

Comparative morphology and mate competition of flightless male fig wasps

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Abstract. The evolution of extreme and disparate male morphology in fig wasps was investigated by reference to differences in mate competition. Five morphological types were distinguished amongst the flightless males collected in Malaysia. Data are presented on three fig wasp species: *Ceratosolen solmsi* (Agaonidae, Blastophaginae), *Apocrypta bakeri* (Torymidae) and *Philotrypesis pilosa* (Torymidae). The three species are commonly found within the same fig receptacles but the males of each species have very different morphologies. The long, narrow, tubular males of *A. bakeri* occur at an intermediate density and are adept at finding mates which are located in the deeper recesses of the fig receptacle; the soldier males of *P. pilosa* also occur at an intermediate density and aggressively defend recently mated females who are distributed more evenly within the fig receptacle; and the males of *C. solmsi*, which are found at high density, and which are not obviously modified for fighting or rapid locomotion, have evolved morphology to counter intense sperm competition. It is suggested that intense sperm competition is a common feature of fig wasps in the family Agaonidae as a consequence of the high density of males and the enclosed female population, and that it accounts for the lack of aggression that is a characteristic of members of the family.

Fig wasps (Chalcidoidea, including the families Agaonidae, Eurytomidae, Pteromalidae and Torymidae) come in an extraordinary variety of shapes and sizes, many of which can be found among the inhabitants of a single fig receptacle (syconium). Even the winged males are quite different from the females of their own species but the wingless and wing-reduced males have been so extremely modified as to lose characteristics of the class Insecta (Grandi 1961), and generally it is not possible to sort the sexes into pairs on morphological grounds alone. Readers unfamiliar with the group can gain an appreciation of the variety of form from the fine colour portraits by A. Watsham (Boucek et al. 1981).

The exaggerated structures of male torymids and the profound sexual dimorphism that is found in all fig wasps were interpreted by Hamilton (1979) as adaptations derived from competition between males for females. Among species with flightless males, the female is frequently mated while still enclosed by her galled flower within the syconium, and apparently she has little opportunity to discriminate between mates. However, differences in male mating behaviour have been described which suggest that the form of male–male competition could vary widely. As Darwin (1871) made abundantly clear, competition between males need not be revealed only in weapons, or other structures

used in overt conflict, but can also be manifested in highly developed sense or locomotive organs. It is possible to divide most secondary sexual characters into three functional classes: those that increase the encounter rate with receptive mates; those that shorten the time required for courtship and fertilization; and those that improve an individual's ability to fight with, struggle against, or displace in some other way those of the same sex (see Thornhill & Alcock 1983, page 74 for a slightly different classification). Morphology that is adapted to serve one function may be incompatible with morphology adapted to other functions. Thus, differences in the relative importance of these three components of mate competition may explain the variability in structure of male fig wasps.

In this paper, I investigate the relationship between male morphology and competition for mates. I shall survey the distribution of male morphologies across a number of fig wasp species, and present a more detailed comparison of morphology and behaviour for three species of fig wasp which inhabit the same syconia of a common species of Old World fig tree.

The males of each of the three species are flightless and possess a highly distinctive morphology. One of the species, *Ceratosolen solmsi*, is a primary sycophile. The females enter through the ostiole (the eye of the fig) to pollinate and oviposit from

