional strategy is an evolutionarily stable strategy (ESS) increases with the degree of asymmetry in

fighting ability (Colegrave 1994). However, such mechanisms are of little importance when the future value is close to zero, and, consequently, the value of the contested resource is higher (Enquist & Leimar 1990) or when the weaker individual cannot leave the resource patch, to evade the fight (e.g. closed systems; Colegrave 1994).

Intense sexual selection leading to male fighting is well documented for fig wasps, and has evolved independently in several lineages of nonpollinating (Hamilton 1979; Murray 1987, 1989, 1990; Bean & Cook 2001) and pollinating (Penaar & Greeff 2003) species. Winged females of agaonid wasps (1) enter the fig (the urn-shaped *Ficus* inflorescences, with the flowers placed internally) through the ostiole, (2) oviposit into the ovary of some of the female flowers and simultaneously (3) pollinate some of the female flowers (Galil 1977; Jusselin et al. 2001; Jusselin et al. 2003). Thus, larvae of pollinating wasps develop in galled ovaries. In addition to pollinating wasps, other nonpollinating wasp species, which usually oviposit externally through the fig wall, develop in flower ovaries or parasitize larvae of primary galling wasps (Bronstein 1992). Mating strategies in fig wasps are represented by winged, sometimes apterous (Greeff & Ferguson 1999; Penaar & Greeff 2003), disperser males, and wingless males that compete locally for females who have

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developed within the same fig. Some species have dimorphic males, with both winged and wingless forms (Hamilton 1979; Cook et al. 1997). Among the wingless species, there exists a large diversity of forms representing fighting and nonfighting morphologies (Hamilton 1979; Murray 1990; Greeff & Ferguson 1999), which seem to be closely linked to variation of mating tactics.

Among the wingless species, the prevalence of fatal fighting seems to be negatively correlated with future mating opportunities (average number of females; West et al. 2001). Within species, fatal fighting seems to be related to the conditions encountered in the particular fig. Murray (1987) proposed that the severity of *Philotrypesis pilosa* combats is determined by the rates of encounters between males, whereas Bean & Cook (2001) observed a positive correlation of severe injuries with both the size of male mandibles and the operational sex ratios (the number of receptive females versus the number of competing males at a particular moment, sensu Greeff & Ferguson 1999) in *Sycosapter australis*.

Despite the report that mandibles are used as weapons and that their sizes reflect fighting ability, previous studies have not found evidence that fig wasps use conditional strategies based on the recognition of competitive asymmetries (Murray 1987; Bean & Cook 2001). The evolution of this conditional strategy may be strongly constrained in fig wasps by the internal fig structure. Male fig wasps have a relatively short life span and the fig cavity, where the male interactions take place, forms a closed system. This causes expectation of future reproductive success to be low and impedes weaker males from leaving the arena to avoid fights. Under these circumstances, strategies based on recognition of competitive asymmetries do little to decrease the risk of injury (Enquist & Leimar 1990; Colegrave 1994).

We carried out detailed observations of wingless males of nonpollinating *Idarnes* fig wasp species that had been previously investigated by Hamilton (1979) in Brazil. In opposition to earlier reports, we observed assessment display and defensive behaviour during the mating period. In addition, males of these species showed, on average, lower scores of physical injuries due to aggressive confrontations (sensu Murray 1987) than reported for other species with similar morphology and expected future mating opportunities (average number of females). Therefore, we addressed the following questions. (1) Can assessment display reduce the incidence of fights? (2) Can defensive behaviour diminish the risk of fatal injuries? (3) Are the observed levels of injury (across figs) consistent with those expected when assessment does occur?

