POLYMORPHISM AND FIGHTING IN MALE FIG WASPS

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ABSTRACT

Male fig wasps (Hymenoptera: Chalcidoidea) exhibit a fascinating range of morphology and behaviour. A cluster analysis, based on descriptions of the males of several hundred species, distinguished six major morphological groups. Behaviourial observations suggest that male morphology is related to the levels of inter-male aggression. Three behaviourial groupings were identified. Fighting species generally mated in the fig cavity, pacifist species mated in the females' galls or outside the figs. Mating sites are thus the primary determinants of male morphology and behaviour. In fighting species males were larger than their females, whereas pacifists and aggressors were equal in size or smaller than conspecific females.

The large males in fighting fig wasps appear to be a consequence of sexual selection because larger males tended to win fights. Within a species there were no differences in the size of the galls that produced males and females, even in species where sexual size differences were present, suggesting that there is a heritable component to wasp size. No alternative advantages for smaller males were detected. Although fights were sometimes fatal, damage was not always a consequence of fighting behaviour and was recorded in both fighting and pacifist species.

Sex ratios in several species were more female biased at higher population densities. Sex ratios of species with 'internally' ovipositing species were heavily female biased, but approached 1:1 in more outbred species with 'externally' ovipositing females.

Levels of matedness, among females ranged from 73% to 99%. No evidence for sperm exhaustion was obtained.

Species of *Philotrypesis* with both winged and flightless males were present only in southern African *Ficus* species from subsections *Platyphyllae* and *Chlamydodorae*. No species had only winged males. The flightless males of some *Philotrypesis* species were themselves polymorphic. In one polymorphic *Philotrypesis* species, winged males were found to be rare at high densities, but common at low densities.

Digitata and *religiosa* males of *Otitesella* differed in coloration, size and behaviour. *Digitata* males were aggressors while *religiosa* males were fighters. *Digitata* males escaped from the figs whereas *religiosa* males remained inside the figs, perhaps because only *digitata* males were attracted to light. Proportionally more *digitata* than *religiosa* males were present in low density populations and females were found to respond differently to the two morphs.

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1 INTRODUCTION

OF DINNER AND DYNASTIES ...

Fig trees (genus *Ficus* L., family Moraceae) have been associated with man since ancient times. In Homer's Iliad and the Odyssey, Ge turned her son Sykeus into a fig tree to save him from Zeus (Storey, 1975). Roman legend would have us believe that the twins, Romulus and Remus, the founders of Rome, were sheltered in infancy by a sacred fig tree, '*Ficus ruminalis*' named after Rumina, the goddess who watched over suckling animals (Condit, 1947). Buddha is supposed to have meditated in the shade of *F. religiosa* L. (Mabberley, 1987) and the Asian fig, *F. benghalensis* L. or banyan tree, derived its name from the 'banians' or traders seen resting in the shade of these trees (Mabberley, 1987).

Figs were also allied to fertility cults. The domestic fig, *F. carica* L. was sacred to the flabby, procreative Greek god, Dionysius and the sycamore fig, *F. sycomorus* L. was sacred to the Egyptian goddess of love, Hathor (Galil, 1967). The highly developed death cult and dry climate of ancient Egypt were conducive to the preservation of fig offerings in tombs that can still be viewed today (Galil, 1967).

Besides featuring in man's religions, fig trees have also served more practical purposes. The milky white latex of *F. elastica* Roxb., the Indian rubber tree, was the basis of a rubber industry. The Assyrians cultivated the domestic fig, *F. carica*, as early as 2000 BC for its fruit, and in time its cultivation spread around most of the countries bordering the Mediterranean (Figure 1.1 a). The epithet *carica* refers to Caria, an ancient region noted for its figs (Storey, 1975). Today *F. carica* is an important fruit crop in many parts of the world, but especially in Middle Eastern countries where the fruit is eaten fresh, dried, as a paste and baked in pastries (Storey, 1975). In ancient Egypt the sycamore fig tree was treasured for its shade, timber and especially its fruit (Figure 1.1 b). The Hebrews, however, used the sycamore tree mostly for its timber (Galil *et al*, 1976). Today, there is renewed interest in wild fig trees as a supplement to the diet of people in Africa (N. Vietmeyer, personal communication).

FIGS AND THEIR POLLINATOR FIG WASPS

While man and his deities have been associated with figs for millennia, the relationship between figs and certain species of wasp dates back much further, to the early Cretaceous period - some hundred million years ago (Galil, 1977). The necessity of tiny wasps for a good fruit set in cultivated figs was recognised more than two thousand years ago by Aristotle and one of his pupils Theophrastus (Hill, 1967).

Each fig species usually supports a unique pollinating wasp belonging to the family Agaonidae, subfamily Agaoninae (Hymenoptera, Chalcidoidea) (Compton, 1990; Galil, 1977; Janzen, 1979c; Michaloud *et al*, 1985; Ramirez, 1970; Van Noort *et al*, 1989;

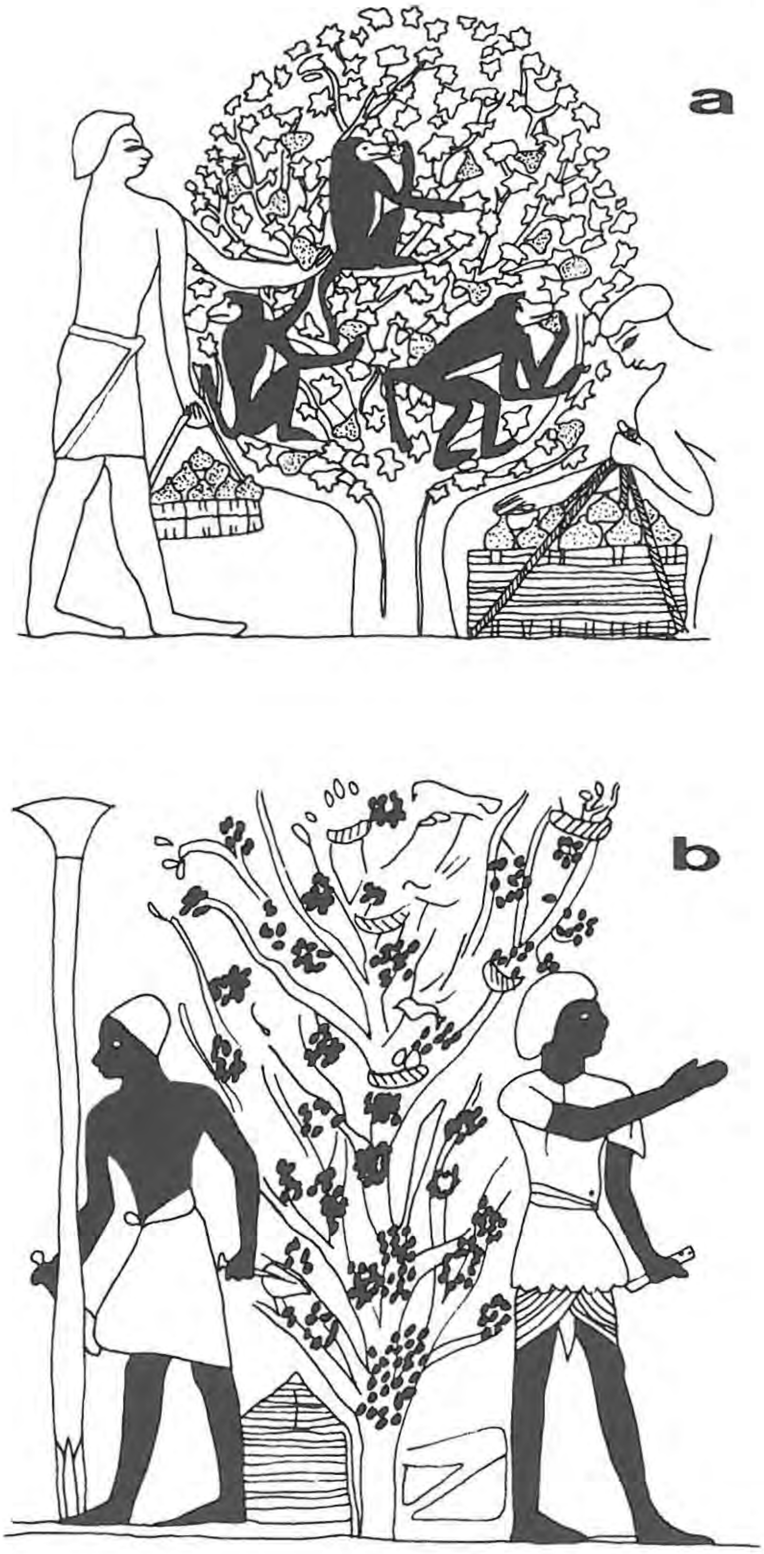


Figure 1.1 Egyptian tomb-wall paintings depicting a) people picking *F. carica* L. figs (modified from Condit, 1947) and b) workers resting under a sycamore fig , *F. sycomorus* L. (modified from Raffle, 1977).

Wiebes, 1979a, 1982a, 1987; Wiebes & Compton, 1990). Figs and agaonids are totally dependent on each other for sexual reproduction: the wasps pollinate the flowers and lay eggs in a proportion of the seeds, the sites for their larval development (Janzen, 1979a, 1979b).

Anatomically, the fig (often referred to as a syconium), is a globular inflorescence. It is most easily envisaged as a hollow ball, the inside of which is lined with many female florets and a few male florets (Janzen, 1979c). The entrance to the fig interior (lumen) is called the ostiole; this consists of a narrow passage lined with inflexed scales, the opening of which is covered by overlapping ostiolar bracts. The female flowers consist of a single ovule surrounded by two to five perianth lobes, depending on the species. They may be sessile or attached to a pedicel of variable length. Each flower has a single style that in most species has a papillate stigma. The staminate (male) flowers generally consist of two introrse stamens, surrounded by some simple and free perianth segments (Verkerke, 1989).

Fig ontogeny passes through a series of stages: 'pre-female', 'female', 'inter-floral', 'male' and 'post floral' (Galil, 1977; Galil & Eisikowitch, 1968a, 1968b). The 'pre-female' is the first stage, before any of the flowers ripen. Female flower maturation (the 'female' stage) corresponds with the opening of the fig ostiole and the release of pollinator-specific volatile attractants (Van Noort *et al*, 1989).

After a female wasp has been attracted to the fig she finds the ostiole and attempts to crawl through it. The anatomy of female agaonids has evolved to facilitate entry through the ostiole (Ramirez, 1976, 1978). These adaptations include the 'controlled' breakage of antennae and loss of wings, dorso-ventral flattening of the head, desclerotisation of some areas of the head (which allow it to collapse while the wasp is passing through the ostiolar scales), a depression that accommodates the antennal scapes, and unique transversely carinate or serrate mandibular processes that facilitate only forward movement through the ostiole (Ramirez, 1976). Despite these adaptations, over one tenth of the female wasps may die during ostiole penetration (Compton *et al*, 1991).

Once a pollinator female has reached the fig lumen she oviposits into the ovaries of some of the female florets and galls them (Galil & Eisikowitch, 1968a, 1968b, 1969, 1974; Verkerke, 1989). She dies shortly afterwards (Galil & Eisikowitch, 1968b). Pollination is carried out by the females of some species of wasps during egg laying by using their forelegs to extract pollen from special baskets on the underside of the body (Ramirez, 1969, 1976, 1978); in more primitive wasps the same result is obtained by regurgitation or accidentally by brushing pollen from the body surface onto the stigmas (Okamoto & Tashiro, 1981; Ramirez, 1969, 1970, 1976, 1978). Only oviposition into or galling of the fig ovules, and not pollination, is essential for continued development of figs beyond the 'female' stage (Galil & Eisikowitch, 1968b; Nefdt, 1989), but pollination is essential for the growth of viable seeds.

Female wasps that have entered the fig die and the ostiole closes as the fig enters the 'inter-floral' stage. Female flowers harbouring wasp larvae develop into galls, where the larvae feed on ovular tissue. The ovules that were pollinated, but not oviposited in, develop as seeds (Galil & Eisikowitch, 1968b). Male flowers develop simultaneously. Their anthers, containing ripe pollen, have matured by the start of the 'male' phase of fig development (Galil & Eisikowitch, 1968b).

During the 'male' phase the adult male agaonids emerge into the fig cavity. They then mate with the females inside their galls and (usually) co-operate to tunnel out through the fig wall and release the females. If too few males develop in the fig, as can happen with *Ceratosolen arabicus* (Agaoninae) in *F. sycomorus*, they are unable to chew a tunnel and the fig becomes a potential death trap for the females (Galil & Eisikowitch, 1968b). The males of *Blastophaga quadraticeps* Mayr (Agaoninae) from *F. religiosa*, are active inside the figs despite the relatively high carbon dioxide concentrations that are present. *B. quadraticeps* females, in contrast, are quiescent (Galil *et al*, 1973). In *F. religiosa* the perforation of the fig wall by the males allows equilibration of the atmosphere within the fig with that outside the fig. The carbon dioxide concentration thus decreases and the inhibition of female wasp activity is removed. Similar effects of carbon dioxide may be present inside figs of other species.

As soon as the female agaonids become active they widen the holes in their galls started by males, emerge into the fig lumen and collect pollen. This activity may be incidental, when the female brushes past the mature male florets (Okamoto & Tashiro, 1981) or deliberate. She may either ingest the pollen (Galil & Eisikowitch, 1968a; Ramirez, 1976, 1978) or lift it with combs on her forelegs to the underside of the thorax and shovel it from there into specialized thoracic pockets (Galil & Eisikowitch, 1974). The female agaonids then leave via the tunnel chewed by the males. Once the females escape from the figs they usually have to fly to another tree in order to lay their eggs, because of within-tree synchrony in fruit production. Once they locate a tree bearing attractive figs the cycle is repeated. When females have vacated their figs (the 'post-floral' stage), the figs ripen and become attractive to birds and bats, which disperse the seeds.

Dioecious *Ficus* species, unlike monoecious species, have distinct 'male' and 'female' figs borne on separate trees. These figs differ from each other in the proportion of seeds and wasps that they produce (Galil, 1973, Verkerke, 1989). This is the consequence of a difference in the length of the styles of the female florets in the two types of figs. Female agaonids can only oviposit in the ovules of flowers with shorter styles (Galil, 1973). Consequently the 'male' figs with short styled flowers produce large numbers of wasps whereas 'female' figs produce large numbers of seeds and few, if any, agaonids.

Worldwide there are approximately 850 species of *Ficus* (Berg, 1989). About 500 species occur in the Asian and Australasian areas, with the rest equally divided between the Americas and

Africa (Wiebes, 1986). *Ficus* species range from large trees, to shrubs, clinging lianas and epiphytes (Janzen, 1979). All four subgenera recognised by Berg (1990a) are represented in Africa, and comprise 105 species. In southern Africa, only one dioecious species (*F. capreifolia*, subgenus *Ficus*) is present, while the monoecious subgenera *Sycomorus*, *Urostigma* and *Pharmacosycea*, have two, 29 and zero representatives respectively. Of these 32, 17 are widespread throughout Africa, nine are shared with East Africa and six are restricted to the area. The subcontinent is therefore characterised by a large proportion of widely distributed species with few endemics (Berg, 1990 b).

NON-POLLINATING FIG WASPS

Agaonines are not the only wasps that inhabit figs, but they are the only ones able to actively pollinate them. Each species of *Ficus* supports several non-pollinating fig wasps, an extreme example being *F. thonningii* Bl. where over 25 species have been recorded (Boucek *et al*, 1981). Boucek (1988) recently reviewed the higher taxonomy of Old World fig wasps (Table 1.1), most of which are now placed in various subfamilies of Agaonidae. Boucek's classification is followed in this thesis, where all the wasps inhabiting figs are collectively referred to as fig wasps. The chalcid and braconid parasitoids of fig-feeding beetle and moth larvae are not covered here.

Table 1.1 The taxonomy of fig wasps *sensu* Boucek (1988).

FAMILY	SUBFAMILY AND TRIBE
EURYTOMIDAE	
TORYMIDAE	
ORMYRIDAE	
AGAONIDAE	
	EPICHRYSOMALLINAE
	OTITESELLINAE
	SYCOECINAE
	SYCORYCTINAE
	Sycoryctini
	Apocryptini
	SYCOPHAGINAE
	AGAONINAE

Non-pollinating fig wasps have been called mess-mates (Wiebes, 1977a), interlopers (Bronstein, 1988), parasites, inquilines and commensals (Joseph, 1984). While there is a large amount of information on the biology of pollinating species there is relatively little on non-pollinators. Their larvae typically feed on galled fig ovules and/or the developing larvae of other fig wasps (Abdurahiman & Joseph, 1978; Bronstein, 1988; Hill, 1967; Joseph, 1959, 1984; Nefdt, 1989; Ramirez, 1988; Wiebes, 1976, 1986b). More rarely they develop in galled fig primordia or galls in the walls of the figs (Compton & van Noort, personal communication). *Philotrypesis caricae* (Sycoryctinae) has been shown to be a parasitoid of the agaonid *Blastophaga psenes* in *F. carica*, but also feeds on the surrounding plant tissue (Joseph, 1959). *P. pilosa* and *Apocrypta bakeri* (Sycoryctinae) are parasites of *Ceratosolen marchali*, the pollinator of *F. hispida* (Abdurahiman & Joseph, 1978), while one *Apocrypta* species is a parasitoid of a non-pollinating galler, *Apocryptophagus* species (Sycophaginae) (Godfray, 1988). Many phytophagous fig wasps are totally independent of the pollinators and are able to prevent unpollinated figs from aborting. Examples include some *Otitesella* species (Otitesellinae) (Neves, 1987), *Sycophaga* (Sycophaginae) (Galil & Eisikowitch, 1968b) and *Odontofroggatia* species (Epichrysomallinae) (Wiebes, 1980b).

