

Mating Strategies and Aggressive Combat in Wingless Neotropical Fig Wasp Males

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ABSTRACT

The aim of this work was to study the wingless males of pollinating (*Pegoscapus tonduzi*) and two nonpollinating fig wasp species, genus *Idarnes*, associated with figs (*Ficus citrifolia*) in Brazil to answer the following questions: 1) Do wingless males of *Idarnes* spp. and *P. tonduzi* show different male-male competition strategies?; and, 2) Do the injury within-species variables correlate with fig/population features? Consistently higher injury levels were observed in the two species of *Idarnes* than in the pollinator species. The results suggested that aggressive confrontations were involved in the mating strategies of *Idarnes*, whereas non-aggressive strategies were shown by males of *P. tonduzi*. Generally, injury variables in *Idarnes* spp. correlated positively with the male encounter rate and negatively with the fig size, thus supporting the contest competition theory. The results pointed out that different species under similar local conditions might follow distinct evolutionary histories. Within species, natural-history particularities might have some influence upon quantified injury levels in wingless males.

Key words: Agaonidae, contest competition theory, *Ficus*, fighting behaviour, Hymenoptera, Moraceae

INTRODUCTION

Sexual selection takes place when individuals of one sex go through competition with other members of the same sex to seize mating opportunities. Such selection favors features (elaborated ornaments or weapon structures, for instance) that increase the ability of a single individual to compete for mating (Alcock, 1998). Conflicts involving the males competing for mates have been reported in many sexual selection studies (Brown et al., 1997). Extensive documentation has been reported on the intense sexual selection occurring among fig wasps and

male fighting has independently evolved in various lineages of nonpollinating (Hamilton, 1979; Murray, 1987, 1989, 1990; Bean and Cook, 2001; Jusselin et al., 2004; Pereira and Prado, 2005) and pollinating (Greeff et al., 2003) species. Winged females of Agaonine wasps (a) enter the fig (inflorescences with internally placed flowers in *Ficus*) through the ostiole, (b) lay eggs into the ovaries of some of the female flowers and, simultaneously, (c) pollinate some of the female flowers (Galil, 1977; Jusselin et al., 2001; Jusselin et al., 2003). The galled ovaries, then, give room to the development of their larvae.

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Besides pollinating wasp species, developing within the flower ovaries or being parasites on larvae of primary galling wasps also occur in other nonpollinating wasp species that commonly lay eggs through the fig wall externally (Bronstein, 1992). Fig wasps may have winged males, apterous disperser males (Greeff and Ferguson, 1999; Pienaar and Greeff, 2003), or wingless males that go through local competition to mate with the females developed inside the same fig. Hamilton (1979) and Cook et al. (1997) point that dimorphic, winged and wingless males can be found in some species. Various forms that represent both the fighting and non-fighting morphological features, can be found among wingless species, suggesting close links to variations in mating tactics (Hamilton, 1979; Murray, 1990; Greeff and Ferguson, 1999).

When the value of the contested resource is high in relation to the expected returns of future fitness, fatal fighting should evolve (Enquist and Leimar, 1990). Hamilton (1979) suggested that high relatedness should reduce fighting in pollinating fig wasp species. However, West et al. (2001) did not find any correlation between fighting levels and estimated relatedness of interacting males. In populations with limited individual dispersal, factors that increase relatedness (and favor altruism) also lead brothers to compete locally, canceling out the benefits of kin-selected altruism (West et al., 2002; Griffin and West, 2002). According to West et al. (2001), the prevalence of fatal fighting suggests a negative correlation to future mating opportunities (i.e., average number of females) among wingless fig wasp species. Conditions found in the particular fig may be related to fatal fighting within species. Encounter rates among males of *Philotrypesis pilosa* can determine combat harshness (Murray, 1987), while a positive correlation of severe injuries involving mandible sizes in males and operational sex ratios (the number of receptive females at a given time, *sensu* Greeff and Ferguson, 1999) is observed in *Sycosapter australis* (Bean and Cook, 2001).

In the present study the same raw dataset analyzed in Pereira and Prado (2005) was used to answer the following questions: 1) Do wingless males of *Idarnes* spp. and *Pegoscapus tonduzi* show different male-male competition strategies?; and, 2) Are injury variables within-species correlated with fig/population features?