METHODS

Study Species

Idarnes is a nonpollinating fig wasp genus associated with *Ficus* species of the subgenus *Urostigma*, section *Americana*. We studied three species of *Idarnes* with wingless males found in figs of *Ficus citrifolia*. In Brazil, *F. citrifolia* is pollinated by *Pegoscapus tonduzi* and associated with 14 nonpollinating chalcid wasp species (Pereira

et al. 2000, referred to as *F. eximia*). Of these nonpollinating genera found in *F. citrifolia*, *Idarnes* is the most represented one, with three species of wingless males, two of *carne* (*Idarnes* sp. 1 and sp. 2) and one of *flavicollis* (sp. 3) groups, and one other species of winged males (*incerta* group). Females of *Idarnes* do not enter the fig but use their long ovipositors to lay eggs through the fig wall into fig ovules. After offspring development in the fig, males eclose first into the lumen, and begin to search for mates. With large mandibles, robust thoraxes, and spikes on the legs, wingless males of *Idarnes* show a morphology consistent with typical fighter forms (Gordh 1975; Hamilton 1979). *Ficus citrifolia* is the same species that Hamilton (1979) had referred to as *Ficus* sp. 2. We examined Hamilton's voucher material left in possession of R. Zucchi at São Paulo University, Ribeirão Preto, Brazil, to confirm wasp identifications.

Behaviour during the Mating Period

We used the methodology presented by Murray (1987) to quantify male behaviour during the mating period. At the beginning of emergence of *Idarnes* males in July 2000, figs were collected from three fig trees growing in the surroundings of the Campinas State University Campus, Brazil (22°54'S, 47°03'W). About one-third of each fig was then removed in the laboratory by cutting off the ostiolar portion. A recently emerged male was marked on its thorax with a small drop of aeromodel ink. The fig was then wrapped in transparent cellophane previously sprayed with de-misting solution for glasses (tensoactive isopropane) to form a window for the observation of the fig's cavity. The focal male was observed under the stereoscope at 10× magnification under cold light illumination.

Behaviour was sampled during 40 min per h, by recording the instantaneous activity of the focal animal at 10-s intervals. We sampled for a total of 33.4 h distributed at 9.8 h for *Idarnes* sp. 1 (five focal animals), 2 h for *Idarnes* sp. 2 (one focal animal), and 21.6 h for *Idarnes* sp. 3 (10 focal animals). The variation in samples across species was caused by the large differences in densities of each species, which prevented a priori determination of the species present in the fig. At the end of each observation period, which varied from 1 to 6 h, we collected all males present in the fig cavity, and measured head width and mandible length of each to the nearest 0.025 mm.

Injury Levels in Wingless Males

Between April 1999 and August 2001, we randomly collected approximately 30 figs from each of eight crops of five fig trees growing in the surroundings of the Campinas State University Campus, prior to wasp emergence. The figs were individually placed in plastic flasks and all the wasps were allowed to emerge prior to freezing for conservation and later counting. Subsequently, we counted and identified morphospecies and sex of all wasps that had developed in the fig, and we scored males for the injuries they had acquired during their lifetime, according

to the sequence of scores proposed by Murray (1987). The scores were rated on a scale of 0–8, according to their severity. As an example, a male that had lost part of one antenna (0.5 points), lost a whole femur (3 points), and had an abdomen severed more than halfway (8 points) received a score of 11.5 points (see Murray 1987 for details). After scoring, we measured the head width and mandible length of each male to the nearest 0.025 mm. We examined 386, 112 and 543 males of *Idarnes* sp. 1, sp. 2 and sp. 3, respectively. For comparison, we also scored 936 males of the pollinating wasp *P. tonduzi*.

The injury level per fig was estimated according to Murray's (1987) variables, which include: (1) 'lifetime extent of injury' (LEI), the average injury scores per fig, providing an estimate of the total cost of fighting, (2) 'injury frequency' (IF), the frequency of injured males per fig, representing the frequency of damaging fights irrespective of their relative intensity, and (3) 'severe injury frequency' (SIF), the frequency per fig of injured males that had injury scores greater than eight points, an estimate of the cost of individual fights.