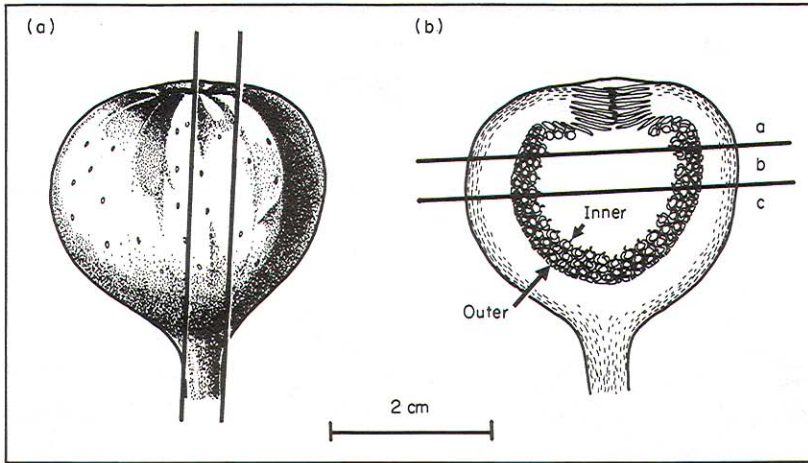


Figure 1. Subsections of the syconium of *F. hispida* used to record the location of fig wasp imagines. (a) Lines indicate slice removed. (b) The slice is divided by solid lines into three subsections: a, ostiole, b, middle, c, stalk. Inner and outer gall layers are also indicated.

within. Usually only one or a small number make this passageway into any one syconium, giving rise to a few large broods. Primary sycophiles include those species that both pollinate and oviposit while within the syconium (i.e. members of the family Agaonidae such as *C. solmsi*), and those species that merely oviposit within the syconium and are therefore parasitic on the fig. The other two species investigated, *Apocrypta bakeri* and *Philotrypesis pilosa*, are secondary sycophiles. The females of this group are parasitic on both the fig and the larvae of primary sycophiles. They oviposit through the wall of the syconium from the outer surface. Typically, a female will visit many syconia depositing a few ova in each so that the larvae developing within any one syconium are likely to be the progeny of many parents.

MATERIALS AND METHODS

All fig wasps were collected from sites close to Kuala Lumpur, Malaysia (3°10' N, 101°40' E) where the climate is moist and hot throughout the year. The collection of species included in the extensive survey is described by Murray (1989). The three species that were studied in more detail were collected from trees of *Ficus hispida* growing wild in the campus gardens of the University of Malaya. The trees fruited regularly every 2 months, and collections were made between March 1981 and January 1982. I recorded the population structure

of fig wasps by enclosing each fruit in a jar with an organdie cloth lid and counting fig wasps after they had emerged.

I investigated the distribution of imagines within the syconia by cutting the fruits in half through the ostiole and stalk (Fig. 1). If males had not yet emerged from their galls, I removed a slice about 5 mm thick from one half and divided it into three subsections according to the distance from the ostiole. I then cut open each gall with fine dissecting forceps to identify the species and sex of the imago. In this way the locations of about one-quarter of all imagines were sampled, with approximately equal numbers in each subsection. To test whether different species have different distributions, I examined the contents of 18 syconia. Within each syconium, the total number of imagines of each species and the proportion of imagines of each species in the subsection containing the ostiole were noted. For each pair of fig wasp species, the data on proportions (from each syconium) were then entered into a Wilcoxon matched-pairs signed-ranks test. I compared the distribution of imagines across gall layers (see Fig. 1) in the same way. The variation in sex ratios depending on location within the syconium was also tested in similar fashion, but comparisons were made within fig wasp species and between subsections or gall layers.

I recorded the location, activity and mating behaviour of fig wasps after slicing off the stalk end of a syconium and wrapping the remainder tightly with transparent kitchen wrap. Individual males