The oviposition behaviour of several species of Sycoryctinae has been described (Ansari, 1967; Abdurahiman & Joseph, 1979; Abdurahiman & Joseph, 1978, 1979; Compton & Nefdt, 1988; Joseph, 1984; Ulenberg, 1985; Ulenberg & Nubel, 1982). The females of these species oviposit through the wall of the fig while standing on its outer surface. Other fig wasps are 'internal' ovipositors, like the agaonines, and enter the figs via the ostiole to lay their eggs down the length of the styles. These include the Sycoecinae (Nefdt, 1989; Newton & Lomo, 1979), *Sycophaga* (other sycophagines are 'external' ovipositors), and some Asian genera of Otitesellinae (Wiebes, 1967b).

Larval development of non-pollinating wasps is also synchronised with the fruiting cycle of fig trees. *Sycophaga* and the sycoecines that enter the fig via the ostiole must enter the figs at the same time as the agaonids, during the brief period in which the ostioles are open. Those that oviposit through the fig wall may do so at any of the 'pre-floral', 'female' or 'inter-floral' stages (Wiebes, 1976b).

THE MALE OF THE SPECIES

Unlike their female counterparts, male agaonids are wingless and vermiform with enlarged fore and hind legs that enable them to push between the flowers inside the fig. Perhaps the most important modification of the male agaonid is the long, tubular, telescopic abdomen which facilitates copulation with the female when she is still immobile in her gall (Ramirez, 1976). Males locate a gall containing a conspecific female, chew a small hole in it and then copulate, as described for *Blastophaga* species (Hamilton, 1979), *Ceratosolen solmsi* (Murray, 1990) and *Allotriozoon heterandromorphum* (Agaoninae) (Newton & Lomo, 1979). Adult male fig wasps are short-lived, dying soon after mating activities finish (Joseph, 1965).

Murray (1987, 1989, 1990) recorded the mating behaviour of the wingless males of certain *Philotrypesis* and *Apocrypta* species, which mate in the galls containing the females. He observed multiple mating in both *P. pilosa* and *A. bakeri*. In *P. pilosa* he also noted that a particular male often returned to a female and mated with her repeatedly.

Hamilton (1979) reported extreme inter-male aggression in the fig lumen between conspecifics of several *Idarnes* species, with some individuals incurring severe, even fatal, injuries while they waited for females to emerge from their galls before mating inside the fig cavity. Murray also reported (1987, 1989, 1990) fighting in *Lipothymus sundaicus* (Otitesellinae), *A. bakeri* and *P. pilosa* males. *P. pilosa* males spent a large part of their time fighting, while *A. bakeri* males accumulated heavy injuries occasionally. Murray (1989) also observed the winged males of certain fig wasp species on the outer surface of the figs, guarding the ostiole and vying for access to holes where virgin females were expected to emerge. Other winged males of the same species waited in the nearby foliage. Winged *Odontofroggatia galili* males also emerge from the figs and wait on their fig surface for females to join them (Joseph, 1984; Abdurahiman & Joseph, 1987). Bronstein (1991) observed similar mating behaviour in an *Aepocerus* species (Otitesellinae, (Boucek, 1988) from *F. pertusa*. The males occurred in two forms, both winged. Individuals of the larger form, with patches on their wings, vied aggressively with each other while they waited on the fig surface for females to emerge, while the smaller males, without wing maculation, did not show any aggressive behaviour and waited elsewhere in the tree for females.

SEX RATIOS, SEXUAL SELECTION, POLYMORPHISM AND FIGHTING

Most animals have populations that contain equal numbers of males and females. This is because in populations with an excess of one sex it pays individuals to produce progeny of the rarer sex, thus leading to the evolutionarily stable strategy of a 1:1 sex ratio (Fisher, 1930; Maynard Smith, 1976, 1978). However, this is not the case where mating is non-random and single foundress females produce broods that are reproductively isolated from other populations. Hamilton (1967) noted that under these circumstances brothers compete to inseminate their sisters (local mate competition (LMC)) and that the evolutionarily stable strategy for foundresses is to produce mainly female progeny. This is because, by producing just enough sons to ensure that all her daughters are mated, a female will maximize the number of her grandchildren. If more than one female contributes to an isolated brood, the intensity of LMC decreases and a less female biased optimal sex ratio would be expected (Hamilton, 1967; Werren, 1980). When the number of foundresses is very large the optimal sex ratio approaches 1:1.

Agaonid fig wasps have provided a useful model for testing sex ratio adjustment. Like most hymenopterans, fig wasps are characterised by male haplodiploidy and arrhenotoky - males originate from unfertilized eggs. Thus a female may be able to control the sex ratio of her offspring via the release or retention of sperm from her spermatheca (Flanders, 1939), which provides a mechanism whereby sex ratios can deviate from 1:1. In three fig species studied by Janzen (1979b), from one to three pollinators entered the figs, while one to 26 pollinators may enter figs of *F. benjamina* (Corlett, 1986). Several agaonine species have sex ratios that show adjustment according to LMC theory, for example, 13 pollinating species from Panama (Herre, 1985, 1987), a *Pegoscapus* species (Agaoninae) from Florida (Frank, 1985a) and two South African, species *Ceratosolen capensis* and *Elisabethiella baijnathi* (Nefdt, 1989).

Average levels of inbreeding at the population level are also thought to influence sex ratio adjustment, so that more highly inbred species have relatively more female biased sex ratios (Herre, 1985, 1987). In agreement with this prediction, fig wasps of species that average a greater numbers of foundresses per fig have relatively more biased sex ratios for a given number of foundresses (Herre, 1985). Thus, observed sex ratios in pollinating fig wasps appear to reflect both average levels of inbreeding and sib-competition (Frank, 1985b). Sex ratios of several non-pollinators have been reported, although not examined from a sex ratio adjustment perspective (Hamilton, 1979; Murray, 1987, 1989, 1990).

Unmated females cannot adjust the sex ratios of their progeny as they are only able to produce male offspring. Hardy and Godfray (1990) called these 'constrained' females. Godfray (1988) studied the proportion of constrained females in several fig wasp species that inhabit *F. hispidioides*. He found that unmatedness was low in *Ceratosolen* and *Sycoscapter* species, but relatively high in an *Apocrypta* species.

Sexual selection results from the struggle between members of one sex, normally males, for mating opportunities with the other sex. Unsuccessful individuals sire few or no offspring and are therefore at a selective disadvantage. Thus, where only a small proportion of the males do the mating there is a greater opportunity for sexual selection than where every male get to mate (Anderson & Bradbury, 1987; Emlen & Oring, 1977). Sexual selection is traditionally measured in relation to the variance in mating success that is correlated with a particular trait of the study organism (Andersson & Bradbury, 1987). However, because there are also other selective processes operating, it is the strength of sexual selection relative to these other selective processes that is important (Wade, 1987). Darwin (1871) developed the idea of sexual selection to explain the elaborate plumage of some male birds and the large mandibles and horns of beetles. He proposed that sexual selection has two components - inter-sexual selection, typically the choice of males by females and intra-sexual selection, usually competition between males for mates. Inter-sexual selection in insects is somewhat contentious, with little empirical evidence to show that active female choice occurs (Thornhill & Alcock, 1983). Intra-sexual selection, on the other hand, is common. Males fight each other in order to gain access to mates, dominance rights and other advantages that increase mating opportunities (Maynard Smith & Price, 1973).

Fighting represents one of the more extreme forms of sexual selection. Ritualistic fighting has been reported in mammals, fish and arthropods, while fatal fighting is almost exclusively restricted to arthropods (Enquist & Leimar, 1990). In male-male contests, increased body size is often an advantage, as in some beetles (Palmer, 1978) and thrips (Crespi, 1986, 1988). In most chalcid wasps, however, the males are smaller than the females (Gauld & Fitton, 1987; Hurlbutt, 1987; Van Den Assem *et al*, 1989). This is explained by the differential impact of variation in body size on reproductive success of males and females. In most species an increase in male size may have less impact on its reproductive success than the same increase in female size, which is often correlated with increased fecundity (Van Den Assem *et al*, 1981). Sexual size dimorphism in fig wasps has not been examined, but the presence of fighting in some species might be expected to result in them having relatively large males, if this assists them during fights.

The occurrence of two or more distinct forms within populations of a species is referred to as a polymorphism/polythenism. The former term implies genetic controls (Ford, 1975) whereas if discrete variation in phenotypes is due to environmental influences this is referred to as polythenism (Harrison, 1980). In this thesis, unless specific information on the mechanism of morph determination is available, the term polymorphism (or dimorphism if two forms are present) is used without any imputation as to how the phenomenon is determined. Sexual dimorphism in flight ability has been recorded in a few hymenopterans, beetles and bugs. Flight dimorphisms are controlled either genetically, by environmental cues or by a combination of the two (Dingle, 1986; Harrison, 1980; Roff, 1986a). Genetic inheritance of flight dimorphisms tends to be polygenic with genotype - environment interactions (Dingle, 1986; Roff, 1986b).

Several fig wasp species with alary dimorphisms have been described. These include *Camarothorax bimasculinus* (Joseph) (Epichrysomallinae) (Joseph, 1959a), *Physothorax deseiger* Mayr (Torymidae) (Burks, 1969) and several *Philotrypesis* species (Boucek *et al*, 1981; Grandi, 1930). Several *Philotrypesis* species have been described with wingless males that show differences in their size and shape (Grandi, 1930; Joseph, 1954). Two wingless forms have also been recorded in *Otitesella digitata* Westwood (Otitesellinae) (Wiebes, 1967c) and *O. clarae* Wiebes (Wiebes, 1974b), which are distinguished by their tarsal structures. Nothing is known about the mechanisms of determination of male form in any of these species.

Hamilton (1979) commented on the combination of winglessness, fighting behaviour and dimorphism in New World fig wasps. He suggested that these characteristics were so common because, as in other insects exhibiting these traits, females were aggregated in reproductively isolated populations. Hamilton also examined why some species have males that fight and others do not. He suggested that species that do not fight are on average more closely related than those species that do. Hamilton had no direct measures of inbreeding, but pointed out that in fig wasps such as agaonines, where the female enters the fig to oviposit, her entire brood is restricted to one fig. Consequently these should on average be more related than those species which oviposit through the fig wall and are able to lay their brood in several figs. He used the examples of *Blastophaga* (a non-fighting agaonine) and *Idarnes* (a fighting, 'external' ovipositing species) to support his argument.

Murray (1987) used *Philotrypesis pilosa*, in figs of *F. hispida*, to test the predictions of his earlier (Murray & Gerrard, 1985) model of contest competition for mates. The model enabled predictions of the cost of fighting at different densities of males and females, and when different sex ratios were present. The model predicted maximum costs at intermediate densities of males and females and when sex ratios were highly skewed. Costs of fighting were measured not only in terms of injuries received, but also the time spent fighting, which might otherwise have been spent searching for mates or inseminating them. Certain predictions of the model were supported, while others were not, apparently because details of the wasps' biology did not correspond with the assumptions of the model (Murray, 1987).

This work was extended when Murray (1989) examined the life-time injury levels of male fig wasps in relation to the genetic relatedness between rival males in several species of Malaysian fig wasps. Murray did not find that species with heavily female biased sex ratios (and presumed greater relatedness) had lower injury levels than other species. Rather, he pointed out that the life histories of some fig wasp species predisposed them to fighting behaviour. He suggested that in those species where large numbers of individuals share a fig it pays males not to fight, but rather to specialise in searching for females and mating with them as soon as possible. In a further study on mate competition between male fig wasps, Murray (1990) re-iterated this idea after showing that males of *C. solmsi*, a 'high density' species, did not fight whereas the males of two 'low density' species *A. bakeri* and *P. pilosa* did.

In his seminal 1979 paper Hamilton also found that the more abundant fig wasp species tended to have wingless males whereas the rarer ones tended to have winged males. His explanation for this was that in abundant species both males and females were likely to find mates within their natal figs and wing loss would not place males at a reproductive disadvantage. In rare species, however, both males and females might die unmated if all males were wingless and restricted their mating opportunities to their natal figs. This explanation led Hamilton to predict that those fig wasp species with both winged and wingless males should exhibit levels of abundance intermediate between those of common and rare species. This prediction has not been tested.

CONTENTS OF THIS THESIS

Fig wasps clearly provide a useful model system for the study of sexual selection and especially fighting behaviour. Male fig wasp species exhibit a wide range of morphology varying from winged individuals similar to their females, to wingless fighters with huge mandibles. This variation may even be exhibited in males of one fig wasp species. In chapter 2 I produce a classification scheme for male fig wasps based on features of their anatomy. These morphological attributes are then shown to be correlated with their behaviour.

As mentioned previously, Hamilton (1979) suggested that species of 'internal' ovipositing fig wasps were less likely to have fighting males than those that are 'external' ovipositors, because the former results in a greater inter-relatedness of individuals inside a fig. In chapter 3 I test the predictions of this hypothesis and produce an alternative hypothesis to explain the presence or absence of fighting males in fig wasps. The relationship between fighting and sexual size dimorphism (SSD) is also examined, and it is demonstrated that males are larger, relative to their females, in species which fight.

In chapter 4 I describe aspects of the fighting behaviour in several fig wasps from *F. burtt-davyi* and look at the consequences of fighting, for both winners and losers. The importance of size in determining the victors in fights is also examined, and related to the male biased SSD in fighting species reported in chapter 3. Chapter 5 examines factors which may determine body size in fig wasps, especially the relationship between the size of galls and the wasps that develop inside them.

Reproductive success in male fig wasps is determined by the number of mates they can obtain. The extreme localisation of mating opportunities in figs makes fighting in some male fig wasps worthwhile because there exists the potential for monopolisation of mating opportunities (Crespi, 1986, 1988; Enquist & Leimar, 1990; Hamilton, 1979). The potential for monopoly is, in part, determined by the local sex ratio of the species. As sex ratios get less female biased, monopoly may be more or less likely, depending on the mating system involved. Because of its closed structure, each fig constitutes a discrete sub-population where local sex ratios may be studied. These are examined in chapter 6.

Hamilton (1979) proposed that more common fig wasp species would have wingless males and rare species winged males, because the likelihood of not being mated within a fig increased as the population density decreased. Levels of unmatedness in females of several fig wasp species are examined in seven and related to where they mate and the morphology of their males.

In chapter 8, the prediction of Hamilton (1979) concerning the occurrence of male flight dimorphisms in species that occur at intermediate densities is examined. The possibility that morph ratios may be flexible, and adapted to local population densities is also investigated by looking for changes in morph ratios in relation to wasp density in a *Philotrypesis* species from *F. burtt-davyi*.

In chapter 9 I quantify morphometric variation in the wingless males of two *Philotrypesis* species to determine whether discrete morphs are present. Anatomical differences between the *'digitata'* and *'religiosa'* morphs of *Otitesella* species are quantified in chapter 10, and in chapters 11 and 12 I describe differences in their fighting and courtship behaviour. Morph ratio changes in relation to population density are also examined. Chapter 13 provides a general discussion of the results presented in the thesis.

2 FIGHTING, FLIGHTLESSNESS AND POLYMORPHISM IN MALE FIG WASPS

2.1 INTRODUCTION

Occurrence of fighting in animals

Fighting for mates is almost exclusively restricted to the male sex. Ritualistic fighting has been recorded in animals as diverse as rattlesnakes, oryx antelope, cichlid fish (Eibl-Eibesfeldt, 1961) and a jumping spider, *Myrmarachne plataleoides* (Moffett, 1991), while fighting that can occasionally result in severe injuries has been reported in mammals such as ungulates (Enquist, 1990; Geist, 1966b) and pinnepeds (Le Boeuf, 1974). Routinely fatal fighting, however, appears to be restricted to arthropods (Enquist & Leimar, 1990), with examples including the spider *Euophrys parvula* (Wells, 1988), a geotrupid beetle, *Typhoeus typhoeus* (Palmer, 1978), the larvae of *Apanteles* braconid wasps (Harvey & Partridge, 1987), aphid larvae (Aoki & Makino, 1982 in Enquist & Leimar, 1990), a water mite, *Unionicola formosa* (Dimock, 1983) and a spider mite *Tetranychus urticae* (Potter, 1981; Potter *et al*, 1976).