Data Analysis

Behavioural data were used to assess the response of males to the particular conditions in the figs. Display and fighting data were analysed with a paired *t* test (Zar 1996) to examine whether sizes of 'winner' and 'loser' males (represented by the cube of head width) were different. The outcomes of observed combats were classified in contingency tables according to two factors: location of the attacked male (fig cavity or sheltered within an empty gall) and occurrence of severe injuries for the attacked male (yes or no). We fitted log-linear models to the data, assuming a Poisson error and using the log-link function in the S-Plus 6.1 software (Insightful Corp., Seattle, Washington, U.S.A.) to test the independence of 'severe injuries' versus 'location'. Initially, we examined the male activities separately by species. Because we did not note marked differences in activities between them (see 'Injury levels in wingless males' in Results), we pooled the species data for all behaviour analyses.

To assess injury level in wingless male *Idarnes*, we considered only those figs that contained at least two conspecific *Idarnes* males, to assure that fights could have occurred. We analysed a total of 188 figs (68, 28 and 92 figs for *Idarnes* sp. 1, sp. 2 and sp. 3, respectively). To evaluate the hypothesis that fighting levels are influenced by average levels of future mating opportunities (average number of females), we graphically compared the LEI values observed for the three *Idarnes* species, in addition to the average value obtained for *P. tonduzi*, to the LEI values of 25 fig wasp species with variable mating strategies (Murray 1989, Tables 1, 2, reprinted with permission from Elsevier). Subsequently, we analysed the local level of injuries (according to particular conditions in the figs). The LEI data were analysed with a linear model (LM); IF and SIF data were analysed with generalized linear models (GLM) with binomial error structures, using the S-Plus 6.1 software. Response variables (LEI, IF and SIF) were mod-

elled as functions of *Idarnes* species (sp. 1, sp. 2 and sp. 3), fig diameter (estimate of fig size), number of conspecific females, number of conspecific males, cube of head width or mandible length (which we have assumed represent fighting ability), and the corresponding *Idarnes* species sex ratios. Because the distribution of the LEI data were skewed to the left, they were square-root transformed to improve their approximation to the normal distribution (Zar 1996). The head width and mandible length data were not simultaneously analysed because their strong colinearity interfered with statistical inference (Belsley 1991). Sex ratios were not significantly correlated with any of the response variables and therefore were not included in the final models. Diagnostic analyses were performed for all models. Explanatory variables did not show strong multicollinearity (Belsley 1991). Residuals did not obviously deviate from the normal distribution and there were no signs of overdispersion when the full models were fitted to the data.

RESULTS

Behaviour during the Mating Period

Idarnes males were the first insects to emerge within the fig cavity and nearly all of their activities occurred prior to the emergence of the pollinating fig wasp males of *P. tonduzi*.

We identified six behaviours performed by *Idarnes* males during the mating period (Fig. 1). 'Investigation' occurred after emergence from their galls when males began to investigate the fig lumen, touching the closed galls with their antennae. 'Opening' occurred when a male found a gall containing a female, charged in, chewed a hole in the gall, and attempted to mate with the female. Sometimes males briefly resumed investigation, but then returned to the female in the gall and continued opening activity. *Idarnes* males are probably able to recognize galls that contain conspecific females. All observed females belonged to the same species as the males that were opening the galls. 'Mating' occurred when the male opened the gall and copulated with the female inside. During mating, the male entered the gall and oriented his mandibles and part of his gaster towards the opening of the gall. This display may work as a defence against rival males; on one occasion, we observed an *Idarnes* male attack and kill another male that was mating. We did not observe multiple mating of the same female. After having mated, females remained inside their galls even after almost all males had died. *Idarnes* females subsequently left their galls simultaneously with the emergence of *P. tonduzi* females, when the exit hole was almost open.