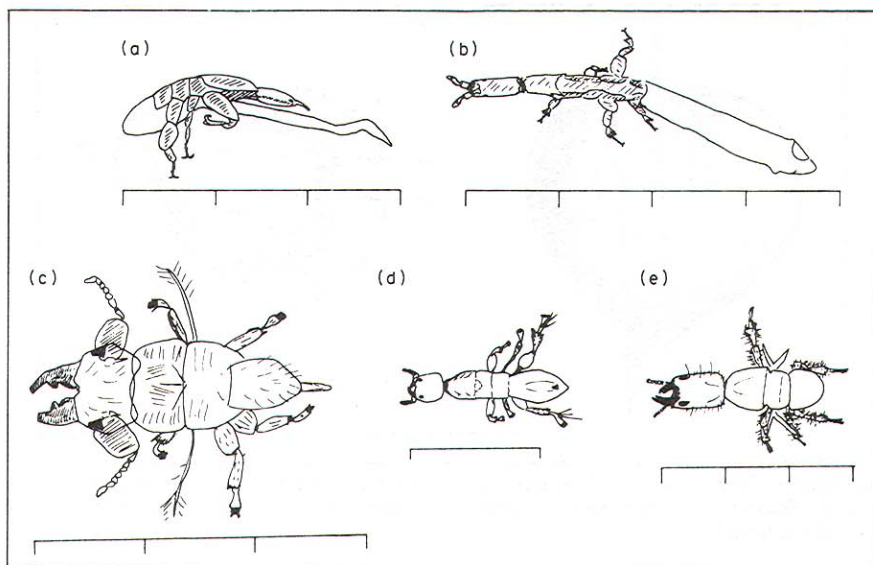


Figure 2. Sketches of Malaysian fig wasps illustrating gross differences in male morphology: (a) *Ceratosolen constrictus* (hooked); (b) *Apocrypta bakeri* (tubular); (c) *Otitesellinae* sp. collected from *Ficus annulata* (hogbacked soldier); (d) *Philotrypesis* sp. collected from *F. annulata* (minute); (e) *Philotrypesis pilosa* (soldier). The sketches are drawn to different scales, indicated by divisions at 1-mm intervals.

were marked with water-soluble paint and their behaviour was observed under a binocular microscope ($\times 10$ magnification) with cold white light. I applied a demisting spray (commonly used for spectacles) beforehand to the undersurface of the cellophane to improve visibility. I sampled the behaviour of individual males of *C. solmsi*, *P. pilosa* and *A. bakeri* for 12, 39 and 10 h, respectively. Activity and location were noted onto check sheets at 10-s intervals, and injuries were assessed at the end of the mating period. Injuries of individual males were rated for severity on a scale of from 0 to 8. These scores were then averaged across all males in a given syconium to give the lifetime extent of injury for the syconium-population. Further details of the methods are given in Murray (1987).

RESULTS

Description of Male Morphology

Five basic morphological patterns were differentiated from amongst the many flightless males collected from over a dozen fig species in Malaysia (Fig. 2, Table I): hogbacked soldiers have an enlarged head and mandibles, and a dorsal convexity with the anterior edge shielding the base of

the head; the head and thorax are heavily sclerotized; soldiers are similar to hogbacked soldiers but the head is not shielded by the thorax which is flat; the powerful legs have long spines; minute males are less than a quarter the weight of a female (Table II shows the range of sexual dimorphism in body size); the head and thorax are narrow and the mandibles small to moderate; tubular males are long and narrow; the abdomen is extremely extendible with forked or paddle-like structures at the tip; the mandibles are small; hooked males have a moderately long and narrow head and thorax; the abdomen is folded over on itself so that the extendible tip is anterior to the head during copulation and the mandibles are small.

The different morphologies do not fall evenly across taxonomic units. The family Agaonidae (which contains the pollinating species of fig wasp) have wingless males which, except for the genus *Alfonsiella*, are all of the hooked type. Among the parasitic wasps, the genus *Apocrypta* are typically of the tubular type (Ulenberg 1985), but other genera, such as *Philotrypesis* and *Sycoryctes* have both minute and soldier males. In some instances, male morphology varied considerably even within the species. *Sycoryctes* males inhabiting syconia of *F. grossularioides* displayed allometric growth in