Dimorphism for fighting behaviour

Some insects and other arthropods have two forms of male; one that fights and another that is a non-fighter. The encyrtid wasp *Pentalitomastix* has a sterile defender morph that kills larvae of other species (Cruz, 1981, Cruz *et al*, 1990). Dimorphism in fighting behaviour has also been reported in some acarid mites (Woodring, 1969) and in the ant *Cardiocondyla wroughtonii*, where the wingless males fight and the winner becomes the only one in the colony, while the winged males do not fight (Stuart, 1987). Only the wingless males of the polymorphic thrips, *Hoplothrips* and *Elaphrothrips* species have developed foreleg armature that is used in fighting other males near communal egg masses, where the females oviposit (Crespi, 1986, 1988). Among females, perhaps the best known polymorphisms are those of social insects; the ants and termites. In termites, castes can be composed of either sex. Minor and major soldiers and workers are distinguished by differences in behaviour and morphology (Wilson, 1953, 1977). The rare case of an apparent soldier caste in bees has been reported in the males of the halictid *Lasioglossum* (Rayment, 1955; Houston, 1970).

Dimorphism in dispersal ability

Sexual dimorphisms in dispersal ability, where the females are apterous and adapted for burrowing in soil, while the males have wings, have been reported in embiopterans (Richards & Davies, 1977) and mutillid, tiphiid and bethylid wasps (Brothers, 1989; Evans, 1967). In strepsipterans the adult female is wingless and usually lives inside her insect host while the male is an active flier (Kirkpatrick, 1937).

Within individuals of the same sex, the presence of both winged and wingless morphs is rare. Examples nonetheless include certain aphids (Harrison, 1980) and ptiliid beetles, *Ptinella* (Dybas, 1978), coccinellid beetles (Hammond, 1985), thysanopterans *Hoplothrips*

(Crespi, 1986) and the sciarid fly *Plastosciara perniciosa* (Stefan, 1973). In the chalcid wasp *Trichogramma*, the female is winged whereas the male may be flightless or winged (Salt, 1937) and in another chalcid, *Melittobia*, both sexes occur in several forms; the female may be apterous or winged while the male has several flightless forms (Balfour-Browne, 1922; Freeman & Ittyeipe, 1982; Schmieder, 1933). An analogous variation in dispersal ability is present in an acarid mite, where the female is dimorphic for structures associated with phoresy on insects, while the male is non-phoretic (Moser & Cross, 1975). Other examples of dispersal dimorphisms are given in Hamilton (1978, 1979) and Roff (1986a).

Variability among male fig wasps

Fig wasps are exceptional insects in that fighting, flightlessness and polymorphism are all relatively common (Hamilton, 1979). Hamilton also suggested that because the offspring of 'internal' ovipositors are, on average, more closely related than those of 'external' ovipositors, the males of these fig wasps species should not fight because of their genetic closeness. All female fig wasps are winged, but males vary greatly in structure between species: some are vermiform and wingless, while others are winged and resemble the females. Moreover, some fig wasp species have two forms of male: a winged morph and a flightless morph. In some cases the flightless males are adapted for fighting with conspecifics (Frank, 1987).

Murray (1989 & 1990) distinguished five morphological groups among some flightless Malaysian male fig wasps he studied: the hooked soldier, tubular soldier, hogbacked soldier, minute soldier and the soldier. In this chapter an alternative classification scheme based on a literature review of several hundred fig wasp species is developed, supplemented by examination of numerous southern African species. Possible correlates of the morphology of male wasps with their life histories and with the oviposition methods of their females are examined. Behaviourial observations and information on sexual size dimorphism (SSD) in a subset of the wasps is then used to relate male structure to reproductive function in fig wasps.

2.2 MATERIALS AND METHODS

2.2.1 Male fig wasp morphology

Basic anatomical features of male fig wasps were obtained from original descriptions in the literature and from examination of specimens, given in Appendix 2, in Dr. S.G. Compton's collection, housed in the Zoology & Entomology Department at Rhodes University, Grahamstown. A list of all the fig wasp species used in this study is given in Appendix 1 with information on their morphology, life history and oviposition behaviour. Specific taxonomic notes are also given there. Fig wasp nomenclature in this thesis follows that in Appendix 1.

Male fig wasp anatomy was defined by five ordinal or binary variables, defined in Table 2.1. The variables were: the degree of antennal and wing reduction, mandible size, the presence or absence of ocelli and the size of the eyes. The range of morphological variation these encompass is illustrated in Figure

2.1. These features were selected because they are consistently mentioned in the taxonomic literature and were liable to minimal subjective judgement. In preliminary analyses, the additional variable of sexual size dimorphism (SSD) was incorporated, as determined by the relative lengths of males and females. However, body length was found to be an unsatisfactory measure of SSD. This was established by comparing the relationships between body length and mass in a range of male fig wasps. Length measurements were obtained from original descriptions in the literature and by measurement of several specimens of each species in Dr. S.G. Compton's collection. Wasp dry mass was determined by weighing individuals with a Cahn-31 micro-balance after they had been dried for 3 days at 40°C.

2.2.2 Statistics

The BMDP 2M statistical software package (Engelman, 1990) was used to perform a hierarchical cluster analysis on male fig wasp morphology.

Cluster analysis is used to divide a set of objects into groups such that the objects within a particular group are more similar (or less dissimilar) to each other than those from other groups (Everitt, 1986;

Table 2.1 Variables used to describe male fig wasp anatomy.

CHARACTER	CODES	DESCRIPTION OF MORPHOLOGY
ANTENNAE	0	antennae show reduction in the number of antennal segments and/or the type or number of antennal sensilla, relative to those of the female
	1	antennal structure of the male is very similar to that of the female, with the equivalent number of segments and few differences in the types and number of sensilla
COMPOUND EYES	1	small eyes less than one quarter the length of the head
	2	medium-sized eyes intermediate in length
	3	large eyes greater than half the length of the head
OCELLI	0	no ocelli
	1	ocelli present
MANDIBLES	1	small, inconspicuous mandibles
	2	medium-sized mandibles less than half the length of the head
	3	large mandibles greater than or equal to half the length of the head
WINGS	0	flight is impossible; male has filamentous or club-shaped wing remnants or none whatsoever
	1	male is fully winged

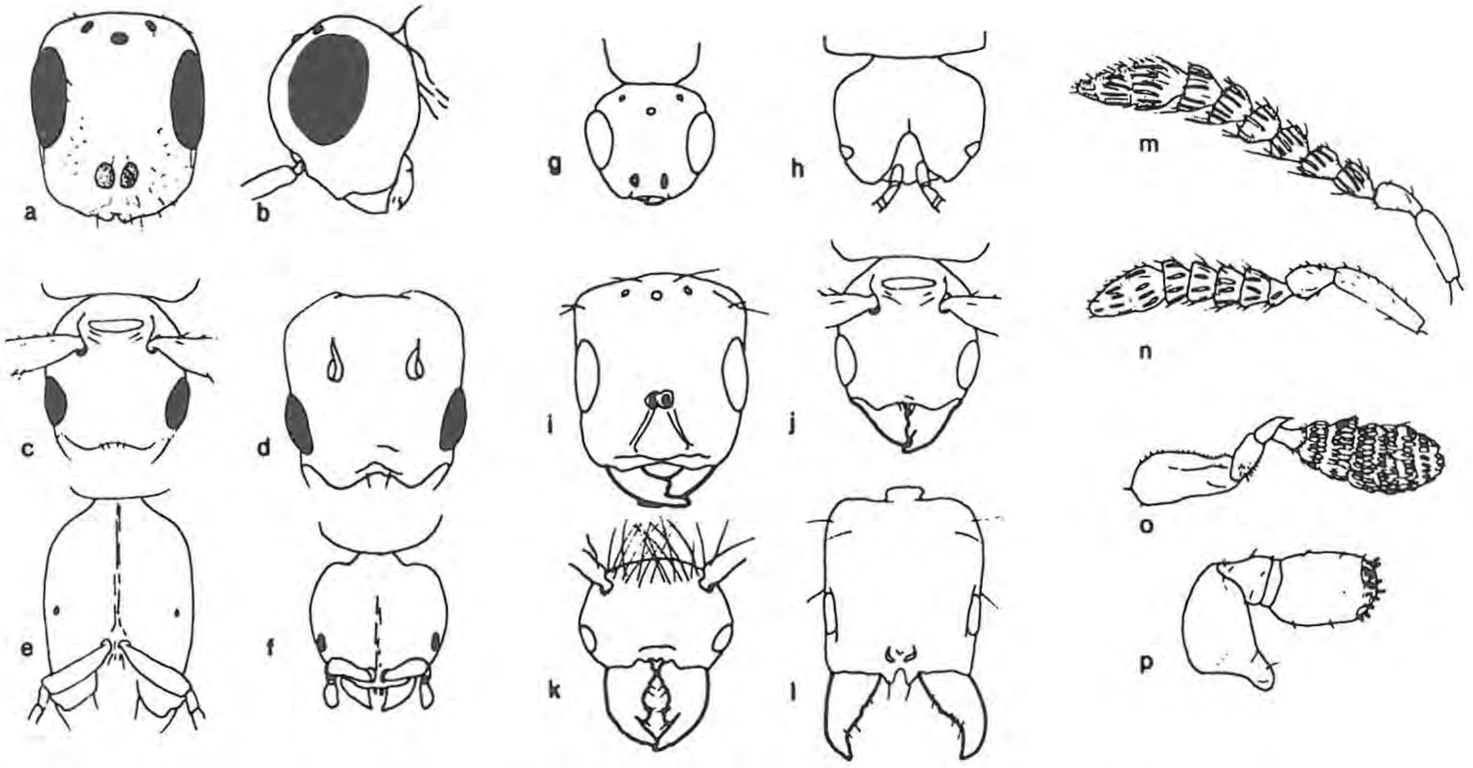


Figure 2.1 Examples of the different eye, mandible and antenna categories used in this classification of male fig wasps. Large eyes, (a-b); medium eyes, (c-d) and small eyes (e-f); small mandibles (g-h); medium mandibles (i-j) and large mandibles (k-l); reduction in the number of male antennal segments and sensilla in comparison to those of the female may be little (m-n) or extreme (o-p). The species illustrated: (a) *Camarothorax equicollis* Boucek, (b) *Sycophila punctum* Boucek, (both from Boucek *et al*, 1981) (c) *O. clarae* Wiebes, the *digitata* morph (from Wiebes, 1974b), (d) *Otitesella tsamvi* Wiebes (from Boucek *et al*, 1981), (e) *A. michaloudi* Wiebes (from Wiebes, 1979b), (f) *Agaon hladikae* Wiebes, (g) *Watshamiella lucens* Wiebes, (h) *Platyscapa etiennei* Wiebes (all from Wiebes, 1981a), (i) *Phagoblastus bouceki* Wiebes, (j) *O. clarae*, the *digitata* morph, (k) *O. clarae*, the *religiosa* morph (all from Wiebes, 1974b), (l) *Sycoscapter cornutus* Wiebes, (m) *Sycotetra serricornis* Boucek female and (n) male (all from Boucek *et al*, 1981), and (n) *Deilagaon chrysolepidis* Wiebes female (from Boucek, 1988) and (o) male (from Wiebes, 1977c). References in brackets below indicate where the drawings were published.

Gordon, 1981). This statistical method has become increasingly popular amongst ecologists, zoologists and taxonomists (Sokal, 1965; Sokal & Rohlf, 1981). Cluster analysis can be divided into hierarchical, clumping and geometrical methods (Gordon, 1981).

Clustering techniques typically begin with the calculation of a 'likeness' or similarity value between entities. This is a similarity co-efficient and it measures the relationship between objects, male fig wasps in this case, given a set of five variates common to those objects (Everitt, 1980). The simple MATCHING coefficient was used here as a similarity measure. Cases were then joined by CENTROID linkage until all cases were combined in one cluster (Engelman, 1990a). Hierarchical classification may be represented as an inverted tree structure or dendrogram which is a diagram illustrating the fusion of cases into clusters at each successive stage of the analysis (Everitt, 1980).

2.2.3 Behaviourial observations

Descriptions of male fig wasp behaviour were obtained from the literature and from observations on fig wasps from *F. burtt-davyi*, *F. ingens*, *F. sur*, *F. sycomorus* and *F. thonningii*. Observations were made both in the field and in the laboratory. For the latter, collected figs were split open and wasp behaviour was observed under a cold light with a binocular dissecting microscope. A subsample of three species of these wasps were examined for damage. Male behaviour was grouped into categories which were then linked with the morphological groupings determined by the cluster analysis.

2.2.4 Polymorphic fig wasps

Where species were polymorphic, with two or more male forms, each form was treated separately in the cluster analysis. The behaviour of each morph was also categorised separately.

2.3 RESULTS

Host *Ficus* species and identifications of fig wasps used from Dr. Compton's collection are given in Appendix 2. For all the tables except Table 2.7 each male form was included separately.

2.3.1 Body length as a measure of sexual size dimorphism (SSD) in fig wasps

The relative body lengths of males and females was found to be an unsuitable character for the cluster analysis because of two problems. Firstly, the length of entire male fig wasps are seldom given in taxonomic descriptions and the weight of the wasps, a more accurate measure of SSD (Gauld & Fitton, 1987), is never provided. Second, there was a poor correlation ($r = -0.239$, $p > 0.05$) between the relative lengths of males to females and the relative mass of males to females (Figure 2.2). This results from the great differences in bodily proportions among males of different fig wasp taxa: some males are short and heavily sclerotised while others are long and soft bodied. The length and weight of female wasps also varies independently, making the use of body length data highly inaccurate for any determination of SSD.

2.3.2 Male fig wasp morphology

Among the several hundred fig wasps examined (Appendix 2), six male morphological types were distinguished in the cluster analysis (Figure 2.3). The character states forming the basis of these types are given in Table 2.2. Type I males are winged, with ocelli, large compound eyes, small mandibles and antennae very similar to those of conspecific females. Type II males are similar to type I males except for having larger mandibles. Type III males were rarely encountered. They have reduced wings, inconspicuous mandibles, medium sized eyes, and although flightless they possess ocelli. Type IV males are similar to type V males except for their smaller mandibles. Types V and VI are the most highly modified males. The former have reduced wings, very large mandibles, medium sized eyes and no ocelli, while type VI males also have reduced wings, but in combination with small mandibles, eyes that are small or vestigial and antennae that are highly reduced (Figure 2.4).

The distribution of the types of males among the taxonomic groupings of fig wasps are summarised in Tables 2.3 and 2.4. Not surprisingly, given that this phyletic classification scheme and the taxonomy of the insects are both based on morphological characters, there is partial concordance between the two. Some taxa nonetheless show great variability in male structure.

2.3.3 Life history characters linked to morphology

Female fig wasps of some species oviposit from the interior of the fig while others oviposit from the outside through the wall of the

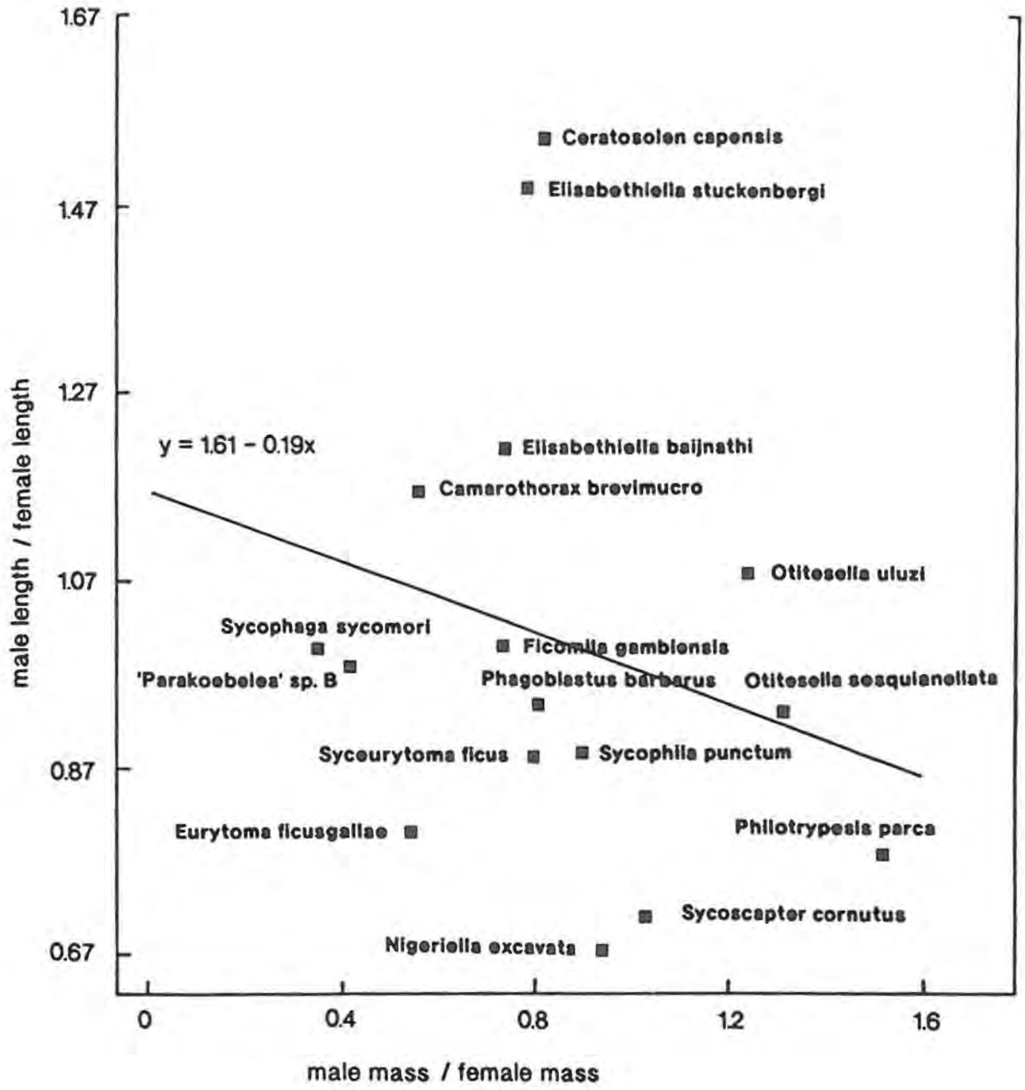


Figure 2.2 Male length/female length versus male mass/female mass for 16 fig wasp species. The correlation is not significant.