MATERIALS AND METHODS

Two species of *Idarnes* with wingless males and the pollinating species, *Pegoscapus tonduzi*, found in figs of *Ficus citrifolia* were studied. In Brazil, *F. citrifolia* is associated with 14 nonpollinating chalcid wasp species (Pereira et al., 2000, referred to as *F. eximia*). Fig wasps belong to the highly diversified group of parasitoid Hymenoptera (Fernández and Sharkey, 2006; Ramalho et al., 2007). *Idarnes* is the most represented genus among the nonpollinating genera found in *F. citrifolia* with three wingless male species, being two of *carne* (*Idarnes* sp. 1 and sp. 2) and one of *flavicollis* (sp. 3) groups, as well as another winged male species (*incerta* group). *Idarnes* sp. 2 occurred in low frequency and density rates and was not considered in the present analyses. Eggs are laid through the fig wall into the fig ovules with the long ovipositors of *Idarnes* females once they do not enter the fig. After developing in the fig, males come out of the egg into the lumen at first, then start searching for mates. The morphological features of wingless *Idarnes* males, i.e., large mandibles, robust thoraxes and spikes on the legs, are consistent with forms typically found in fighters (Gordh, 1975; Hamilton, 1979). *Pegoscapus tonduzi* males are also wingless but exhibit nonfighting morphology (less robust body, small mandibles and telescopic gaster). Hamilton (1979) referred *Ficus citrifolia* as *Ficus* sp. 2.

Approximately 30 figs were collected at random, prior to the emergence of wasps from each of the 11 crops out of eight fig trees in the surroundings of the Campinas State University campus (22°54'S; 47°03'W), from April 1999 to August 2001. For further counting, each fig was placed in a plastic flask and wasps were allowed to emerge before freezing steps occurred. Morphospecies were identified and all specimens of each sex were counted. Wingless males were ranked down on a sequence of scores according to the injuries they had suffered throughout their lifetime, as proposed by Murray (1987). Such scores rated on a 0-8 scale of severity (for further details, please check Murray, 1987). In the last eight sampled crops, The head width of each male was measured as to a minimum of 0.025 mm. The head measure has been used to estimate fig wasp sizes in other studies (Bean and Cook, 2001; Moore et al., 2004). In the last nine sampled crops, injuries were scored only in *Idarnes* spp. for partial analyses pointed out the absence of aggressivity in *P.*

tonduzi. In addition, the fig diameter was used as a covariate that estimates the fig sizes.

The injury level per fig was estimated according to Murray's (1987) variables, which included: (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. Only those figs that contained at least two conspecific *Idarnes* males were considered, to assure that fights could have occurred. 936 (46 figs), 420 (69 figs) and 574 (107 figs) males of *P. tonduzi*, *Idarnes* sp. 1, and *Idarnes* sp. 3 were analysed, respectively. All analyses were performed in the S-Plus 6.1 software (Insightful Corp., Seattle, Washington, U.S.A.).

To evaluate the population and the injury patterns, the differences of population variables (total brood size and sex ratio between species (including *P. tonduzi*) were tested with ANOVA. In *Idarnes* spp., the LEI data were analysed with linear model (LM) and IF and SIF data were analysed with generalized linear models (GLM) with binomial error structures. Counts of *P. tonduzi* offspring were square-root transformed and the sex ratios were arcsine square-root transformed. 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).

To evaluate the relationship between injury variables and fig/population features, LEI data were analysed with LMs. LMs were weighted by the number of males per fig to avoid bias associated with variable sample sizes. IF and SIF data were analyzed with GLM. Response variables (LEI, IF and SIF) were modeled as functions of fig diameter (estimate of fig size), number of conspecific females, number of conspecific males,

average head width, and the corresponding *Idarnes* species sex ratios. The explanatory variables were retained in the minimum adequate model, depending on their statistical significance. 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

The total brood size was approximately ten times larger in *P. tonduzi* than in both *Idarnes* spp. (Table 1: $F_{2, 219} = 611.6$, $P < 10^{-4}$). The brood sex ratio was significantly lower in *P. tonduzi* when compared to *Idarnes* spp. (Table 1: $F_{2, 219} = 23.7$, $P < 10^{-4}$), but not significantly different between *Idarnes* spp. *Idarnes* spp. had significantly higher LEI and IF values than *P. tonduzi* (Table 1). *Idarnes* spp. did not differ significantly in LEI, IF or SIF (LEI: $F_{1, 174} = 0.42$, $P = 0.52$; IF: $\chi^2_1 = 0.87$, $P = 0.35$; SIF: $\chi^2_1 = 1.32$, $P = 0.25$).