Table I. Male morphology and injury scores for fig wasps

Fig wasp species	Male morphology	Mean lifetime extent of injury
<i>Eupristina adempta</i>	Hooked	0.046
<i>Ceratosolen</i> sp.	Hooked	0.322
<i>Deilagaon annulatae</i>	Hooked	0.428
<i>Lipothymus sundaicus</i>	Hogbacked soldier	0.429
<i>Sycoscapter</i> sp. 2	Soldier	0.445
<i>Ceratosolen solmsi</i>	Hooked	0.458
<i>Blastophaga</i> sp.	Hooked	0.743
<i>Ceratosolen constrictus</i>	Hooked	0.748
<i>Eujacobsonia genalis</i>	Hogbacked soldier	1.032
<i>Apocrypta varicolor</i>	Tubular	1.195
<i>Philotrypesis</i> sp. 2	Soldier	1.199
<i>Eukoebelea</i> sp. 1	Tubular	1.676
<i>Apocrypta bakeri</i>	Tubular	1.816
<i>Philotrypesis</i> sp. 1	Minute	1.875
<i>Sycoryctes</i> sp. 2	Soldier	2.846
<i>Epichrysomallinae</i> sp.	Soldier	3.001
<i>Otitesellinae</i> sp.	Hogbacked soldier	3.534
<i>Philotrypesis pilosa</i>	Soldier	4.175
<i>Sycoscapter</i> sp. 1	Soldier	4.250
<i>Sycoryctes</i> sp. 1	Minute	4.625
<i>Philotrypesis</i> sp. 3	Soldier	4.865
<i>Eukoebelea</i> sp. 2	Tubular	5.273
<i>Sycoscapter</i> sp. 3	Soldier	5.420
<i>Philotrypesis spinipes</i>	Soldier	5.423
<i>Arachonia</i> sp.	Soldier	5.496

head size which gave rise either to small-headed individuals who behaved like tubular males or to large-headed soldiers. A peculiar divergence was noticed in one species (subfamily Otitesellinae) reared from syconia of *F. annulata*. The males were uniformly large, each with a rounded hog's back and shovel-like mandibles, but they could be separated into two distinct forms by a marked difference in the size of the scape and by other detailed features of the head and thorax (one form is illustrated in Fig. 2c). In one other species (subfamily Epichrysomallinae), which was common in the small syconia of *F. benjamina*, there were winged and wingless males, an extreme form of male dimorphism that is discussed by Hamilton (1979).

Of the three species collected from syconia of *F. hispida*, the males of *C. solmsi* were of the hooked type, the males of *A. bakeri* were tubular, and those of *P. pilosa* were of the soldier type (the latter two

species and *C. constrictus*, a species congeneric with *C. solmsi* and with similarly shaped males, are illustrated in Fig. 2).

Distribution and Sex Ratio

Most syconia of *F. hispida* contained two or three species of fig wasp with the pollinator *C. solmsi* being the most abundant species (Table III). *Ceratosolen solmsi* was distributed evenly across the three subsections of the syconium and across the three layers of galls (Table IV). The two parasites (*P. pilosa* and *A. bakeri*) were more commonly found in the subsection nearest the ostiole where the syconium wall is thinnest. They were also more abundant in the outer layer of galls (i.e. that closest to the fleshy wall of the syconium) which is presumably easier for a female to reach when she is searching for a suitable site for oviposition. The distribution of *A. bakeri* was the most extreme with 90.3% of imagines infesting the outer layer of galls in the ostiole subsection. Many of these were in a ring of galls underlying the male flowers that surround the ostiole. Consequently, the larvae of the pollinator species, *C. solmsi*, suffered a higher incidence of parasitism from the other two species in the outer gall layer than in the inner one (8% versus 2%) and in the ostiole subsection than in the stalk subsection (11% versus 1%).

All species had a higher proportion of males in galls of the inner layer (i.e. those galls that form the surface to the hollow central chamber Table V). Males emerging from galls of the inner layer were able to move freely within the central chamber. Sex ratios did not vary between subsections of the syconium.