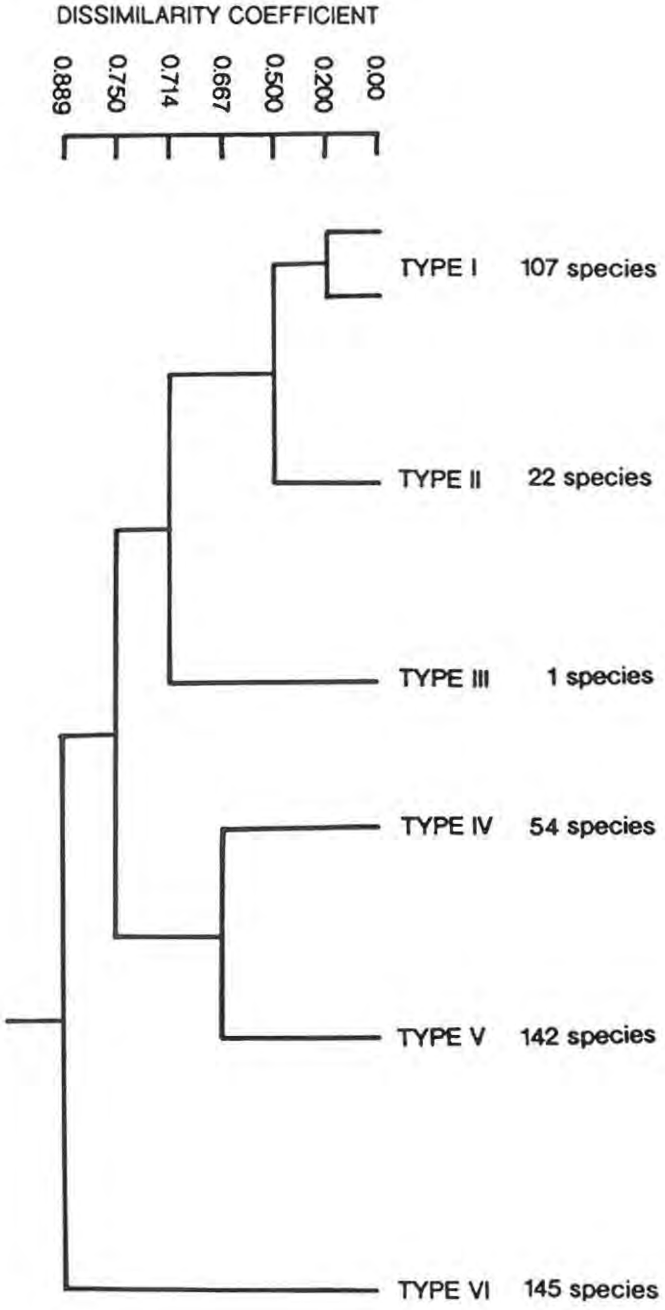


Figure 2.3 Dendrogram summarising the hierarchical cluster analysis on male fig wasp morphology and the 'number' of species in each class. Different male morphs were included separately in the analysis.

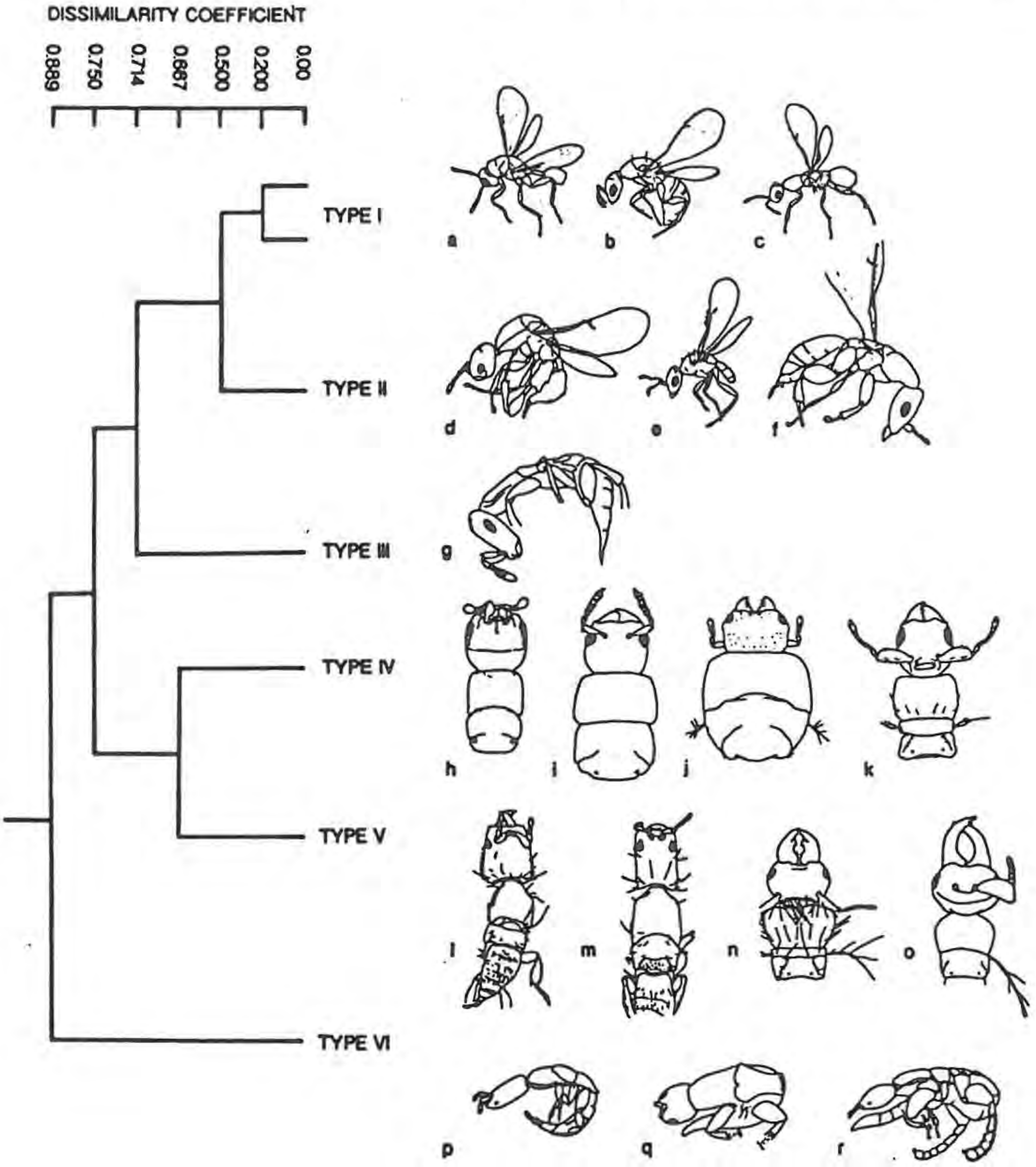


Figure 2.4 Dendrogram summarising the hierarchical cluster analysis on male fig wasp morphology, illustrated with examples from each class. Type I (a - c), type II (d - f), type III (g), type IV (h - k), type V (l - o) and type VI (p - r). Species illustrated are; (a) *Sycophila flaviclava*, (b) *Philotrypesis parca*, (c) *Camarothorax equicollis* (all from Boucek *et al*, 1981), (d) *Odontofroggatia galili* (from Wiebes, 1980), (e) *Crossogaster odorans* (from Boucek *et al*, 1981), (f) *Dobunabaa longula* (from Boucek, 1988), (g) *'Camarothorax'* sp. T (original), (h) *Nigeriella fusciceps* (from Wiebes, 1974a), (i) *Lipothymus panchoi* (from Wiebes, 1974b), (j) *Grandiana wassae* (from Wiebes, 1961), (k) *Otitesella clarae*, digitata form (from Wiebes, 1974b), (l) *Sycoscapter monilifera*, (m) *Philotrypesis anguliceps* (both from Wiebes, 1967c), (n) *Otitesella clarae*, religiosa form (from Wiebes, 1974b), (o) *Walkerella temeraria* (from Wiebes, 1967c), (p) *Apocrypta* species (from Wiebes, 1982a), (q) *Elisabethiella stuckenbergi* (from Boucek *et al*, 1981) and (r) *Ceratosolen* species (from Wiebes, 1982a). References in brackets indicate where the drawings were first published.

Table 2.2 Character states displayed by the six groups of male fig wasps identified in the cluster analysis. Both antennal character states were present in type I males, as indicated.

CHARACTER	CHARACTER STATE	CHARACTER STATES OF MORPHOLOGICAL TYPES					
		I	II	III	IV	V	VI
ANTENNAE	0	+	+	+	+	+	+
	1	+					
MANDIBLES	1	+		+			+
	2		+		+		
	3					+	
COMPOUND EYES	1	+	+				
	2			+	+	+	
	3						+
OCELLI	0				+	+	+
	1	+	+	+			
WINGS	0			+	+	+	+
	1	+	+				

Table 2.3 A summary of the fig wasp species used in the classification scheme in relation to their male types. * represents polymorphic species.

TYPE I	TYPE II	TYPE III	TYPE IV	TYPE V	TYPE VI
EURYTOMIDAE	AGAONIDAE	AGAONIDAE	AGAONIDAE	AGAONIDAE	TORYMIDAE
40 *Sycophila*	EPICHRYSOMALLINAE	EPICHRYSOMALLINAE	OTITESELLINAE	OTITESELLINAE	*1 *Physothorax*
1 *Pseudisa*	3 *Odontofroggatia*	*1 *Camarothorax*	*5 *Otitesella*	24 *Otitesella*	
2 *Eurytoma*			3 *Grandiana*	*5 *Otitesella*	AGAONIDAE
1 *Syceurytoma*	SYCOECINAE		1 *Lipothymus*	1 *Walkerella*	SYCORYCTINAE
8 *Ficomila*	1 *Diazella*		1 *Micrognathorphora*	2 *Sycobiella*	Sycoryctini
2 genus indet.	6 *Crossogaster*		1 *Gaudalia*	1 *Tetrastiozoon*	*1 *Watshamiella*
	8 *Phagoblastus*		1 *Grasseiana*	2 *Philosycus*	12 *Sycoscapteridea*
TORYMIDAE	1 *Philocaenus*		1 *Eujacobsonia*		Apocryptini
1 *Physothorax*	3 *Seres*		1 genus indet.	SYCORYCTINAE	2 *Apocrypta*
*1 *Physothorax*				Sycoryctini	
			SYCOECINAE	42 *Philotrypesis*	SYCOPHAGINAE
ORMYRIDAE			2 *Robertsia*	40 *Sycoryctes*	4 *'Eukoebelea'*
5 *Ormyrus*				24 *Sycoscapter*	5 *'Idarnes'*
			SYCORYCTINAE	*1 *Sycoscapter*	4 *'Parakoebelea'*
AGAONIDAE			Sycoryctini		3 *Sycophaga*
EPICHRYSOMALLINAE			*1 *Sycoscapter*		
1 *Neosycophila*			27 *Philotrypesis*		AGAONINAE
2 *Acophila*			1 *Dobunabaa*		4 *Pleistodontes*
*3 *Camarothorax*					3 *Deilagaon*
1 *Parapilkhanivora*			AGAONINAE		6 *Waterstoniella*
19 *'Camarothorax'*			7 *Alfonsiella*		49 *Ceratosolen*
1 *Sycobia*			3 *Nigeriella*		5 *Blastophaga*
1 *Sycophiloides*					5 *Kradibia*
2 *Sycotetra*					2 *Dolichoris*
					1 *Wiebesia*
SYCORYCTINAE					11 *Agaon*
Sycoryctini					3 *Allotriozoon*
*7 *Philotrypesis*					6 *Courtella*
8 *Watshamiella*					8 *Elisabethiella*
*1 *Watshamiella*					8 *Platyscapa*
					2 *Pegoscapus*

Table 2.4 Distribution of male morphological types among taxa of fig wasps. Each data point represents a species or a morph within a species.

FAMILY/ SUBFAMILY AND TRIBE	MORPHOLOGICAL TYPES					
	I	II	III	IV	V	VI
EURYTOMIDAE	53	0	0	0	0	0
TORYMIDAE	2	0	0	0	0	1
ORMYRIDAE	5	0	0	0	0	0
AGAONIDAE						
EPICHRYSOMALLINAE	32	3	1	0	0	2
OTITESELLINAE	0	0	0	14	35	0
SYCOECINAE	0	19	0	2	0	0
SYCORYCTINAE						
Sycoryctini	17	0	0	29	107	13
Apocryptini	0	0	0	0	0	2
SYCOPHAGINAE	0	0	0	0	0	16
AGAONINAE	0	0	0	10	0	110

fig. Species with females that oviposit from the interior of the fig have type I, type IV or type VI males, while 'externally' ovipositing species have all six types of males, but with types I and V males predominating (Table 2.5). Here, as later, it is inappropriate to statistically compare frequencies of male types possessed by 'internally' and 'externally' ovipositing wasps, because of the links of taxonomy with male form, and our uneven sampling of taxa. Consequently, certain cells, such as internal ovipositing species with type VI males, for example, are over-represented because of the thorough taxonomic treatment that pollinating fig wasps have received.

Gallers and parasitoids also appear to differ in their distribution of male morphological types (Table 2.6). The significance of this is difficult to assess because various life-history features are inter-linked (for example all parasitoids are external ovipositors) and are also subject to phylogenetic constraints (Table 2.7). Information on the methods of oviposition are based mainly on female anatomy. Larval feeding biologies have been extrapolated from the limited numbers of species in each subfamily for which information is available (Compton & Van Noort, in preparation).

2.3.4 Male behaviour and morphology

On the basis of the observations on the subset of the species included in the cluster analysis, the wasps may be divided into three behaviourial categories; pacifists, aggressors and fighters (Table 2.8). No aggressive behaviour whatsoever was observed in pacifists. *Ceratosolen capensis*, for example, which clamber

Table 2.5 Oviposition behaviour of fig wasps and morphological types of their males. Each data point represents a species or a morph within a species.

OVIPOSITION BEHAVIOUR	MORPHOLOGICAL TYPES					
	I	II	III	IV	V	VI
INTERNAL	0	19	0	14	0	113
EXTERNAL	109	3	1	41	142	31

Table 2.6 Life history and male morphological types of fig wasps. Each data point represents a species or a morph within a species.

LIFE HISTORY	MORPHOLOGICAL TYPES					
	I	II	III	IV	V	VI
GALLER	32	22	1	25	35	128
PARASITOID	77	0	0	30	107	16

Table 2.7 The relationship between fig wasp taxa, method of oviposition and larval feeding biology. Each data point represents a species or a morph within a species that was used in the analyses.

FAMILY SUBFAMILY AND TRIBE	OVIPOSITION		LARVAL FEEDING BIOLOGY	
	INTERNAL	EXTERNAL	GALLER	PARASITOID
EURYTOMIDAE	0	53	0	53
TORYMIDAE	0	2	0	2
ORMYRIDAE	0	5	0	5
AGAONIDAE				
EPICHRYSOMALLINAE	0	35	35	0
OTITESELLINAE	2	39	41	0
SYCOECINAE	21	0	21	0
SYCORYCTINAE				
Sycoryctini	0	133	0	133
Apocryptini	0	2	0	2
SYCOPHAGINAE	3	13	16	0
AGAONINAE	120	0	120	0

Table 2.8 Definitions of behaviourial categories used in the text.