Approximately 70% of the injuries observed in *Idarnes* spp. occurred in the antennae and tarsi. In *P. tonduzi*, injuries occurred mainly in the coxa, femur and tibia (Fig. 1). Injuries observed in males of *P. tonduzi* occurred predominantly in their mid legs (94.7%), whereas in *Idarnes* spp. injuries were even distributed between fore (33.1%), mid (38.5%) and hind (28.4%) legs.

The best model to explain LEI was represented by positive correlations with the number of both conspecific females (marginally significant) and males in *Idarnes* sp. 1. In *Idarnes* sp. 3 the best model to explain LEI variation included a negative correlation with the fig diameter and a positive correlation with the number of conspecific males (Table 2). Non-significant variables (fig diameter in *Idarnes* sp. 1, number of females in *Idarnes* sp. 3, and sex ratio and head width in both species) were excluded from the models.

Table 1 - Population and injury variables of *P. tonduzi* and *Idarnes* spp. Values are mean \pm SE per fig. LEI = lifetime extent of injury, IF = injury frequency, SIF = severe injury frequency. Means followed by different letters (brood size and sex ratio) were significantly different by Tukey test.

Species	n	Brood size	Sex ratio	LEI	IF	SIF
<i>P. tonduzi</i>	46	249.9 \pm 7.6a	0.078 \pm 0.007b	0.07 \pm 0.03	0.018 \pm 0.006	0.002 \pm 0.002
<i>Idarnes</i> sp1	69	23.4 \pm 2.2b	0.314 \pm 0.028a	0.99 \pm 0.14	0.398 \pm 0.045	0.012 \pm 0.006
<i>Idarnes</i> sp3	107	21.6 \pm 2.0b	0.364 \pm 0.028a	1.11 \pm 0.11	0.463 \pm 0.035	0.025 \pm 0.007

Table 2 - LMs used to explain lifetime extent of injury in wingless males of *Idarnes* spp. (*Idarnes* sp. 1: adjusted $r^2 = 0.22$, $F_{2,66} = 10.6$, $P < 10^{-3}$; *Idarnes* sp. 3: adjusted $r^2 = 0.067$, $F_{2,103} = 4.784$, $P = 0.01$).

Variables	<i>Idarnes</i> sp. 1 (n = 69)			<i>Idarnes</i> sp. 3 (n = 106)		
	Standardized b	t	P	Standardized b	t	P
Constant	0.000	9.224	$<10^{-4}$	0.000	11.816	$<10^{-4}$
Fig diameter	-	-	-	-0.214	-2.272	0.0252
N. of females	0.206	1.995	0.0502	-	-	-
N. of males	0.280	3.263	0.0017	0.124	2.138	0.0349

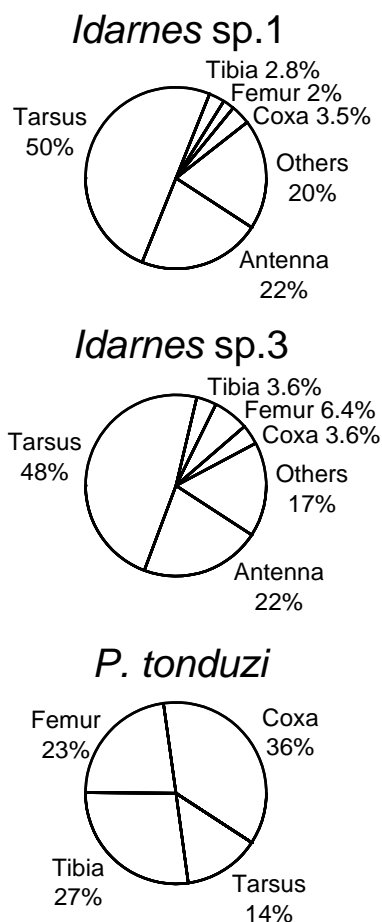


Figure 1 - Injury distribution between different body parts in *P. tonduzi* and *Idarnes* spp. wingless males. "Others" include injuries on head, gaster, thorax and bruises on any body part.