Searching for Females

On opening a syconium at the right stage, it is at once obvious that the males of each species have quite distinct forms of locomotion. A *C. solmsi* male crawls across the galls in a slow ponderous manner that is reminiscent of the movements of hypometabolic mammals (such as the slow loris, *Nycticebus coucang*, or the sloths *Choloepus* and *Bradypus*). He searches for females by crawling along the surface layer of galls that lines the inner chamber of the syconium (at about 0.3 mm/s), and periodically squeezing outwards towards the wall of the syconium, through densely packed galls. In the latter manoeuvre, his progress is very slow.

Table II. Weights of fig wasps inhabiting syconia of *F. annulata*

Species	Mean live mass of males		Mean live mass of females		Sexual dimorphism $\left(\frac{\text{male mass}}{\text{female mass}} \right)$
	μg	<i>N</i>	μg	<i>N</i>	
<i>Deilagaon annulatae</i>	270	20	210	20	1.286
<i>Eujacobsonia genalis</i>	260	17	270	22	0.963
<i>Arachonia</i> sp.	320	9	320	22	1.000
<i>Otitesellinae</i> sp.	470	25	580	8	0.810
<i>Philotrypesis</i> sp.	64	11	290	17	0.220

Table III. Fig wasp population sizes and sex ratios in syconia of *F. hispida*

Fig wasp	Median number (M + F)	Range	Median sex ratio M/(M + F)	Range	Number of syconia
<i>C. solmsi</i>	816.0	210–1579	0.258	0.131–0.672	39
<i>P. pilosa</i>	18.3	3–116	0.357	0.0–0.579	43
<i>A. bakeri</i>	20.8	2–101	0.321	0.0–1.0	42

Table IV. The location of fig wasps in different subsections and layers within the syconium before emergence from galls

Fig wasp	Ostiole/ Outer layer %	Middle %	Stalk/ Inner layer %
Different subsections			
<i>C. solmsi</i>	89.5	96.8	98.9
<i>P. pilosa</i>	5.8	2.5	1.1
<i>A. bakeri</i>	4.7	0.7	0
Mean number of galls in subsection			
	107.5	101.8	115.4
Different layers			
<i>C. solmsi</i>	92.2	96.8	98.1
<i>P. pilosa</i>	4.0	3.2	1.7
<i>A. bakeri</i>	3.8	0.1	0.2
Mean number of galls in layer			
	132.2	98.8	93.8

Averages from 18 syconia are presented.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Statistics refer to the probability that different species share the same distribution in the syconium (see Methods).

Eventually, his investigations complete, the male reverses back by the same route to the inner chamber. In marked contrast, the soldier males of *P. pilosa* are agile and quick; their bodies are raised

clear of the galls on strong legs to aid their rapid progress (1–3 mm/s) during their excursions across the inner chamber. They investigate the deeper galls by biting open short passages but make only slow

Table V. Sex ratios, M/(M + F), in different localities of the syconium

Fig wasp	Number of syconia with at least one wasp	Sex ratio			<i>P</i>
		Ostiole/ Outer layer	Middle	Stalk/ Inner layer	

Different subsections					
<i>C. solmsi</i>	18	0.282	0.277	0.260	NS
<i>P. pilosa</i>	12	0.485	0.232	0.367	NS
<i>A. bakeri</i>	14	0.364	0.111	—	
Different layers					
<i>C. solmsi</i>	18	0.187	0.285	0.384	**
<i>P. pilosa</i>	12	0.173	0.671	0.722	*
<i>A. bakeri</i>	14	0.339	1	1	

The mean number of individual fig wasps sampled in each locality is given in Table IV.

* $P < 0.01$; ** $P < 0.001$. Statistics refer to the probability that sex ratios from different localities (ostiole versus stalk subsection or outer versus inner gall layer) have the same distribution (see Methods). There were insufficient data for a test on the distribution of sex ratios in *A. bakeri*.