Aggressive behaviour was observed during the investigation and opening activities, whenever two conspecific males met. 'Assessment' was observed as a recurrent display, consistent with assessment behaviour. In this display, two males faced each other with their mandibles completely open and almost touching each other, in a threatening display (Fig. 2). We noted that the antennae were positioned in line with the mandibles and that

Table 1. Population* (*N*) and injury (*n*) characteristics of wasps within sampled figs

Species	<i>N</i>	Females	Males	Total per fig	Sex ratio	<i>n</i>	LEI	IF	SIF
<i>P. tonduzi</i>	618	168.8±79.5	20.3±19.0	189.1±91.1	0.103±0.066	46	0.07±0.18	0.018±0.042	0.002±0.012
<i>Idarnes</i> sp. 1	382	16.3±16.3	5.2±6.4	21.5±20.1	0.270±0.207	69	0.99±1.19	0.398±0.377	0.012±0.046
<i>Idarnes</i> sp. 2	342	14.3±14.5	6.9±8.4	21.2±21.0	0.318±0.192	47	1.23±2.13	0.370±0.414	0.055±0.182
<i>Idarnes</i> sp. 3	477	14.0±14.5	6.0±6.1	20.0±17.7	0.329±0.224	107	1.11±1.14	0.463±0.362	0.025±0.074
<i>Idarnes</i> sp.†	1	15	54	69	0.783	1	2.093	0.222	0.074

Means are given ± SD; LEI = lifetime extent of injury; IF = injury frequency per fig; SIF = severe injury frequency per fig (scores ≥ 8 points). *Long-term data from crops sampled during 1992–1993 on the campus of the Londrina State University (23°18'S, 51°09'W), and from crops sampled during 1996–2001 near the campus of the Campinas State University.

†Murray's (1987) scores were used to quantify the LEI in a fig based on Hamilton's (1979) descriptions of the injuries suffered by the males.

smaller males tended to give up fighting after this display, suggesting that some assessment of fighting ability occurred in that moment. 'Fighting' occurred when males grasped different body parts of opponents (mandibles, head, thorax, propodeo and gaster). *Idarnes* males were extremely aggressive in combat, which resulted sometimes in death of one opponent. On one occasion, a male spent several minutes biting and lacerating the gaster of the opponent he had killed in fighting. 'Sheltering' often occurred after aggressive interactions, when attacked males took shelter within empty galls and remained with their mandibles placed at the openings. We observed assessment between sheltered and nonsheltered males.

The mean percentage of total time spent by *Idarnes* spp. in assessment display (3.95%, 95% confidence limit = 1.9–6.1%) was approximately four times the mean percentage of time spent in fights (1.08%, 0.5–1.8%). Usually, after an assessment display, the smaller male retreated, avoiding the fight. On four of five occasions of assessment display, in which we measured the males involved, the cube of head width of the loser was smaller than that of the winner. Despite this tendency, however, the sample size was too small to permit the detection of potential significant differences ($\bar{X}_{\text{winner-loser}} \pm \text{SD} = 0.01 \pm 0.02 \text{ mm}^3$; paired *t* test: $t_4 = 1.1$, $P = 0.353$, power = 0.124).

We observed that male size, represented by the cube of head width, appears to reflect fighting ability. In 12 of 17 observed confrontations (fights or assessment displays), the losers were smaller ($\bar{X}_{\text{winner-loser}} \pm \text{SD} = 0.01 \pm 0.02 \text{ mm}^3$; paired *t* test: $t_{16} = 2.2$, $P = 0.044$, power = 0.308). The losers of fights suffered severe injuries, which left them in a moribund condition. We found that a focal male's likelihood of winning was correlated with his relative body size (focal:other; GLM: slope = 3.8, $\chi^2_1 = 3.8$, $P = 0.050$).

Sheltering within empty galls was an effective protection against severe injuries. We observed four serious injuries (Murray's scores ≥ 8) during 17 fights that occurred in the fig cavity versus no serious injury during six combats when one male was sheltering in an empty gall ($G_2 = 15.46$, $P = 0.0004$).

Injury Levels in Wingless Males

Table 1 shows the characteristics of wasps within the sampled figs. At the species level, pollinating *P. tonduzi* was approximately 10 times more abundant than the non-pollinating *Idarnes* species and had the lowest average values for proportion of males and injury variables. The LEI, IF and SIF values were not significantly different among the three *Idarnes* species studied (Table 2).