BEHAVIOURIAL CATEGORIES	DEFINITIONS
PACIFIST	males exhibit no aggression towards other males
AGGRESSOR	males exhibit aggressive behaviour but seldom damage opponents
FIGHTER	males regularly injure and maim opponents

around the inside of the figs searching for galls containing conspecific females. They apparently ignored other males of their species. *Apocrypta* and *Sycophaga* species males, also pacifists, did not exhibit overt aggressive behaviour, but would push and shove each other, and other wasps, out of the way while crawling amongst galls and searching for those containing their females. Aggressor males, for example, the *digitata* form of *Otitesella* sp. I, were observed to fight, biting other conspecific males they encountered, but I seldom saw any debilitating injuries incurred. Winged *Phagoblastus* sp. B were also aggressive towards conspecific males, often flicking their wings and occasionally biting them, but rarely inflicting injuries. Altercations between aggressor males were not common. Males of several *Philotrypesis*, *Sycoryctes* and *Otitesella* species were observed to fight. These males searched among the galls in the fig lumen for females. Upon encountering a conspecific male, a male would either ignore it or fight. Fights were intensive: each male grabbing his opponent, on any part of the body, and holding on. This continued until one male was severely injured or retreated to hide amongst the galls. These fights were common and dangerous, resulting in serious, debilitating injuries that often proved fatal. However, small males of certain *Philotrypesis* species were not seen to fight as ferociously as their larger counterparts and apparently 'avoided' aggressive encounters.

Males of types VI and I did not exhibit any aggressive behaviour. Types II and IV males exhibited some aggressive behaviour, but seldom injured opponents, whereas type V males exhibited extreme aggressive behaviour, often maiming and killing opponents. Behaviour and morphology show a close correspondence: fighting fig wasps look as though they are fighters (Table 2.9). Type I and VI males are consistently pacifists, type II and IV males aggressors and type V males fighters. These distinctions cut across taxonomic relationships; for example, type IV aggressors are recorded from species from Agaoninae, Sycoryctinae and Otitesellinae and type V fighters are recorded from Sycoryctinae and Otitesellinae.

Male morphology and inter-male interactions are related in Table 2.10, which also includes species where information on male behaviour is available from the literature. The latter were generally consistent in their behaviour to conspecifics observed in the present study, but the aggression recorded in *Apocrypta bakeri* by Murray (1990) is an exception.

2.3.5 Polymorphism in male fig wasps

17 of the several hundred species included in the cluster analysis had males of two or more morphological types (Table 2.11). Two distinct types of polymorphism were exhibited by these wasps: species with combinations of flightless and winged males and (more rarely) species with two distinct wingless male forms. The morphology and behaviour of different male forms within a species again corresponded: type I males are pacifists while type V males are fighters and type IV and II males are aggressors, threatening but seldom injuring opponents in fights (Table 2.10).

Table 2.9 The relationship between behaviourial and morphological groupings of male fig wasps. No observations were available for Type III males. Each data point represents a species or a morph within a species.

BEHAVIOUR TYPE	MORPHOLOGICAL TYPES				
	I	II	IV	V	VI
PACIFIST	13	0	0	0	10
AGGRESSOR	0	2	9	0	0
FIGHTER	0	0	0	13	0

Table 2.10 The relationship between male morphological types and fighting behaviour. In polymorphic species each morph is treated separately.

FAMILY SUBFAMILY SPECIES	MORPHOLOGICAL TYPE	MALE-MALE INTERACTIONS	SOURCE
EURYTOMIDAE			
Sycophila punctum	I	no aggression	personal observations
Sycophila sp. V_3	I	no aggression	personal observations
Sycophila sp. V_4	I	no aggression	personal observations
Eurytoma ficusgallae	I	no aggression	personal observations
Syceurytoma ficus	I	no aggression	personal observations
Ficomila gambiensis	I	no aggression	personal observations
AGAONIDAE			
EPICHRYSOMALLINAE			
Camarothorax brevimucro	I	no aggression	personal observations
C. equicollis	I	no aggression	personal observations
Camarothorax sp. A	I	no aggression	personal observations
	VI	no aggression	personal observations
Odontofroggatia galili	I	no aggression	Abdurahiman & Joseph (1987)
OTITESELLINAE			
Otitesella sesquianellata	V	extreme aggression	personal observations
O. tsamvi	V	extreme aggression	personal observations
O. uluzi	V	extreme aggression	personal observations
Otitesella sp. I	V	extreme aggression	personal observations
	IV	aggression	personal observations
SYCOECINAE			
Phagoblastus barbarus	II	aggression	personal observations
Phagoblastus sp. B	II	aggression	personal observations

Table 2.10 *continued*

FAMILY SUBFAMILY SPECIES	MORPHOLOGICAL TYPE	MALE-MALE INTERACTIONS	SOURCE
SYCORYCTINAE			
Sycoryctini			
Philotrypesis parca	I	no aggression	personal observations
	IV	aggression	personal observations
	V	extreme aggression	personal observations
P. pilosa	V	extreme aggression	Murray (1987 & 1990)
Philotrypesis sp. C	I	no aggression	personal observations
	IV	aggression	personal observations
	V	extreme aggression	personal observations
Philotrypesis sp. N	IV	aggression	personal observations
	V	extreme aggression	personal observations
Sycoscapter sp. K	V	extreme aggression	personal observations
Sycoryctes remus	V	extreme aggression	personal observations
Sycoryctes sp. D	V	extreme aggression	personal observations
Sycoryctes sp. M_3	V	extreme aggression	personal observations
Sycoscapteridea sp. G	VI	no aggression	personal observations
Apocryptini			
Apocrypta bakeri	VI	aggression	Murray (1990)
A. guineensis	VI	no aggression	personal observations
A. longitarsus	VI	no aggression	personal observations
SYCOPHAGINAE			
Eukoebelea sycomori	VI	no aggression	personal observations
'Idarnes' sp. A	VI	no aggression	personal observations
'Idarnes' sp. B	VI	no aggression	personal observations
'Parakoebelea' sp. B	VI	no aggression	personal observations
'Parakoebelea' sp. C	VI	no aggression	personal observations
Sycophaga cyclostigma	VI	no aggression	personal observations

Table 2.10 *continued*

FAMILY SUBFAMILY SPECIES	MORPHOLOGICAL TYPE	MALE-MALE INTERACTIONS	SOURCE
S. sycomori	VI	no aggression	personal observations
AGAONINAE			
Alfonsiella fimbriata	IV	aggression	Michaloud (1982), Michaloud (1988), identification corrected in Wiebes (1988)
Elisabethiella baijnathi	VI	no aggression	personal observations
E. stuckenbergi	VI	no aggression	personal observations
Platyscapa soraria	VI	no aggression	personal observations
Ceratosolen capensis	VI	no aggression	personal observations
C. solmsi	VI	no aggression	Murray (1990)

Table 2.11 Morphological types of fig wasps with polymorphic males. Sources of information are listed in Appendix 1. *P. finitimorum* has two type V males. Although small type IV and large type V male forms were observed in several *Philotrypesis* species they are not included in this table.

FAMILY SUBFAMILY SPECIES	MORPHOLOGICAL TYPES					
	I	II	III	IV	V	VI
TORYMIDAE						
Physothorax deseiger	+					+
EPICHRYSOMALLINAE						
Camarothorax sp. A	+					+
'*Camarothorax*' sp. T	+		+			
C. bimasculinus	+					+
OTITESELLINAE						
Otitesella clarae				+	+	
O. digitata				+	+	
O. serrata				+	+	
Otitesella sp. I				+	+	
Otitesella sp. R				+	+	
Philotrypesis anguliceps	+				+	
P. finitimorum					++	
P. parca	+				+	
Philotrypesis sp. C	+				+	
Philotrypesis sp. F	+				+	
Philotrypesis sp. G	+				+	
Philotrypesis sp. L	+				+	
Philotrypesis sp. M	+				+	
Watshamiella fictitia	+					+

Eight of the species where both flightless and alate males were recorded belonged to the genus *Philotrypesis*. The alate forms of these species were type I pacifists and their flightless forms type IV aggressors and/or type V fighters. Four polymorphic species were also recorded from the Epichrysomallinae. The flightless males in these families were type VI pacifists, except for that of *'Camarothorax'* sp. T, which was the only example of a type III male detected (Figure 2.5 a). Behaviourial observations were not made on this species, but its morphology suggests that it will be a pacifist. The alate male of this species and the other polymorphic epichrysomallinae are typical type I pacifists (Figure 2.5 b).

Otitesella species belonging to the *digitata* species group exhibit an unusual kind of male dimorphism, where the two morphs are easily distinguished by their tarsal structure (chapter 10). In these species the larger forms are type V fighters and the smaller type IV aggressors. *Sycoscapter reticulatus* Wiebes also has two flightless male forms (Wiebes, 1966). The large forms are type V fighters while the smaller are type IV aggressors (Table 2.3). Distinct 'big' and 'small' flightless male forms were also present in several *Philotrypesis* species (see chapter 8). This has previously been observed by Grandi (1930) and Joseph (1954). Species with 'big' and 'small' males were not included in Table 2.11.

P. finitimorum has two distinct flightless type V fighter males, one with very reduced wings and another with half-sized wings, very reduced in length, but hardly in width. Similarly, *Watshamiella fictitia* has winged type I pacifist males and rather similar type VI

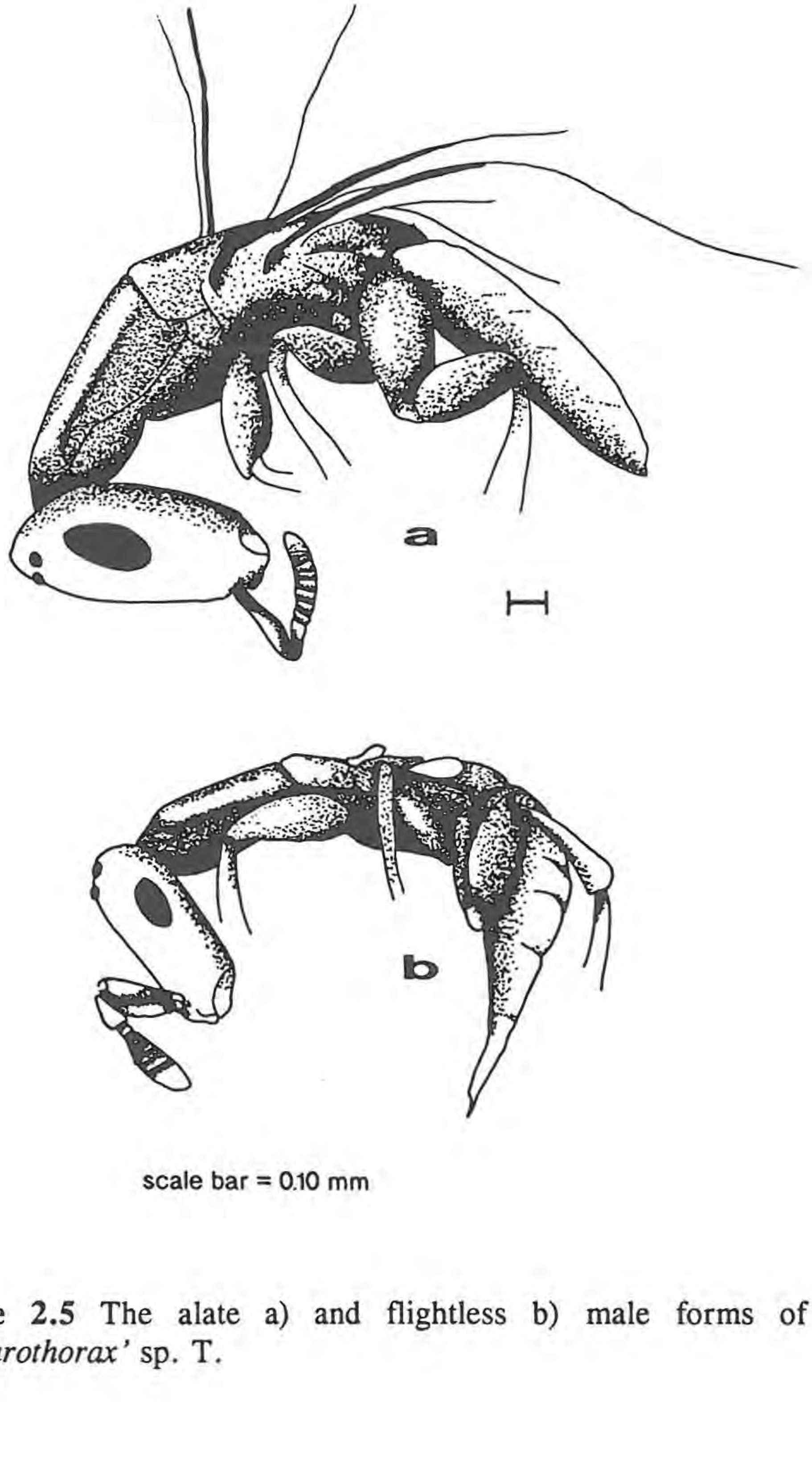


Figure 2.5 The alate a) and flightless b) male forms of *'Camarothorax'* sp. T.

pacifist males with no ocelli and half-sized wings (Figure 2.6 a). A single male *Watshamiella* sp. A had wings that are reduced in width but not length, but unlike the half-winged male of *W. fictitia,* it had medium sized mandibles typical of type II aggressor males (Figure 2.6 b & c).

Aberrant males or genuine polymorphisms?

Where two or more morphologically distinct male morphs are encountered frequently, one can be confident that a polymorphism is present (but see chapter 8). However, where certain males with reduced wings are rarely encountered, as for example in *'Camarothorax'* sp. T, these individuals could be mere aberrants. In this case the wasps concerned were not deformed and appeared transitional between some of the other male forms. Furthermore, changes in 'suites' of characters were sometimes involved. Nonetheless, only further collections can confirm whether these individuals are aberrations or genuine polymorphisms.

More clear cut cases of apparent aberrations were observed. Among large numbers of *Camarothorax* sp. A males, two atypical specimens were collected, one of which showed characters intermediate between those of the two male morphs. In this first specimen (Figure 2.7 a), the head is similar to that of the type II alate male (Figure 2.7 f), but the antennae are like those of the typical flightless type VII male (Figure 2.7 d). The thorax is also similar to that of the flightless male of this species, with parapsidal grooves widely separated where they meet the scutellum, but differs from either morph by having short, non-functional wing

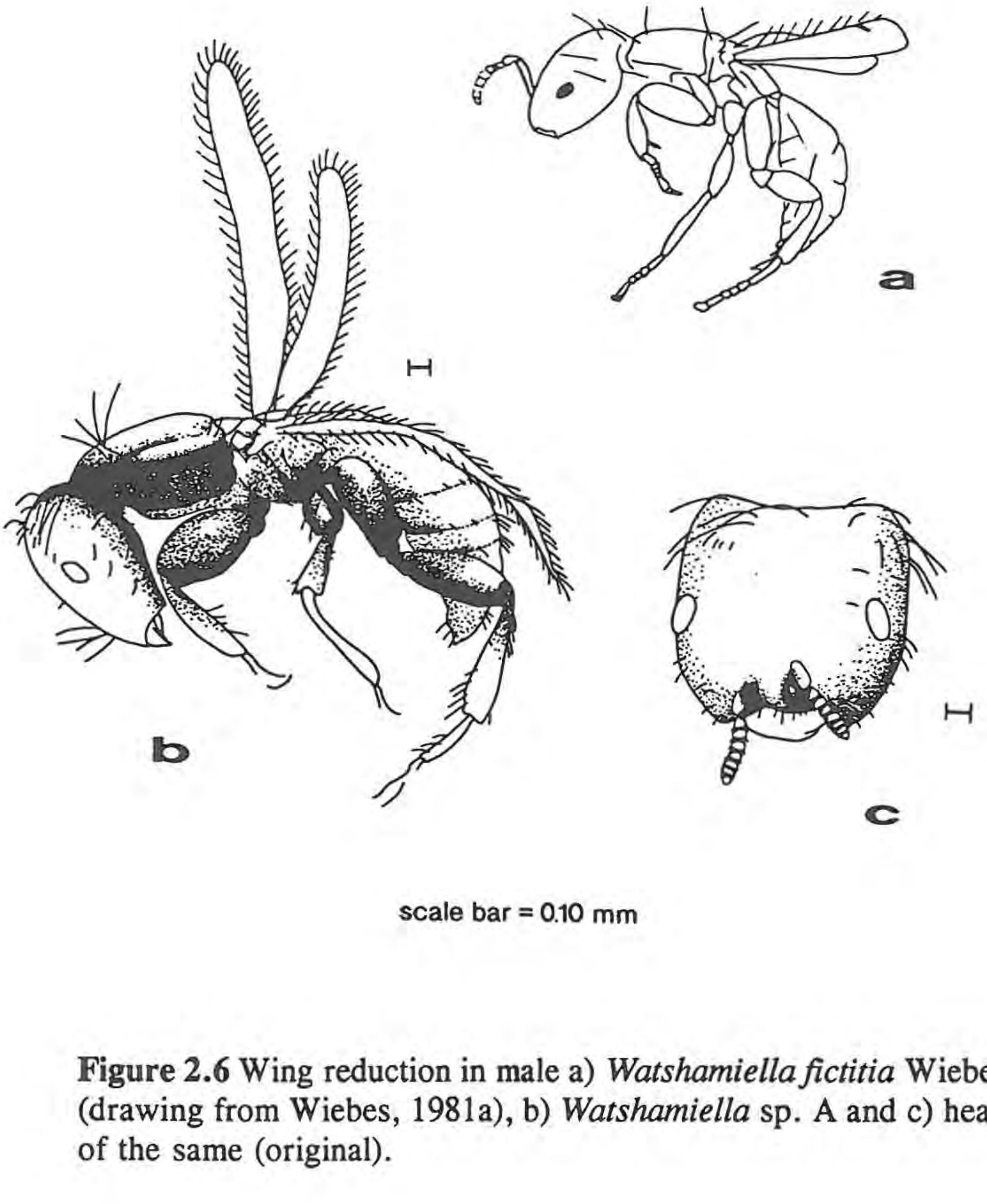


Figure 2.6 Wing reduction in male a) *Watshamiella fictitia* Wiebes (drawing from Wiebes, 1981a), b) *Watshamiella* sp. A and c) head of the same (original).