Table 3 - GLMs used to explain injury frequency in wingless males of *Idarnes* spp. (*Idarnes* sp. 1: $r^2_L = 0.245$, $\chi^2_2 = 41.3$, $P < 10^{-8}$; *Idarnes* sp. 3: $r^2_L = 0.148$, $\chi^2_3 = 23.6$; $P < 10^{-4}$). χ^2 values correspond to the change in deviance caused by the removal of the factor from the full model.

Variables	<i>Idarnes</i> sp. 1 (n = 68)				<i>Idarnes</i> sp. 3 (n = 92)			
	Slope.	d.f.	χ^2	P	Slope.	d.f.	χ^2	P
Fig diameter	-0.96	2	26.23	$<10^{-5}$	-1.41	2	20.00	$<10^{-4}$
N. of females	0.02	1	6.11	0.013	-	-	-	-
N. of males	-	-	-	-	0.06	1	18.24	$<10^{-4}$
Head width	-	-	-	-	5.92	15	34.26	0.003

In *Idarnes* sp. 1 IF was better explained by a negative correlation with fig diameter and by a positive correlation with the number of conspecific females. In *Idarnes* sp3, the best model to explain IF included, (1) a negative correlation with fig diameter, (2) a positive correlation with the number of conspecific males and (3) a positive correlation with the head width (Table 3). The SIF data was not significantly correlated with the study variables in both *Idarnes* species (*Idarnes* sp. 1: $\chi^2_4 = 2.33$, $P = 0.676$, n = 69 figs; *Idarnes* sp. 3: $\chi^2_4 = 2.79$, $P = 0.593$, n=107 figs).

DISCUSSION

Consistently higher injury levels in the two study *Idarnes* species were observed, than in the pollinator *P. tonduzi*. Results suggested that aggressive confrontations were involved in *Idarnes* mating strategies, whereas non-aggressive strategies were shown by *P. tonduzi* males. Results supported previous reports of aggressive confrontations in wingless males of *Idarnes*, as well as other nonpollinating species (Hamilton, 1979; Murray, 1987, 1989, 1990; West et al., 2001; Bean and Cook, 2001). However, the injury levels observed were smaller than those ones reported for nonpollinating fig wasps (mainly for those species belonging to the Sycoryctinae subfamily, Berg and Wiebes, 1992) from Australia and the Malaysia (Murray, 1989; Bean and Cook, 2001). The lower injury level observed in *Idarnes* might be related to a particular behavior shown by males during mating periods. Wingless *Idarnes* males show assessment displays and defensive behaviors (mating inside female galls and sheltering within empty galls) that seem to

play an important role to avoid fatal combats (Pereira and Prado, 2005).

The comparison of injury patterns observed in *P. tonduzi* and *Idarnes* spp. suggested some insights about mating strategies adopted by such fig wasp males. *Idarnes* males suffered injuries mainly in antennae and tarsi. These structures are probably more vulnerable during combats. *P. tonduzi* males suffered injuries predominantly throughout mid legs, which are morphologically smaller than fore and hind ones (Bouček, 1993). The high injury percentage pattern in mid legs (~95%) suggests that such injuries should be accidentally caused by fig manipulation instead of male confrontations. No evidence of aggressiveness in *P. tonduzi* males was found, giving support to previous reports on some pollinating fig wasp species (Hamilton, 1979; Murray, 1989, 1990). However, male aggressiveness in pollinating species has been recently reported for several genera of fig wasps (Greeff et al., 2003). Greeff et al. (2003) found a series of traits that co-occurred along with fighting behaviors. These included falcate mandibles, large head, long antennal scape, non-forward projecting antennae, often located in separate toruli instead of in a central depression, elongate legs, narrower tibia and femur, reduced dents on fore tibia, pronotum broader than long, mesonotum, metanotum and propodeum strongly fused. Such traits were not found in *P. tonduzi*; these give support to the present results, *i.e.*, the absence of an aggressive behavior in this species. The present results support the contest competition theory (Murray and Gerrard, 1985) since LEI and IF generally correlated positively with male encounter rates. Fig diameter, which estimates fig size, correlated negatively with IF in both *Idarnes* species and correlated negatively with LEI in *Idarnes* sp. 3. This scenario suggests that the probability of rival males to meet one another would be high in smaller figs. Moreover, higher densities of conspecific males would increase mating competition. An unexpected

result was the positive correlation between number of conspecific females and LEI, in *Idarnes* sp. 1. However, this positive correlation could be an indirect effect of a third variable, the number of males. Number of conspecific males and number of conspecific females were positively correlated in *Idarnes* sp. 1 ($r_{67} = 0.516, P < 10^{-4}$).