Table 2. Linear (LEI) and generalized linear (IF, SIF) models used to explain injuries in wingless males of *Idarnes* spp.

Effect	LEI			IF				SIF			
	Standardized slope	<i>t</i>	<i>P</i>	Slope	df	χ^2	<i>P</i>	Slope	df	χ^2	<i>P</i>
	$R^2_{\text{adj}} = 0.24$, $F_{6,181} = 11.0$, $P < 10^{-9}$			$R^2_l = 0.167$, $\chi^2_6 = 63.1$, $P < 10^{-10}$				$R^2_l = 0.094$, $\chi^2_6 = 8.0$, $P = 0.24$			
Species	—	0.3*	0.755	—	2	1.06	0.588	—	2	3.16	0.21
Fig diameter	−0.20	−2.8	0.005	−0.20	1	17.59	< 10^{-4}	−0.10	1	0.52	0.473
Females	0.06	0.7	0.484	0.004	1	0.65	0.421	0.01	1	0.97	0.323
Males	0.32	3.8	0.010	0.05	1	20.46	< 10^{-5}	−0.04	1	1.46	0.227
Cube of head width	−0.09	−1.3	0.210	7.10	1	1.66	0.198	−25.51	1	1.78	0.183

LEI = lifetime extent of injury; IF = injury frequency per fig; SIF = severe injury frequency per fig (scores ≥ 8 points). Chi-square values correspond to the change in deviance caused by the removal of the factor from the full model. *N*: *Idarnes* sp. 1 = 68, *Idarnes* sp. 2 = 28 and *Idarnes* sp. 3 = 92 (total of 188 figs).

**F* value obtained by the removal of the variable 'species' from the model.

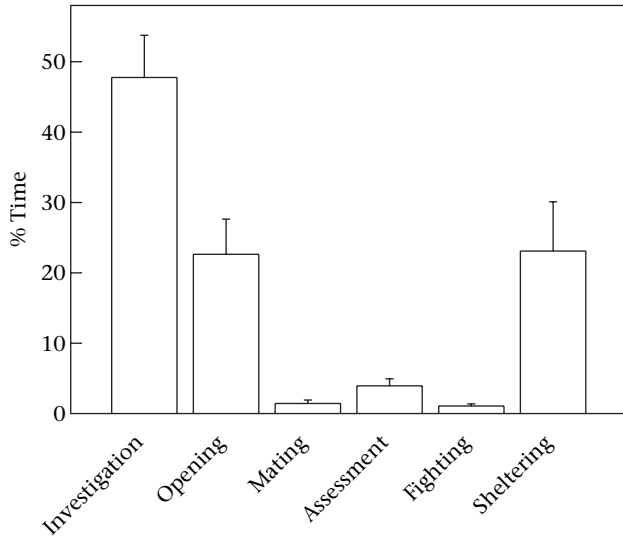


Figure 1. Percentage of time spent ($\bar{X} \pm SD$) on the six activities identified in wingless males of *Idarnes* spp.

Average LEI observed in *Idarnes* spp. was in general lower than that reported for other species with similar morphology and expected future mating opportunities (average number of females; Fig. 3). In an extreme case of physical injuries described by Hamilton (1979) that we quantified using Murray's (1987) scores, the LEI (2.1 points; Table 2) was also low in relation to most other fighting fig wasp species. The plot of LEI versus the mean number of females per fig (Fig. 3) showed that the species of *Idarnes* studied fell in a particular group with low values for both expected future mating opportunities (average number of females) and LEI. This group was represented by species without fighting morphology with the exception of two species with 'soldier' morphology.

Both LEI and frequency of injured males per fig (IF) were negatively correlated with fig diameter and positively correlated with the number of males per fig, but not with the cube of head width (Table 2). The inclusion of mandible length instead of head width did not qualitatively change the results. Nevertheless, the frequency of severely injured males (SIF) was not significantly correlated with the variables studied (Table 2).

DISCUSSION

Can Assessment Display Prevent Fights?