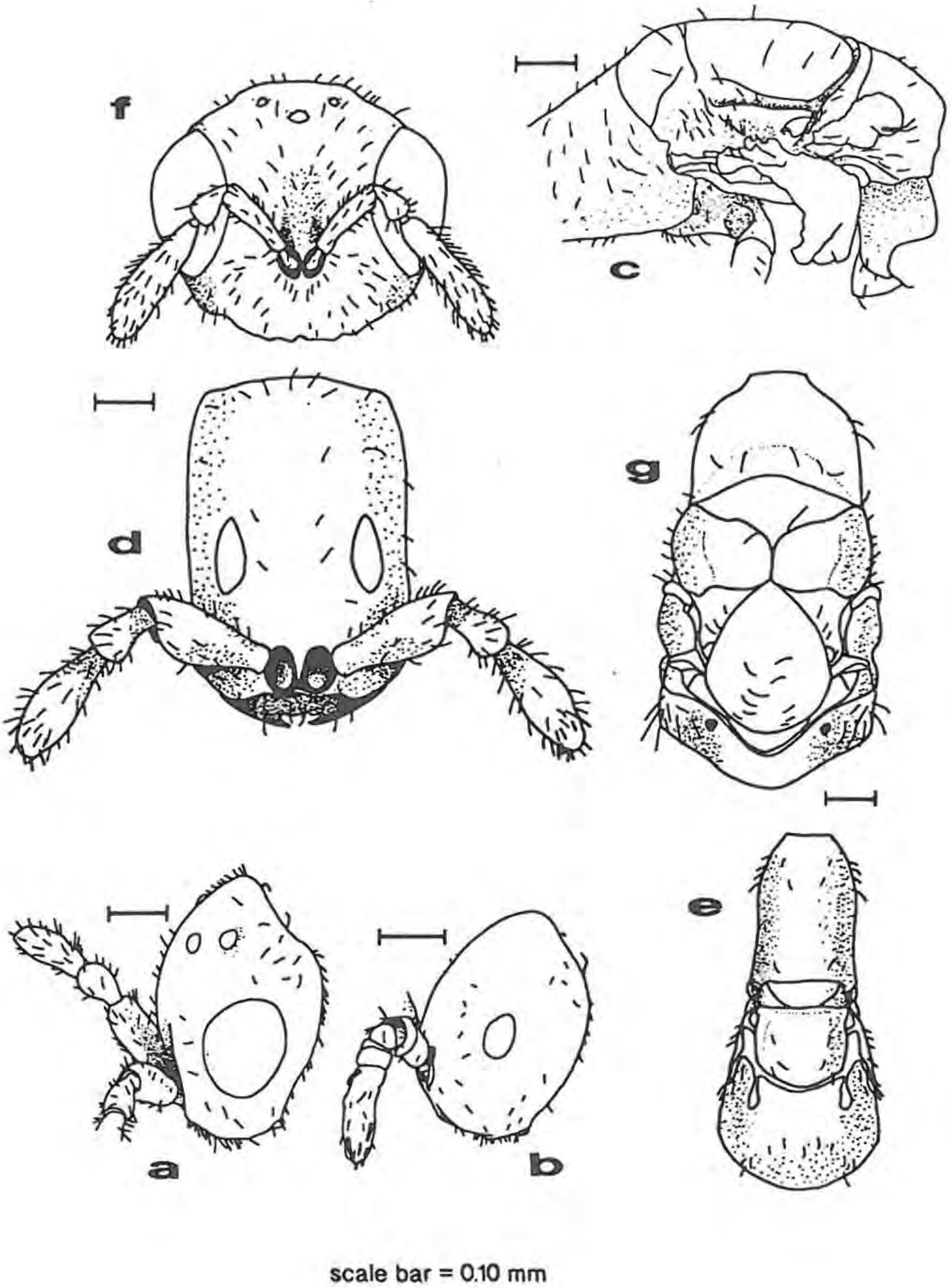


Figure 2.7 Morphology of *Camarothorax* sp. A from *Ficus ingens*; (a), (b), head and (c) thorax of aberrant males; (d), head and (e), thorax of apterous male; (f) head, of alate male and (g), thorax of the female which is very similar to that of the alate male.

stumps (Figures 2.7 c, e & g). The second aberrant male (Figure 2.7 b) was very similar to the typical wingless form, but had more antennal segments.

2.4 DISCUSSION

Hamilton (1978; 1979) listed several insects exhibiting combinations of alary polymorphism and fighting. He pointed out common factors that linked these examples: high levels of inbreeding, biased sex ratios and claustral habitats. Many fig wasps epitomise these conditions. Progeny of only one or two female pollinator fig wasps may develop within a single fig, leading to high levels of sib-mating. Extremely female biased sex ratios are typical of some pollinating fig wasps (Frank, 1985b; Herre, 1985; 1987; Nefdt, 1989). Hamilton (1979) suggested that wings are an encumbrance inside figs and pointed out that wing reduction occurs in similar claustral habitats such as soil and rotting wood (Hamilton, 1978) and caves (Barr, 1967). Loss of wings in male fig wasps can therefore be seen as an adaptation to mating in the confined space of the fig interior.

A loss of ocelli has been linked with the loss of wings in adult insects (Kalmus, 1945), although ocelli have also been lost in some adult female fig wasps, for example *Alfonsiella fimbriata, A. michaloudi* (Wiebes, 1988) and *Agaon spatulatum* (Wiebes, 1968c). Wing loss in insects is often also associated with a reduction in the size of the eyes. The flightless forms of both male and female *Ptinella* beetles have vestigial eyes (Dybas, 1978) and the apterous males of two parasitic *Melittobia* eulophid wasps (Freeman &

Ittyeipe, 1982) also have no eyes and occasionally no ocelli. However, the flightless males of *Trichogramma* do have ocelli (Salt, 1937). Flightless male fig wasps usually have reduced eyes and no ocelli, but the apterous form of the *'Camarothorax'* sp. T is exceptional as it has ocelli combined with reduced compound eyes.

In fig wasps six male morphological types were distinguished. The groupings do not correspond closely with the taxonomy of the wasps, suggesting that the evolution of male structure from that of the putative ancestral winged form (type I) has resulted in both convergence and divergence. Examples of convergence include the highly modified type V males that are present in the Otitesellinae and Sycoryctinae and the equally highly modified type VI males occurring in the Sycophaginae, Agaoninae and Epichrysomallinae. More detailed anatomical features nonetheless clearly separate the males of these various taxa. A clear 'linkage' is present between male anatomy and the form of male-male interactions. The morphological classification developed here (and other studies (Frank, 1987; Hamilton, 1979; Murray, 1987; 1989; 1990)) therefore effectively also divides fig wasps according to the degree of their fighting behaviour.

Probably the most characteristic feature of fig wasps that fight is their large mandibles. The development of such weaponry is to be expected, given the evolution of fighting behaviour in the wasps (Enquist & Leimar, 1990; Geist, 1966a, 1966b; Geist, 1971). Parallel examples include the male *Hoplothrips* that have developed leg armature which they use in male combat (Crespi, 1986) and the fighting males of the ant *Cardiocondyla wroughtonii* that have enlarged mandibles (Stuart, 1987). The elaborate horns and mandibles of some beetles similarly function as unconventional weapons that are mainly used to pry loose or lift rivals rather than to inflict injuries (Eberhard, 1980).

There are limits to the effectiveness of the classification scheme described here. Fig wasp mandibles also serve purposes apart from fighting, such as chewing into galls containing females. In *Odontofroggatia galili*, classified as a type II aggressor here, the male has medium sized mandibles which it uses to chew a tunnel through the fig wall (Abdurahiman & Joseph, 1987). The species may thus be wrongly classified from a behaviourial perspective because of this alternative mandible function. Only direct observations of the wasps' behaviour can clarify this point. For example, *Phagoblastus barbarus* Grandi males are also classified as type II aggressors, but observations showed that although they exhibit aggressive behaviour towards conspecific males, they also use their mandibles to hold a female during copulation. Clearly, in cases where only the description of the fig wasp is available it cannot be known with certainty whether or not the wasps actually exhibit fighting behaviour. Nonetheless, male fig wasp morphology, in most cases, is consistent with behaviour.

3 BIG MALES AND SMALL MALES: Inbreeding and mating sites as determinants of male anatomy and sexual size dimorphism in fig wasps

3.1 INTRODUCTION

Sexual dimorphism

Sexual dimorphism has provoked intense interest ever since Darwin developed the theory of sexual selection. He cited examples of birds, mammals, amphibians, reptiles, fish and numerous insects which exhibited differences in coloration, morphology and size between the sexes. Amongst insects, Darwin was particularly impressed by the elongated pincer-like mandibles and horns of some male Scarabaeinae beetles that they use to pry off or pick up opponents (Eberhard, 1980). Other insect examples of sexual dimorphism related to inter-male aggression come from Brentidae, Scolytidae, Drosophilidae and Coreidae (Thornhill & Alcock, 1983), while sexual dimorphism in relation to dispersal ability is present in some wasps (Evans, 1969), strepsipterans (Kirkpatrick, 1937) and aphids (Dixon, 1985; Dixon *et al*, 1968) among others. Sexual dimorphism in fig wasps is often pronounced and involves differences in both fighting and dispersal ability. Some examples are illustrated in Figure 3.1.

Sexual size dimorphism (SSD), the relative body sizes of the sexes, has been studied in birds (Downhower, 1976; Höglund, 1989; Orians,

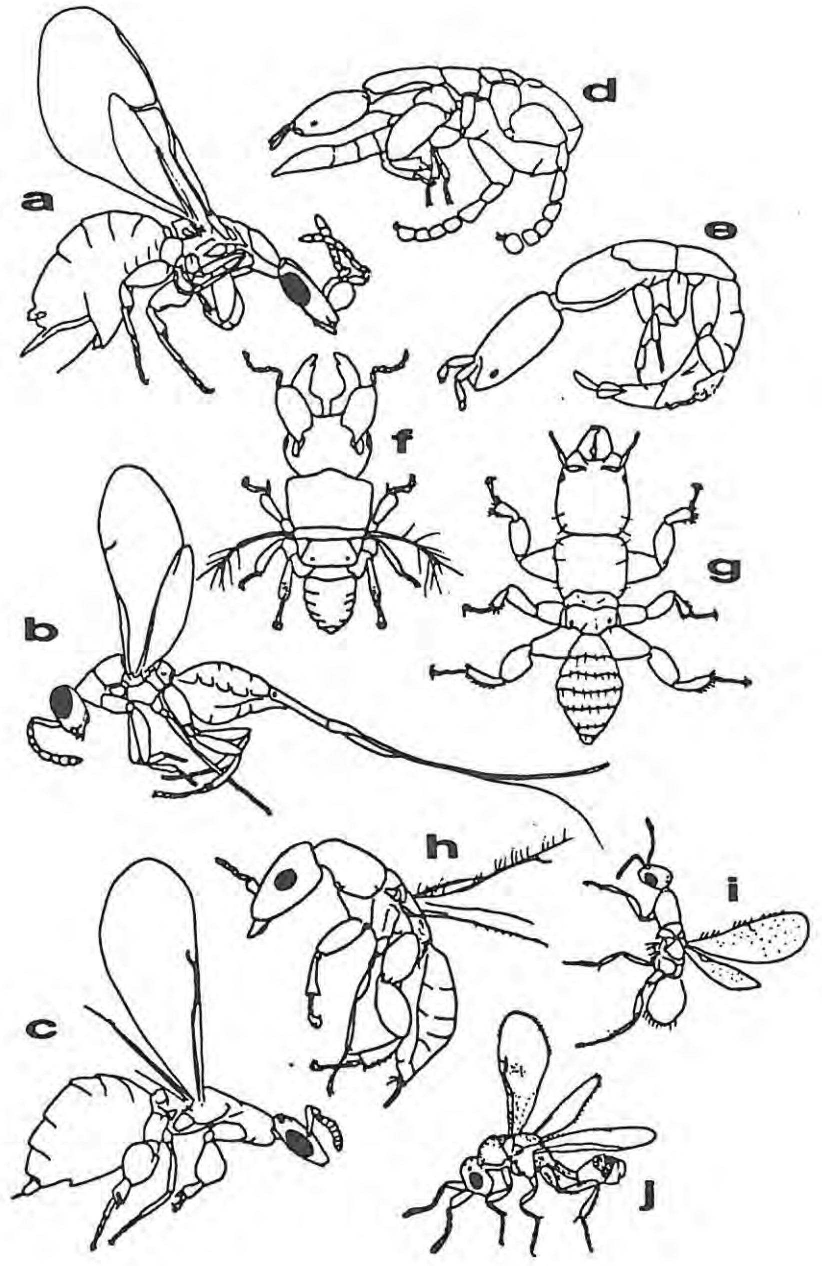


Figure 3.1 Several female (a-c) and male (d-j) fig wasps to illustrate sexual dimorphism and differences in male morphology; (d-e) type VI males, (f-g) type V males, (h) a type II male and (i-j) type I males. Fig wasps illustrated; a) a *Ceratosolen* species, b) an otiteselline, c) a sycoryctine, d) a *Ceratosolen* species, e) an *Apocrypta* species, f) a *Grasseiana* species, g) a *Sycoryctes* species (all from Wiebes, 1982a), h) a *Dobunabaa* species (from Boucek, 1988), i) *Camarothorax equicollis* (from Boucek *et al*, 1981) and j) a *Sycophila* species (from Watsham, 1977).

1969; Selander, 1966, 1972), mammals (Clutton-Brock *et al*, 1977; Crook, 1972; Jarman, 1983; Myers, 1978; Packer, 1983; Ralls, 1976, 1977), amphibians (Howard, 1981; Shine, 1979; Woolbright, 1983) and lizards (Carothers, 1984; Cooper & Vitt, 1989), but there is a paucity of information on SSD in invertebrates. Exceptions include studies of ichneumonid wasps (Gauld & Fitton, 1987; Hurlbutt, 1987), amphipod crustaceans (Ward, 1988), gerrid waterstriders (Faribairn, 1990) and satyrid butterflies (Harvey, 1988). Females are usually the larger sex, but where males are larger than females it is generally believed to be a consequence of intra-sexual selection (competition between males). This is because large size is often an advantage in fighting (Carothers, 1984; Clutton-Brock *et al*, 1977; Crook, 1972, Höglund, 1989; Orians, 1969; Selander, 1972; Trivers, 1972; Woolbright, 1983). Male fig wasps that are adapted for fighting might therefore be expected to be larger, relative to their females, than those of non-fighting species.

Hamilton's hypothesis

Fighting behaviour and dispersal ability vary greatly among fig wasps (Hamilton, 1979). Why should some fig wasp species have wingless males adapted for fighting, while others do not? Hamilton (1979) attempted to answer this question by linking fighting to levels of inbreeding. Closely related male wasps are predicted to be less likely to fight with each other because of their genetic closeness (Grafen, 1979; Hamilton, 1964, 1979). Although levels of inbreeding are generally not known in fig wasps (Herre, 1985, 1987), fig wasps may be conveniently divided into two groups on the basis of their oviposition behaviour. The offspring of 'external' ovipositing species can be assumed to be, on average, less related to each other than are those of 'internal' ovipositors. This is because 'internal' ovipositors (except some *Phagoblastus* species and perhaps some other Sycoecine fig wasps (Nefdt, personal communication) are restricted to laying their entire brood in one fig, while 'externally' ovipositing species may oviposit in any number of figs. Consequently, opportunities for sib-mating are far greater in the former group. Hamilton (1979) therefore proposed that, if levels of inbreeding play a role in influencing the likelihood of fighting, then species with males adapted for fighting should be more common among those which oviposit from the outside of the fig.