Table VI. Time spent in different localities of the syconium and in fighting by individual male fig wasps after leaving their natal galls

Fig wasp	Location			Fighting %	Hours of activity sampled
	Inner chamber %	Within galls %	Between galls %		
<i>C. solmsi</i>	54.4	0	45.6	0	15
<i>P. pilosa</i>	50.2	11.5	38.3	3.6	37
<i>A. bakeri</i>	6.5	52.8	40.7	0.8	9

progress in this way. The long slender males of *A. bakeri* slide apparently effortlessly between the tightly packed galls. Sometimes a male will anchor himself to a gall by lodging the inflated tip of his abdomen on the inside of a narrow entrance hole (see Mating and Fertilization below) or exit hole. Once secure, the male makes forays outwards to the full length of his extremely extendible abdomen, periodically pulling himself backward before setting off in a different direction. Curiously, the males do not make use of their paddle-like flaps at the tip of the abdomen in these manoeuvres, although the tubular males of the genus *Eukoebelia* use the forked tip to their abdomens as an anchor. Relatively rapid movement is possible between galls (0.1–0.2 mm/s), but progress over the surface of galls is not necessarily easy (speeds ranging from 0.1 to 1.0 mm/s) as the short-legged male may become temporarily

stranded with his legs waving uselessly in the air; however, little time is spent on the surface of the gall layer within the inner chamber (Table VI).

Mating and Fertilization

Ceratosolen solmsi

On locating a new gall, the male of *C. solmsi* will first make a few brief scrapes on its surface with his mandibles and then, using his antennae, appear to test in some way whether the occupant is of the right sex and species. If the occupant is judged suitable, he will continue biting until a small hole has been formed, taking an average of 84 s to complete it. Despite this time investment, the male only occasionally makes use of pre-existing holes, so that most surface galls have five or six perforations

Table VII. The mating history of female *C. solmsi* (see Fig. 3)

Hour since emergence of males	Virgin females remaining	No. of copulations (all females)	Copulations per female per h	Duration of copulations (min)		Copulations per mating attempt (%)
				Mean	SD	
0-1	19	30	1.58	2.41	1.57	69.8
1-2	6	18	0.95	2.97	2.27	69.2
2-3	3	13	0.68	2.09	0.99	65.0
3-4	2	13	0.68	1.10	1.03	56.5
4-5	1	8	0.42	1.07	0.60	61.5
18-19	1	5	0.53	0.78	0.98	62.5

within a few hours of the start of mating activity. Care must be taken when estimating the duration of each copulation as the male often continues to enlarge the entrance hole even after the tip of his abdomen has slid forward along the underside of his head and entered the gall.

Several anecdotal observations indicate that males may have difficulty initiating copulation when the female is unreceptive. On one occasion a non-virgin female was seen to whirl rapidly round just as a second male introduced his head through a second entrance hole; the male promptly withdrew and moved off. On two other occasions, a male was observed to make persistent attempts to copulate with a non-virgin female over a span of more than 5 min. The male repeatedly introduced the tip of his abdomen through a hole in the gall only to withdraw it again after a few seconds investigation. In these two cases, the female may have been biting at the male's abdomen as was observed in the pollinator (*Blastophaga* sp.) of *F. grossularioides*, where the females caused dark bruising of the aedeagus (penis) and surrounding tissues. Thus, females of *C. solmsi* probably become less receptive and less easy to mate with after their first mating. Nevertheless, males that persist manage to copulate with females that have been mated many times before.

Among 18 females who were observed continuously over several hours (and who were mated at least once in that period) 17 were mated successfully by their first suitors. Of 115 subsequent mating attempts, 70 were successful. The proportion of successful matings did not decrease with time elapsed after the first mating, suggesting that females were unable to increase the degree to which they could block males attempting to mate (Table VII). In nature, the mating phase probably lasted