We have described an assessment display adopted by the wingless *Idarnes* wasp males that appears to be used to implement conditional strategies (engage in fight or withdraw without fighting). A similar display of mandible spreading was observed in males of the South African *Otitesella longicauda* and *O. rotunda* nonpollinating fig wasps (J. C. Moore, personal communication). Two findings support the notion that the assessment display in *Idarnes* is used to detect fighting ability. First, when males faced each other, antennae were positioned in line with the opened mandibles in a way that should permit size comparisons. Second, smaller males (head width) tended to retreat without fighting. This assessment display was probably important in reducing the number of fights because *Idarnes* males spent approximately four times more time assessing than engaging in fights. Moreover, the number of fights observed in *Idarnes* (0.7 fights/h) was very low in relation to the number reported by Murray (1987) for *Philotrypesis pilosa* (5.7 fights/h).

Although costs associated with fighting favour the assessment of relative fighting ability over indiscriminate attacks on all opponents (Parker 1974; Maynard Smith & Parker 1976), an assessment display has previously not been reported in fig wasps (Murray 1987; Bean & Cook 2001). The evolution of assessments may be strongly constrained in fig wasps by the internal fig structure (forming closed systems), which accounts for both the low expectation of future reproductive success and the impossibility of the weaker individual evading combat by leaving the territory. These two factors render conditional strategies, based on intrasexual recognition of competitive asymmetries, of little importance in decreasing the intensity of fights (Enquist & Leimar 1990; Colegrave 1994).

Why then does assessment occur in *Idarnes* when conditions do not seem to favour this behaviour? The value of the contested resource (female mates) is probably high in *Idarnes*, because males spend the greater part of their activities finding and obtaining access to the resource (about 70% of the time is spent investigating and opening galls containing females; Fig. 1). The relatively

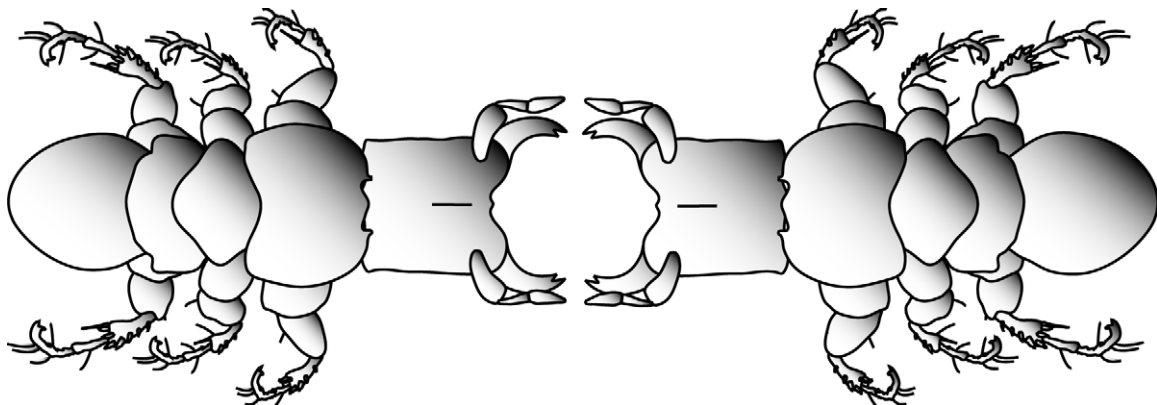


Figure 2. Sketch of the assessment display in wingless males of *Idarnes*.