Resource competition and mating sites

Murray (1987, 1989, 1990) looked at competition between male fig wasps for mating opportunities with females inside their galls. He viewed the variable morphology of male fig wasp species in terms of the varying importance of different components of competition such as searching and fighting. He suggested that species such as *Ceratosolen solmsi* (a pacifist) became better competitors by specialising in locating galls containing their females prior to eclosion, rather than in fighting (Murray, 1990). Compton & McLaren (1989) suggested that the environment inside certain figs (including those pollinated by *Ceratosolen*) were not conducive to the evolution of fighting, and had favoured adaptations which allowed males to search for females as early as possible, before other competing males.

In the previous chapter male morphology was shown to be linked with the grades of inter-male aggressive behaviour. Types I, III and VI males were pacifists, types II and IV were aggressors and type V males were fighters. Here patterns of SSD in the different male morphological types are examined and are related to the differing behaviours of the insects in order to determine whether male aggression is linked to SSD. I also put forward and test an alternative hypothesis to explain the variation in the occurrence of fighting behaviour in fig wasps. This is that mating sites are the predominant determinant of the presence or absence of intra-specific aggression.

3.2 MATERIALS AND METHODS

Mature figs were collected from several African fig trees (Appendix 2). The figs were either split open or placed intact in netting covered jars and the wasps allowed to emerge. Fig wasps were then killed and stored for subsequent identification. The relative dry masses of the males and females were used as a measure of SSD. To compare male and female weights, samples of wasps were dried for three days at 40 °C and then weighed on a Cahn C-31 microbalance. Only intact specimens were used.

Fighting and mating behaviour were observed under a binocular dissecting microscope with a fibre optic cold white light. The different categories of inter-male aggressive behaviour that were recognised; pacifists, aggressors and fighters, have already been described in chapter 2.

Information on oviposition behaviour and larval ecology of fig wasps was obtained from Compton & Van Noort (in preparation). Some of the assumptions that were made are listed in Appendix 1. The larvae of gallers feed entirely on plant tissue whereas the eggs of parasitoids (and 'inquilines') are laid in galls already occupied by the larvae of other fig wasps. Consequently parasitoid larvae develop at the expense of other fig wasp larvae.

3.3 RESULTS

Information was obtained on the mating sites, methods of oviposition and SSD of 39 species of fig wasps, from three families and six subfamilies (Tables 3.1 and 3.2). In the 6 polymorphic species that are included, the different male forms were compared separately with females of their respective species. A total of 47 pairings (including the polymorphic species) formed the data on SSD in fig wasps. Females were larger than their respective males in 31 instances, in species belonging to the Eurytomidae, Ormyridae, Epichrysomallinae, Sycoecinae, Sycoryctinae, Sycophaginae and Agaoninae. In another seven pairings, in species from the Eurytomidae, Sycoryctinae and Agaoninae, males were equivalent to the females in weight. In the remaining nine pairings, males from the Otitesellinae and Sycoryctinae were heavier than their females (Table 3.1). Thus there were characteristic SSD values among the subfamilies represented in

Table 3.1 A comparison of the means and variances of male and female dry weights in 39 species of fig wasps.

SUBFAMILY AND SPECIES	MALE MASS (mg)			FEMALE MASS (mg)			MANN-WHITNEY U		LARGER SEX	LEVENE F	
	N	MEAN ± SD	RANGE	N	MEAN ± SD	RANGE	U	*P*		F	*P*
EURYTOMIDAE											
Eurytoma ficusgallae	20	0.474 ± 0.208	0.138-0.900	20	0.891 ± 0.137	0.690-1.110	24.00	***	FEMALE	1.80	NS
Ficomila gambiensis	5	0.385 ± 0.082	0.280-0.470	12	0.439 ± 0.129	0.270-0.620	24.00	NS	NEITHER	4.10	NS
Syceurytoma ficus	20	0.403 ± 0.164	0.230-0.900	20	0.522 ± 0.084	0.380-0.660	88.00	**	FEMALE	3.25	NS
Sycophila sp. V_3	14	0.166 ± 0.034	0.110-0.230	16	0.173 ± 0.033	0.090-0.220	97.50	NS	NEITHER	0.03	NS
Sycophila sp. V	82	0.089 ± 0.050	0.010-0.270	20	0.224 ± 0.052	0.130-0.320	64.00	***	FEMALE	0.06	NS
S. punctum	16	0.365 ± 0.078	0.240-0.480	17	0.432 ± 0.116	0.250-0.710	88.00	NS	NEITHER	1.46	NS
ORMYRIDAE											
Ormyrus sp. A	20	0.142 ± 0.052	0.080-0.233	20	0.374 ± 0.090	0.250-0.530	0.00	***	FEMALE	4.61	NS
EPICHRYSOMALLINAE											
Camarothorax brevimucro	11	0.114 ± 0.028	0.070-0.160	10	0.223 ± 0.057	0.120-0.300	5.99	***	FEMALE	4.36	*
C. equicollis	20	0.205 ± 0.056	0.100-0.280	20	0.425 ± 0.068	0.320-0.540	0.00	***	FEMALE	1.75	NS
'Camarothorax' sp. D	20	0.224 ± 0.101	0.023-0.360	20	0.955 ± 0.155	0.720-1.390	0.00	***	FEMALE	0.67	NS
Camarothorax sp. A											
winged pacifist	20	0.049 ± 0.009	0.029-0.070	20	0.201 ± 0.023	0.160-0.250	0.00	***	FEMALE	12.88	***
flightless pacifist	18	0.026 ± 0.005	0.014-0.036	-	-	-	0.00	***	FEMALE	23.11	***
OTITESELLINAE											
Otitesella sesquianellata	21	0.051 ± 0.012	0.032-0.081	19	0.044 ± 0.016	0.026-0.092	280.50	*	MALE	0.42	NS
O. tsamvi	20	0.079 ± 0.026	0.021-0.137	20	0.061 ± 0.014	0.036-0.095	309.50	***	MALE	4.76	*
O. uluzi	26	0.065 ± 0.008	0.053-0.086	20	0.054 ± 0.008	0.035-0.069	321.00	**	MALE	0.54	NS

Table 3.1 *continued*

SUBFAMILY AND SPECIES	MALE MASS (mg)			FEMALE MASS (mg)			MANN-WHITNEY U		LARGER SEX	LEVENE F	
	N	MEAN ± SD	RANGE	N	MEAN ± SD	RANGE	U	*P*		F	*P*
Otitesella sp. I											
flightless fighter	27	0.060 ± 0.013	0.035-0.088	20	0.037 ± 0.018	0.007-0.071	88.50	***	MALE	2.40	NS
flightless aggressor	20	0.021 ± 0.010	0.007-0.043	-	-	-	6.00	***	FEMALE	0.20	NS
SYCOECINAE											
Phagoblastus barbarus	20	0.034 ± 0.005	0.026-0.044	20	0.043 ± 0.004	0.035-0.050	42.50	***	FEMALE	0.56	NS
Phagoblastus sp. B	17	0.029 ± 0.011	0.015-0.044	20	0.039 ± 0.006	0.022-0.051	95.50	*	FEMALE	12.04	**
SYCORYCTINAE											
Philotrypesis sp. C											
flightless fighter	47	0.057 ± 0.021	0.022-0.101	46	0.031 ± 0.013	0.020-0.789	1899.5	***	MALE	21.84	***
flightless aggressor	16	0.011 ± 0.005	0.005-0.028	-	-	-	20.50	***	FEMALE	3.53	NS
winged pacifist	14	0.026 ± 0.004	0.016-0.031	-	-	-	284.00	NS	NEITHER	4.87	*
Philotrypesis sp. H											
flightless fighter	29	0.052 ± 0.011	0.020-0.32	20	0.050 ± 0.006	0.035-0.06	171.00	*	MALE	10.65	**
flightless aggressor	27	0.019 ± 0.006	0.010-0.040	-	-	-	517.00	***	FEMALE	0.59	NS
Philotrypesis sp. N											
flightless fighter	34	0.036 ± 0.006	0.023-0.048	20	0.024 ± 0.007	0.016-0.039	580.00	***	MALE	1.36	NS
flightless aggressor	14	0.020 ± 0.007	0.011-0.035	-	-	-	75.50	*	FEMALE	0.00	NS
P. parca											
flightless fighter	30	0.061 ± 0.017	0.028-0.115	20	0.045 ± 0.010	0.028-0.062	451.00	**	FEMALE	5.32	*
flightless aggressor	16	0.019 ± 0.005	0.013-0.033	-	-	-	5.00	**	FEMALE	6.63	*
winged pacifist	20	0.024 ± 0.003	0.019-0.034	-	-	-	9.00	***	FEMALE	15.29	***
Sycoryctes sp. X	5	0.032 ± 0.004	0.029-0.040	14	0.026 ± 0.005	0.016-0.036	57.50	*	MALE	0.40	NS
Sycoryctes sp. D	20	0.032 ± 0.010	0.015-0.047	20	0.020 ± 0.003	0.013-0.029	334.00	***	MALE	48.59	***
S. remus	20	0.043 ± 0.006	0.034-0.059	20	0.049 ± 0.011	0.023-0.068	136.50	NS	NEITHER	9.25	**

Table 3.1 *continued*

SUBFAMILY AND SPECIES	MALE MASS (mg)			FEMALE MASS (mg)			MANN-WHITNEY U		LARGER SEX	LEVENE F	
	N	MEAN ± SD	RANGE	N	MEAN ± SD	RANGE	U	*P*		F	*P*
Sycosapter cornutus	11	0.042 ± 0.005	0.030-0.050	20	0.046 ± 0.008	0.020-0.060	94.00	*	FEMALE	1.21	NS
Sycoscapter sp. K	20	0.119 ± 0.014	0.090-0.139	20	0.119 ± 0.025	0.080-0.160	209.00	NS	NEITHER	14.15	***
SYCOPHAGINAE											
Parakoebelea sp. B	20	0.175 ± 0.026	0.120-0.22	20	0.378 ± 0.043	0.310-0.520	0.00	***	FEMALE	1.64	NS
P. gigas	20	0.310 ± 0.060	0.22-0.43	20	0.772 ± 0.110	0.440-0.970	0.00	**	FEMALE	2.20	NS
Sycophaga sycomori	20	0.046 ± 0.008	0.024-0.057	20	0.145 ± 0.043	0.085-0.220	0.00	***	FEMALE	46.97	***
AGAONINAE											
Alfonsiella binghami	20	0.063 ± 0.012	0.050-0.084	20	0.082 ± 0.008	0.059-0.094	44.00	***	FEMALE	2.76	NS
A. michaloudi	19	0.037 ± 0.005	0.028-0.051	19	0.043 ± 0.006	0.030-0.057	83.00	***	FEMALE	0.41	NS
Elisabethiella baijnathi	20	0.021 ± 0.003	0.012-0.030	20	0.030 ± 0.006	0.020-0.045	34.50	***	FEMALE	7.79	**
E. stuckenbergi	20	0.026 ± 0.004	0.019-0.038	20	0.034 ± 0.006	0.025-0.049	69.00	***	FEMALE	1.69	NS
Nigeriella excavata	20	0.030 ± 0.007	0.019-0.050	20	0.034 ± 0.006	0.023-0.047	144.00	NS	NEITHER	0.20	NS
N. fusciceps	20	0.067 ± 0.009	0.050-0.083	20	0.093 ± 0.011	0.070-0.110	15.00	***	FEMALE	1.14	NS
Ceratosolen capensis	20	0.104 ± 0.009	0.089-0.123	20	0.128 ± 0.010	0.099-0.140	21.00	***	FEMALE	0.05	NS
C. galili	18	0.061 ± 0.007	0.050-0.075	20	0.084 ± 0.012	0.060-0.105	21.00	***	FEMALE	5.05	*
Platyscapa soraria	20	0.025 ± 0.004	0.017-0.035	20	0.050 ± 0.006	0.040-0.062	0.00	***	FEMALE	2.42	NS
P. binghami	20	0.021 ± 0.004	0.011-0.029	20	0.031 ± 0.002	0.027-0.037	3.00	***	FEMALE	3.67	NS

NS = not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Table 3.2 Oviposition behaviour, larval ecology, male morphology and sexual size dimorphism in 39 species of fig wasps. Information on the larval ecology and oviposition behaviour of the fig wasps was obtained, partly from Compton & Van Noort (in preparation).

SUBFAMILY AND SPECIES	LARVAL ECOLOGY	OVIPOSITION METHOD	MALE MORPHOLOGY/ BEHAVIOUR	PRIMARY MATING SITE	MALE/FEMALE MASS(SSD)	
					N MALE/ FEMALE PAIRS	SSD
EURYTOMIDAE						
Eurytoma ficusgallae	parasitoid	external	I, alate pacifist	exterior	20	0.540
Ficomila gambiensis	parasitoid	external	I, alate pacifist	exterior	5	0.731
Syceurytoma ficus	parasitoid	external	I, alate pacifist	exterior	20	0.802
Sycophila sp. V	parasitoid	external	I, alate pacifist	exterior	14	0.956
Sycophila sp. V_3	parasitoid	external	I, alate pacifist	exterior	20	0.475
S. punctum	parasitoid	external	I, alate pacifist	exterior	16	0.907
ORMYRIDAE						
Ormyrus sp. A	parasitoid	external	I, alate pacifist	exterior	20	0.361
EPICHRYSOMALLINAE						
Camarothorax brevimucro	galler	external	I, alate pacifist	exterior	11	0.561
C. equicollis	galler	external	I, alate pacifist	exterior	20	0.504
'*Camarothorax*' sp.D	galler	external	I, alate pacifist	exterior	20	0.265

Table 3.2 *continued*

SUBFAMILY AND SPECIES	LARVAL ECOLOGY	OVIPOSITION METHOD	MALE MORPHOLOGY/ BEHAVIOUR	PRIMARY MATING SITE	MALE/FEMALE MASS(SSD)	
					N MALE/ FEMALE PAIRS	SSD
Camarothorax sp. A	galler	external	I, alate pacifist	exterior	20	0.249
			VI, pacifist	gall	20	0.132
OTITESELLINAE						
Otitesella sesquianellata	galler	external	V, fighter	lumen	19	1.310
O. tsamvi	galler	external	V, fighter	lumen	20	1.351
O. uluzi	galler	external	V, fighter	lumen	20	1.243
Otitesella sp. I	galler	external	V, *religiosa* fighter	lumen	20	1.046
			IV, *digitata* aggressor	exterior	18	0.480
SYCOECINAE						
Phagoblastus barbarus	galler	internal	II, alate aggressor	exterior/ lumen	20	0.807
Phagoblastus sp. B	galler	internal	II, alate aggressor	exterior/ lumen	17	0.744
SYCORYCTINAE						
Philotrypesis sp. C	parasitoid	external	V, fighter	lumen	46	1.791
			IV, aggressor	lumen	16	0.298
			I, alate pacifist	exterior	14	0.761
Philotrypesis sp. H	parasitoid	external	V,fighter	lumen	20	1.049
			IV, aggressor	lumen	20	0.390

Table 3.2 *continued*

SUBFAMILY AND SPECIES	LARVAL ECOLOGY	OVIPOSITION METHOD	MALE MORPHOLOGY/ BEHAVIOUR	PRIMARY MATING SITE	MALE/FEMALE MASS(SSD)	
					N MALE/ FEMALE PAIRS	SSD
Philotrypesis sp. N	parasitoid	external	V, fighter	lumen	20	1.713
			IV, aggressor	lumen	14	0.939
P. parca	parasitoid	external	V, fighter	lumen	20	1.517
P. parca	parasitoid	external	IV, aggressor	lumen	16	0.501
			I, alate pacifist	exterior	20	0.562
Sycoryctes sp. X	parasitoid	external	V, fighter	lumen	5	1.367
Sycoryctes sp. D	parasitoid	external	V, fighter	lumen	20	1.635
S. remus	parasitoid	external	V, fighter	lumen	20	0.943
Sycosapter cornutus	parasitoid	external	V, fighter	lumen	11	1.033
Sycoscapter sp. K	parasitoid	external	V, fighter	lumen	20	1.101
SYCOPHAGINAE						
Parakoebelea sp. B	galler	external	VI, pacifist	gall	20	0.457
P. gigas	galler	external	VI, pacifist	gall	20	0.415
Sycophaga sycomori	galler	internal	VI, pacifist	gall	20	0.355
AGAONINAE						
Alfonsiella binghami	galler	internal	IV, aggressor	gall	20	0.779
A. michaloudi	galler	internal	IV, aggressor	gall	20	0.876
Elisabethiella baijnathi	galler	internal	VI, pacifist	gall	20	0.733

Table 3.2 *continued*

SUBFAMILY AND SPECIES	LARVAL ECOLOGY	OVIPOSITION METHOD	MALE MORPHOLOGY/ BEHAVIOUR	PRIMARY MATING SITE	MALE/FEMALE MASS(SSD)	
					N MALE/ FEMALE PAIRS	SSD
E. stuckenbergi	galler	internal	VI, pacifist	gall	20	0.786
Nigeriella excavata	galler	internal	IV, aggressor	gall	20	0.944
N. fusciceps	galler	internal	IV, aggressor	gall	20	0.732
Ceratosolen capensis	galler	internal	VI, pacifist	gall	20	0.813
C. galili	galler	internal	VI, pacifist	gall	18	0.730
Platyscapa soraria	galler	internal	VI, pacifist	gall	20	0.494
P. binghami	galler	internal	VI, pacifist	gall	20	0.694

the samples. 14 SSD measurements were obtained for the six polymorphic species. Females were heavier than the males in nine pairings, males were heavier than females in four pairings and the sexes were equal in weight in the remainder (Table 3.1).