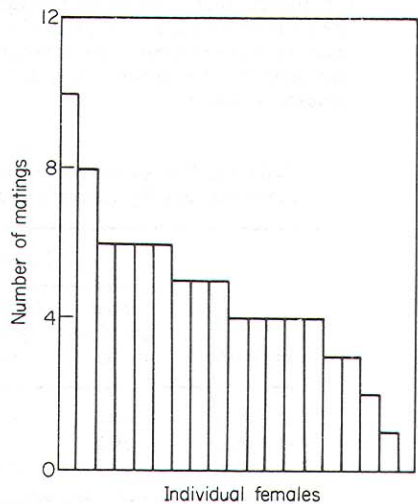


Figure 3. Distribution of the number of matings per female *C. solmsi*. Individual females are ranked from highest to lowest according to the number of matings observed in a 5.5-h period following emergence. Females were still being mated 13 h later. By extrapolation, each female is estimated to have averaged seven extra copulations in this 13-h period.

from 8 to 16 h, but in the case of syconia under observation in the laboratory, I could confirm copulation with females located in surface galls 24 h after the start of male activity by applying drops of ether to mating pairs and dissecting open the galls. Thus, females of *C. solmsi* must frequently be mated up to a dozen times or more before leaving the syconium (Fig. 3). For their part, the males of *C. solmsi* initially averaged five matings each per h, declining to about half that rate 2 h later (Table VIII). Thus, a total of 35 matings would be about average in a lifetime which included (say) 12 h of

Table VIII. Mating history of male fig wasps

Fig wasp	Matings per h	Number of h sampled	Duration of copulations† (min)	Range (min)	Number of copulations
<i>C. solmsi</i>					
First 2 h of activity	5.0	6			
Overall	3.8	10	2.02	0.17– 9.00	75 } NS
<i>P. pilosa</i>	1.2	39	2.03	0.17– 8.83	62 } *
<i>A. bakeri</i>	0.5	10	22.50	4.67–68.50	5 } *

* $P < 0.001$. Statistics refer to the probability that copulations have the same duration in two different species.

†In *A. bakeri*, copulation refers to periods of continuous occupation by the male and female within the same gall.

mating activity. The mean duration of matings decreased with the time elapsed since a female had first mated (Spearman's $r = -0.47$, $P < 0.001$, Table VII).

Philotrypesis pilosa and Apocrypta bakeri

Multiple mating of females was also observed in the two parasitic fig wasps but to a lesser degree. Females of *P. pilosa* were mated 2.53 times on average ($N = 30$ females) with a range of one to eight matings per female per lifetime, but usually the same male mated on each occasion and the time interval from the first to the last mating by a female was in the order of 20 min (Murray 1987). Males of *A. bakeri* averaged only one mating each for every 2 h of activity and guarded their mates for longer than the other two species (Table VIII). Overall, the males of *P. pilosa* and *A. bakeri* copulated less often than those of *C. solmsi*, and the females of the two parasitic species were more frequently in a receptive state when mated.

Mate Guarding and Fighting

In common with males of the other agaonids collected in Malaysia, those of *C. solmsi* had low injury scores (Table I). Fighting, shoving or other signs of overt conflict were not observed between males of *C. solmsi*. Sometimes two males would bite entrance holes into the same gall, their heads touching, but with no outward sign of aggression; only after one had started to copulate would the other give up and wander elsewhere. Individuals did not tend to stay in any particular locality and regularly traversed the interior.

When soldier males of *P. pilosa* were searching for females, they soon developed an attachment to small sites within the syconium, and after they had found and mated a female they would defend the site for some minutes (Murray 1987). They spent an unusually high proportion of their active life in fighting, which engendered a high risk of injury in the lifetime of a male (Tables I, VI). The enlarged head and mandibles of this species, and the heavily sclerotized plates which cover the thorax are useful adaptations for fighting. The tubular males of *A. bakeri* also guarded females after mating, and spent a considerable proportion of their time within galls (Table VI). They also fought intensely, and sometimes accumulated a heavy injury load (Table I). Although the males of *P. pilosa* and *A. bakeri* suffered a high frequency and intensity of fighting injuries, high scores for the lifetime extent of injury were not necessarily associated with soldier and tubular morphologies in males of other species. In fact, a wide scatter of injury scores in four of the five basic morphologies (i.e. those other than the hooked type) was apparent (Table I).