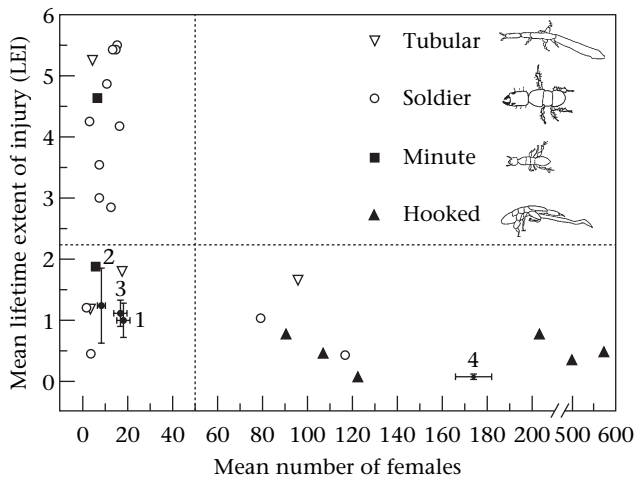


Figure 3. Mean lifetime extent of injury (LEI) versus mean number of females per fig for fig wasps found in *F. citrifolia* in the present study and for 25 fig wasps studied by Murray (1989, 1990). Numbers 1–3 represent *Idarnes* spp. 1–3 and number 4 represents *P. tonduzi*. Horizontal and vertical bars indicate the 95% confidence intervals. Dotted lines were drawn arbitrarily. Sketches representing male morphology were modified from Murray (1990, reprinted with permission from Elsevier).

short life spans of fig wasps would not favour routine surrender of a contested resource; therefore, indiscriminate fatal fighting should be expected. However, peculiar features of the host fig should favour unexpected assessment display. Figs of *F. citrifolia* have large internal cavities, an exception within the section *Americana* (Kjellberg et al. 2005), that remain open during fig development and when adult males emerge. Our hypothesis is that the large internal cavity increases the importance of intrasexual assessment as a conditional strategy. Large internal space could allow weaker males to successfully evade combat and then search for female galls in other fig parts (including those located at deeper ovary layers, which are less accessible to large males), increasing the expected future reproductive success. Another particularity was that *Idarnes* did not show a male-biased operational sex ratio (OSR), because females emerged simultaneously at the end of the mating phase, when almost all males had died. Thus, OSR in *Idarnes* seems to be less male biased than in other studied species because it is determined by male searching efficiency rather than female emergence rates (Greeff & Ferguson 1999; Bean & Cook 2001). This pattern would increase the number of mating opportunities and favour the evolution of assessment. Under this scenario, most contests could be resolved by assessment displays or by less dangerous behaviour (Enquist & Leimar 1990).

Observations in *Courtella michaloudi*, a pollinator of *F. bubu* that has figs with large cavities, seem to support our results. Males of *C. michaloudi* have a nondangerous aggressive behaviour that consists of using their long mandibles to grab other males by the thorax, lift them up, and throw them to one side within the fig (Greeff et al. 2003). On the other hand, in the nonpollinator *Sycoscapter australis*, found in *F. macrophylla* that has figs with small cavities (F. Kejjelberg, personal communication), Bean &

Cook (2001) reported high levels of fatal fights, but no evidence of assessment display.

In opposition to our findings, Murray (1987) did not describe assessment in *Philotrypesis pilosa* associated with *F. hispida* figs with large internal cavities. However, *P. pilosa* shows behavioural particularities not observed in *Idarnes*. Females in *P. pilosa*, unlike those in *Idarnes*, mate several times. Males remain with their female mates and mate with them again when an intruding male approaches (Murray 1987). This characteristic could favour fatal fighting if it improves defensibility.

Can Defensive Behaviour Diminish the Risk of Fatal Injuries?

Certain behaviour observed in *Idarnes* males, such as mating inside the female gall and sheltering in empty galls, seems to be associated with defensive strategies. Our data suggest that defensive behaviour reduces the risk of death during the mating period. Entering into the female gall to mate was one particular behaviour, whereas males of other reported nonpollinating fig wasp species mate from outside the gall, inserting only part of the gaster (e.g. *P. pilosa*; Murray 1987), or mate in the fig lumen when females emerge from their galls (Greeff & Ferguson 1999; Bean & Cook 2001; Pienaar & Greeff 2003). Mating in *Idarnes* probably has a high cost for males because they spent more than 20% of the sampled time opening the female galls to mate. On one occasion, we observed an *Idarnes* male attacking and killing another male that was mating. Entering and positioning their mandibles at the gall opening must work as a protection against rival males. The other defensive behaviour in *Idarnes* males, sheltering in empty galls, described by Hamilton (1979) and confirmed here by us, was also reported in *P. pilosa* (Murray 1987), suggesting that it is probably widespread through other fighting fig wasp species.