Male size, estimated by head width, does not seem to be important when explaining the total fight cost, since no correlation between the average head width and LEI was found. But head width was positively correlated with injury combat frequency in *Idarnes* sp. 3. This might reflect the occurrence of fighter-sneak morphology and suggests that larger males are able to injury one another more frequently, as reported in *Sycosapter australis* males (Bean and Cook, 2001).

Neither *Idarnes* species showed significant correlation between severe injury frequency and the study variables, as observed in other studies (Murray, 1987; Bean and Cook, 2001). The lack of correlation might be explained by the assessment behavior of relative fighting ability and defensive behaviors used by wingless *Idarnes* males during mate periods (Pereira and Prado, 2005). In *Idarnes* (Pereira and Prado, 2005) and *Philotrypesis pilosa* (Murray, 1987), combat costs seem to be high, since the probability of suffering a serious injury rises with fighting length. These high fighting costs might favor mechanisms that limit the risk of severe injury during combats, such as the assessment of relative fighting ability (Enquist and Leimar, 1983, 1990).

Brood sex ratio, used to estimate relatedness of interacting males, was not important to explain the total fighting cost (LEI) and the frequency of males with injuries or severe injuries. Between species, there is some empirical (West et al., 2001), experimental (Griffin et al., 2004) and theoretical (West et al., 2002; Griffin and West, 2002) evidence that kin-selected altruism is cancelled by competition among relatives in populations with limited individual dispersal. Our results suggest that this selective conflict could occur within species in *Idarnes* or, alternatively, that wingless *Idarnes* males are not able to assess relatedness among them.

Another question is why aggressive strategies did not evolve in *P. tonduzi* and other pollinating fig wasps (Murray, 1989, 1990;

Zammit and Schwarz, 2000). By considering the general female-biased sex ratio in pollinating fig wasp species, males that monopolized a greater number of females via aggressive behavior tactics should have higher fitness (Hamilton, 1979). However, in several pollinating fig wasp species, male-male competition seems to follow a less aggressive path than some nonpollinating species. Relatively larger brood sizes in the pollinating species, as observed in *P. tonduzi*, seem to decrease the value of contested resources to levels inferior to their expected future fitness returns (Enquist and Leimar, 1990). Moreover, larger broods lead to strong sperm competition, favoring morphological specializations (telescopic gaster and large sperm production) and behaviors that allow males to mate repeatedly (Murray, 1989, 1990). Therefore, male-male competition in these pollinating fig wasps occurred as a scramble competition (Murray, 1989, 1990; Zammit and Schwarz, 2000).

Results pointed out that different species under similar local conditions may follow distinct evolutionary histories. Within species, natural-history particularities might have some influence upon quantified injury levels in wingless males.

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RESUMO

Estudamos machos ápteros da espécie polinizadora (*Pegoscapus tonduzi*) e de duas espécies não-polinizadoras, gênero *Idarnes*, de vespas de figo associadas à *Ficus citrifolia* no Brasil, para responder as seguintes questões: 1) Os machos ápteros de *Idarnes spp.* e *P. tonduzi* apresentam estratégias diferentes de competição entre machos?; e 2) As variáveis associadas às injúrias são correlacionadas às características populacionais de cada espécie? Os níveis de injúrias foram maiores nas duas espécies de *Idarnes*. Nossos resultados sugerem que combates agressivos fazem parte da

estratégia de acasalamento de *Idarnes*, ao passo que machos de *P. tonduzi* adotam estratégias não agressivas. Em geral, as variáveis de injúria correlacionaram-se positivamente à taxa de encontros entre machos e negativamente ao tamanho do figo, apoiando a teoria de competição direta. Nossos resultados apontaram que espécies diferentes sob condições similares podem seguir histórias evolutivas distintas. Particularidades da história natural das espécies podem influenciar o nível de injúria quantificado nos machos ápteros.

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