DISCUSSION

The distinctive morphologies of the males of the three fig wasp species inhabiting syconia of *F. hispida* can be related to specific features of mate competition. The high frequency of multiple mating by individual females of *C. solmsi* is presumably associated with intense sperm competition among males. The morphology of the *C. solmsi* male is well adapted to sperm competition: his relatively narrow head and thorax affords him easy

access to females lying in deeply recessed galls; his extendible and directionally mobile abdomen enables him to mate even when the female is unreceptive and poorly positioned in the gall for copulation; and his large abdomen may provide a capacious storage space for sperm. The decline in duration of copulations of *C. solmsi* after 2 h of mating activity suggests that the male's supply of sperm may eventually become depleted, as occurs in other parasitic wasps following multiple copulations (Van den Assem 1986).

It is tempting to conclude that the large head and mandibles of fighting males, such as those of *P. pilosa*, are hallmarks of aggressive behaviour. Within species, the larger individuals are often the most active fighters. Between species, however, the relationship breaks down. The wide scatter of injury scores among species in four of the five major types of male morphology demonstrates that the degree of sexual dimorphism in body size, the relative size of mandible, and the presence of heavily sclerotized plates on the thorax are not related to the intensity of fighting, or risk of injury, in a simple way.

In male fig wasps, soldier morphology may evolve only if unconstrained by selection for structures that serve other functional aspects of mate competition. The narrow head and body of the tubular males of *A. bakeri* were clearly adaptations for movement in a tightly constricted environment. The females of *A. bakeri* were invariably deeply recessed within the gall layers, and were rarely numerous. Locating these females would have taken many hours of laborious excavation by large-headed soldier males. The morphology of the tubular males of *A. bakeri* (and that of minute males in syconia of other *Ficus* species) enabled the males to search rapidly, so reducing the time taken to encounter receptive mates.

The incidence of fighting morphology in the three species of fig wasp in syconia of *F. hispida*, and in the larger sample included in Table I, was not restricted to a narrow range in the density of males. The locality of male conflict within, and the inner architecture of, the syconium probably influenced the detailed evolution of soldier morphology. From the distribution of female fig wasps alone, one might suspect a general tendency for males to start searching for mates that are in galls lining the inner chamber, and then to work outwards through the tightly packed layers to the outer galls lining the syconium wall. Much of the fighting between

P. pilosa males took place in the early stages, within the interior chamber, where males could strike at each other unimpeded by physical obstacles. In monoecious species of *Ficus*, which often have syconia with little or no central chamber, the fighting males have enlarged thoraces dorsally, giving them a hogbacked appearance. In amongst the tightly packed galls and male flowers, the large size of one of these heavily armoured males was sometimes sufficient in itself to block the access of a rival to a gall containing a receptive female.

The males of *C. solmsi* occur at a relatively high density within syconia, do not suffer from fighting injuries, and do not possess fighting morphology. In these respects, they are representative of the males of most other agaonid species. I have previously predicted that the overall cost of fighting per male fig wasp will decline at high male densities, because of the low escalation cost of individual fights (Murray 1987). The prediction has been supported by comparative data on injuries in 25 species of Malaysian fig wasp (Murray 1989). However, a large part of the observed variation in injury levels was accounted for by phylogenetic differentiation between primary and secondary sycophiles. I suggest that the high male density in agaonid populations initially gave rise to multiple mating and intense sperm competition; that specialized morphology then evolved to combat sperm competition, possibly partially replacing previous morphology used in fighting; that this in turn allowed males to mate repeatedly with unreceptive females; and that, in consequence, the contest value of each mating was substantially reduced, further decreasing the usefulness of aggressive behaviour and fighting morphology.

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