Defensive behaviour that increased the chance of male survival could be favoured by selection. Sheltering within empty galls was an effective protection against severe combat-related injuries. The risk of death in combat seems to be high in *Idarnes*, because mandibles are used as an efficient weapon to severely damage opponents (Hamilton 1979) and larger males tend to win combats (this study). Data from *F. citrifolia* figs in which all except one wingless *Idarnes* males were dead (samples from Barro Colorado Island, Panama; S. A. West, unpublished data) also support our observation that male size reflects fighting ability. In 10 of 11 figs, the average head width of the living male was larger than that of the dead ones, ($\bar{X}_{\text{alive}} \pm \text{SD} = 0.418 \pm 0.052$ mm, $\bar{X}_{\text{dead}} \pm \text{SD} = 0.352 \pm 0.051$ mm, paired t test: $t_{10} = 2.9$, $P = 0.016$). Such asymmetry in fighting ability increases the range of conditions over which conditional strategies are an evolutionarily stable strategy (Colegrave 1994).

Are Observed Injury Levels Consistent with Expectations?

The average levels of physical injuries quantified in *Idarnes* spp. and *P. tonduzi* support the proposal by West

et al. (2001) that the prevalence of fatal fights across species is negatively correlated with future mating opportunities (average number of females). However, the injury levels in wingless males of *Idarnes* were less than those reported for other nonpollinating fig wasps with similar morphology and average number of females per fig (Murray 1989). Bean & Cook (2001) reported the occurrence of severe injuries in 25% of males of *Sycosapter australis*, which is higher than the 1.2–5.5% incidence observed in *Idarnes* spp.

On a more refined scale, the positive correlation between variables of injury scores and number of males per fig, revealed by LM and GLM analyses, support the conclusion that the intensity of combats is locally determined by the rates of the encounters between males, as proposed by the contest competition model (Murray & Gerrard 1985; Murray 1987). However, in *Idarnes*, the occurrence of severe injuries seems not to be related to encounter rates between males, because we did not observe significant correlations between the variables studied and SIF.

Therefore, we suggest that *Idarnes* males showed lower injury scores as a result of their ability to locally assess competitive asymmetries, which could be used to resolve most contests without dangerous behaviour (Maynard Smith & Parker 1976; Enquist & Leimar 1990). With assessment, escalated contests tend to occur when individuals of similar sizes meet. This would explain the observed positive correlation between number of conspecific males and both LEI and IF per fig, because elevated numbers of males increased the meeting probability of individuals of similar sizes. If intrasexual assessment display was not important to avoid fights, injury level should be correlated with the mean male size (not number of males per fig; Bean & Cook 2001). An interesting test of our hypothesis would be to investigate whether it is more difficult to assess fighting asymmetry when the size difference between males is smaller. We might expect that assessment would be less likely to settle the debate when males are more even in size.

The negative correlation observed between fig size and both LEI and IF might indicate that avoiding fights through adoption of a conditional strategy is difficult in restricted spaces (Colegrave 1994). Curiously, we did not find significant correlations between the variables studied and the frequency of severe injury. This might suggest that both the assessment display and defensive behaviour observed in *Idarnes* males were efficiently working to reduce the fight intensity, as expected by theory (Colegrave 1994). It would be interesting to test whether conditional strategies based on recognition of competitive asymmetries are also unimportant in *Idarnes* species associated with *Ficus* species having smaller cavities.

We have reported behaviours and levels of injury scores that are consistent with models of asymmetric contest competition. Our results also indicate that defensive behaviour and particular internal features of figs may increase the importance of the recognition of competitive asymmetries as a conditional strategy in closed systems. This opens new opportunities to investigate the mating competition of fig wasps.

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