As measured by the Levene F test females were more variable than males in 10 of the 17 cases where the variance in the weights of the sexes differed while in the remaining seven the converse was true (Table 3.1). Thus there was no indication that male variability (within morphs) was generally higher than that of females.

The pattern of SSD varied in relation to the different male morphological types, a few examples of which are illustrated in Figure 3.1. Females tended to be larger than males in species with pacifist type I, III, VI and aggressor type II and IV males, whereas males were larger if they were V fighters (Tables 3.2 & 3.3).

As with other chalcids (Askew, 1971) male fig wasps emerge before the females. They then mate in one or more of three sites in and around the figs in which they developed. The mating sites are in galls containing the females, in the lumen of the fig or on the outside of the fig (Table 3.4). While each species/morph had a clear primary mating site, males were nonetheless occasionally observed mating elsewhere. Winged males of *Phagoblastus* species, for example, typically wait for females to emerge, but were observed to climb back into the figs and may sometimes mate there. Males that fight were found to mate in the lumen of the fig, whereas pacifists and aggressors mated either in the galls or on the

Table 3.3 Sexual size dimorphism (male dry mass/female dry mass) in relation to male morphology. No data were obtained for species with type III or IV males. Each datum represents a species or a morph within a species.

SSD	MORPHOLOGICAL TYPES				
	I	II	IV	V	VI
FEMALE LARGER	9	2	8	1	10
EQUAL SIZE	4	0	1	2	0
MALE LARGER	0	0	0	10	0

Table 3.4 The three mating sites of fig wasps.

MATING SITES	DESCRIPTIONS
GALL	Male wasps mate with females before they leave the galls where they developed. The males either enter the galls or have telescopic gasters.
LUMEN	Male wasps wait for females to eclose from their galls and mate in the cavity formed by the enlargement of the fig at the 'male' stage *sensu* Galil (1977).
EXTERIOR	Male wasps emerge from the fig and wait until females also emerge, whereupon they mate on the fig surface or elsewhere on the tree.

outside of the fig (Chi-square$_{[2]}$ = 36.42; $P < 0.001$) (Table 3.5). These statistics must however be viewed cautiously because of confounding factors such as taxonomic constraints, as pointed out in chapter 2.

The correspondence between mating site and male behaviour is evident in several replicate fig wasp communities from different *Ficus* species (Table 3.6). *F. sur* is exceptional, with no fighting species, while the other three *Ficus* each species have at least three species with males that exhibit extreme fighting behaviour. Pacifists consistently mate in galls or outside the figs while fighters mate in the lumen of the fig.

Further evidence for a link between mating sites, male anatomy and fighting behaviour comes from some polymorphic species, where different male forms of the same species have contrasting reproductive behaviour. If morphological types of several polymorphic species are examined in relation to their mating sites, it is evident that Types I, III and VI pacifists and Type II aggressors mate either in galls or outside the figs, whereas Type IV aggressors and Type V fighters mate in the lumen of the fig (Table 3.2). For example, *'Camarothorax'* sp. A has two male morphs, a type VI male that is a non-fighter and is a gall mater, and a type I male which mates outside the fig. Similarly, the aggressor type IV males of *Otitesella* sp. I are adapted for mating outside the figs (chapter 11) while the type V fighter males of this species mate in the lumen of the fig, as do the type V fighter males of *Philotrypesis* sp. C and *P. parca*. However, the type I

Table 3.5 Fighting behaviour in relation to mating sites, based on information from Table 3.2. Each datum represents a species or a morph within a species.

MATING SITE	PACIFIST	AGGRESSOR	FIGHTER
GALL	10	4	0
LUMEN	0	4	13
EXTERIOR	13	3	0

Table 3.6 Mating sites and male behaviour of fig wasps from four *Ficus* species.

FICUS SPECIES	FIG WASP	BEHAVIOUR	MATING SITE
F. sur	*Ceratosolen capensis*	PACIFIST	GALL
	Apocrypta guineensis	PACIFIST	GALL
	Sycophaga cyclostigma	PACIFIST	GALL
F. ingens	*Platyscapa soraria*	PACIFIST	GALL
	Philotrypesis sp. H	FIGHTER	LUMEN
	Sycoryctes sp. M	FIGHTER	LUMEN
	Camarothorax sp. A	PACIFIST (FLIGHTLESS MORPH)	GALL
		PACIFIST (ALATE MORPH)	EXTERIOR
	Otitesella sp. I	AGGRESSOR	EXTERIOR
		FIGHTER	LUMEN
F. burtt-davyi	*Elisabethiella baijnathi*	PACIFIST	GALL
	Otitesella uluzi	FIGHTER	LUMEN
	O. sesquianellata	FIGHTER	LUMEN
	Sycoryctes sp. D	FIGHTER	LUMEN
	Phagoblastus sp. B	AGGRESSOR	EXTERIOR
	Philotrypesis sp. C	PACIFIST (ALATE MORPH)	EXTERIOR
		FIGHTER (FLIGHTLESS MORPH)	LUMEN
F. thonningii	*Elisabethiella stuckenbergi*	PACIFIST	GALL
	Otitesella tsamvi	FIGHTER	LUMEN
	Sycoryctes remus	FIGHTER	LUMEN
	Camarothorax brevimucro	PACIFIST	EXTERIOR
	Phagoblastus barbarus	AGGRESSOR	EXTERIOR
	Philotrypesis parca	PACIFIST (ALATE MORPH)	EXTERIOR
		FIGHTER (FLIGHTLESS MORPH)	LUMEN

pacifist males of both of these species mate outside the figs. Sexual size dimorphism also varies in relation to mating site and fighting behaviour (Tables 3.7 & 3.8 and Figure 3.2). Fig wasp species that mate in the lumen of the fig tend to be fighters and have males larger than their females, whereas those that mate in either the galls containing females or outside the figs tend to be either pacifists or aggressors and have males that are smaller than conspecific females. The SSD pattern is clearly evident within the fig wasp communities associated with single host trees, as in *F. burtt-davyi* (Figure 3.3).

Table 3.9 shows that there is considerable taxonomic conservatism within fig wasps in relation to certain life history styles. Whether or not a species fights and where it mates is largely determined by which higher taxon it belongs to. In most cases therefore, the appropriate comparison between mating site and fighting behaviour must be at the level of subfamily or tribe, not the individual species (Felsenstein, 1985). A link with larval biology is nonetheless evident - no internally ovipositing species are parasitoids. This is perhaps not surprising, given the danger of very limited oviposition possibilities when restricted to hosts in a single fig.

There are three groups of African fig wasps that have 'internally' ovipositing females - agaonines, sycoecines and *Sycophaga* (Sycophaginae). The first and last mate inside the galls and have either pacifist or aggressor males, while sycoecines mate primarily on the fig surface, and perhaps occasionally in the lumen, and are

Table 3.7 Sexual size dimorphism in fig wasps (SSD) in relation to mating site, based on data from Table 3.1. Each datum represents a species or a morph within a species.

MATING SITE	FEMALE LARGER	EQUAL	MALE LARGER
GALL	16	1	0
LUMEN	1	2	10
EXTERIOR	14	3	0

Table 3.8 Sexual size dimorphism (SSD) in fig wasps in relation to fighting behaviour, based on Tables 3.1 & 3.2. Each datum represents a species or a morph within a species.

SSD	PACIFIST	AGGRESSOR	FIGHTER
FEMALE LARGER	19	10	1
EQUAL	4	1	2
MALE LARGER	0	0	10

Table 3.9 Summary of the oviposition behaviour, male morphology and life history styles of the fig wasps studied.

FIG WASP SUBFAMILY	OVIPOSITION BEHAVIOUR	LIFE HISTORY	MATING SITES	MALE TYPES
AGAONINAE	INTERNAL	GALLER	GALL	IV, VI
SYCOECINAE	INTERNAL	GALLER	OUTSIDE	II
EPICHRYSOMALLINAE	EXTERNAL	GALLER	OUTSIDE	II
OTITESELLINAE	EXTERNAL	GALLER	LUMEN and few OUTSIDE	IV, V
SYCOPHAGINAE	BOTH	GALLER	LUMEN	VI
SYCORYCTINAE				
apocryptini	EXTERNAL	PARASITOID	LUMEN	VI
sycoryctini	EXTERNAL	PARASITOID	LUMEN OUTSIDE	I, IV, V, VI
ORMYRIDAE	EXTERNAL	PARASITOID	OUTSIDE	I
EURYTOMIDAE	EXTERNAL	PARASITOID	OUTSIDE	I

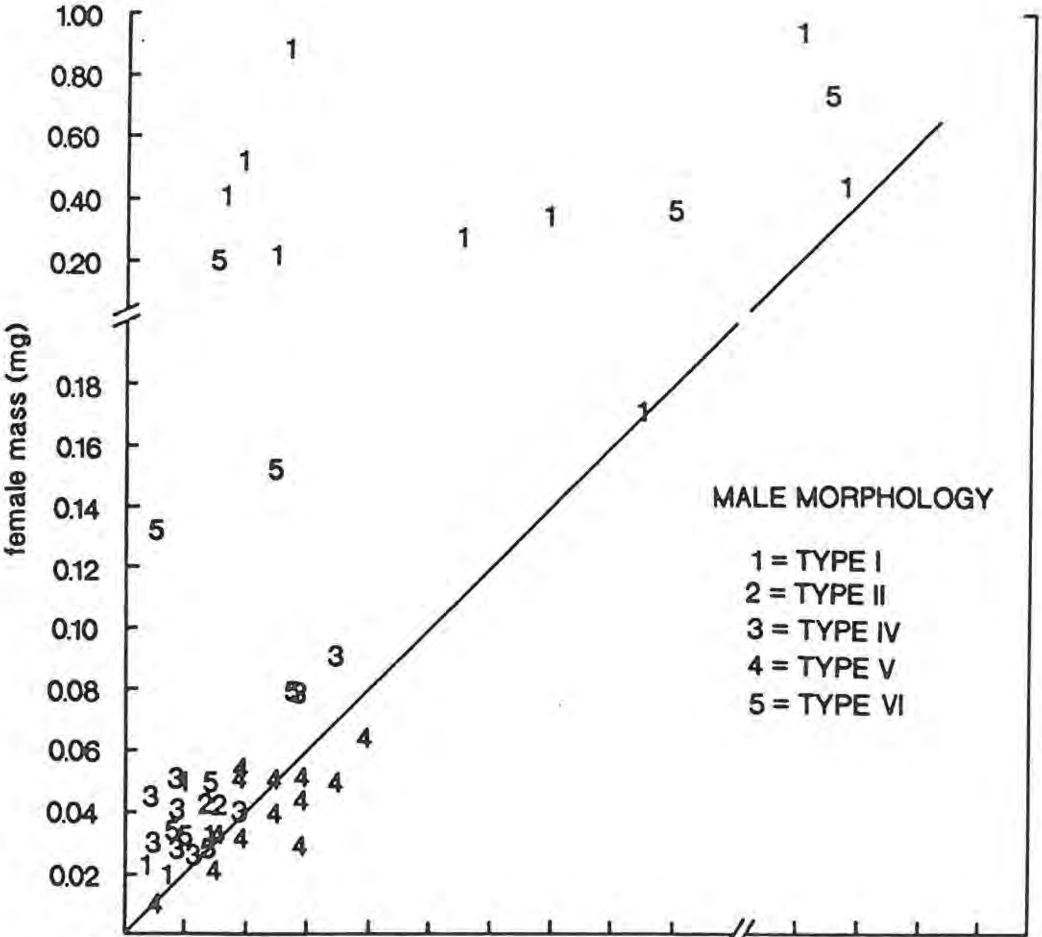


Figure 3.2 SSD in fig wasps in relation to male morphology, summarising data from Tables 3.1 and 3.2. No data on type III males were available. Male mass equals conspecific female mass along the 45° line, points above the line represent species where females are heavier than conspecific males and points below it represent species where males are heavier than conspecific females. Each data point represents a species or a morph within a species.

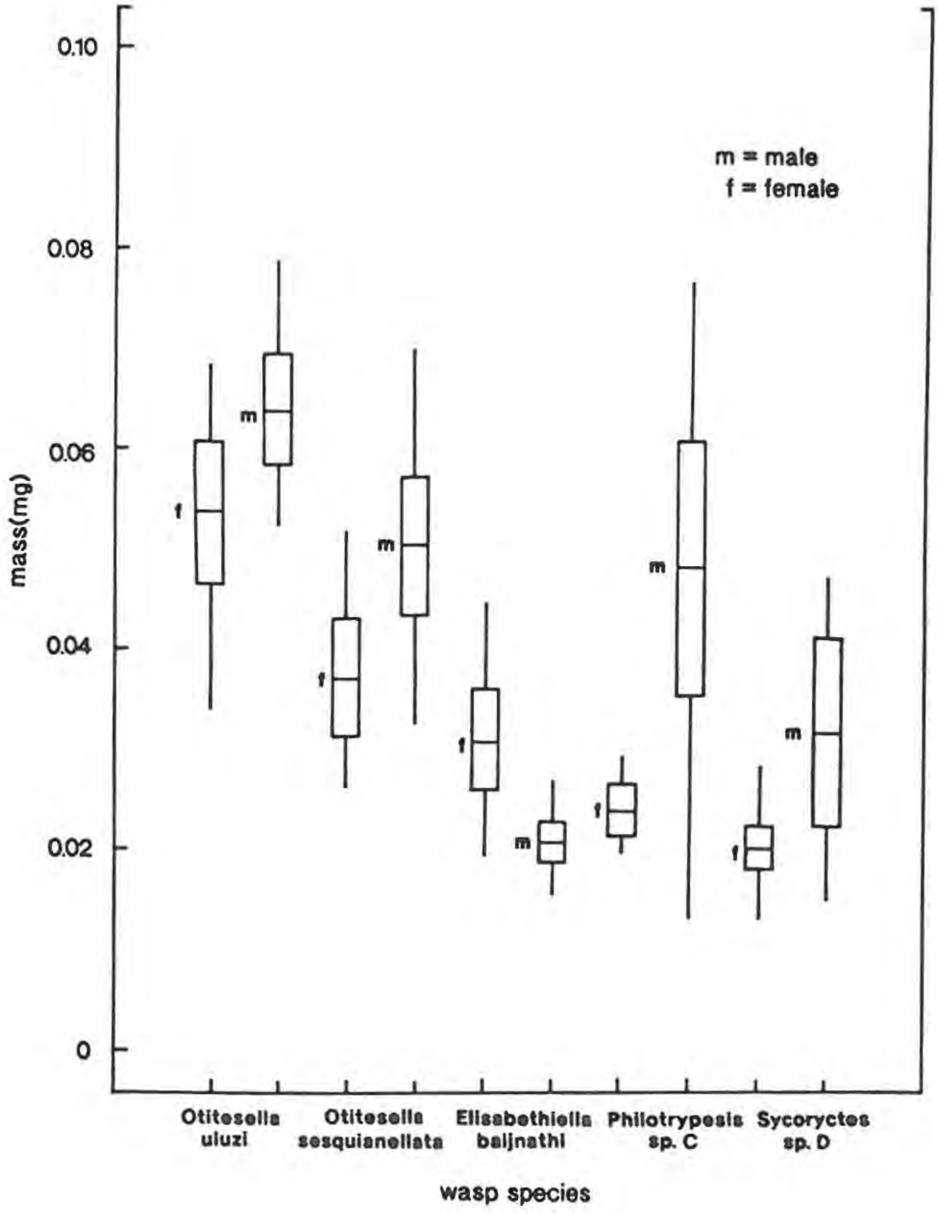


Figure 3.3 The dry weights of fig wasps associated with *Ficus burtt-davyi*. Mean, SD and range are indicated. *Elisabethiella baijnathi* is the only pacifist species illustrated, and the only species where males are smaller than females.

aggressors. That no fighting males are recorded from 'internally' ovipositing species is in agreement with Hamilton's predictions,although some sycoecine females can oviposit in several figs, and mate on the outside of the figs, and are therefore likely to be hardly more inbred than many of the 'externally' ovipositing species. *Sycophaga* is particularly interesting because all other Sycophaginae are 'externally' ovipositing species. Despite the likely increase in inbreeding that has resulted, *Sycophaga* and genera such as *Apocryptophagus* have males that are so similar that they are currently indistinguishable. Outside of Africa, two genera of Otitesellinae are adapted for internal oviposition (*Eujacobsonia* and *Grasseiana*). Their males have a Type IV morphology and are therefore likely to be aggressors, whereas most otitesellines have fighting males. However, some 'externally' ovipositing otitesellines also have Type IV males and this is therefore not conclusive proof of a 'decline' in fighting ability associated with the change of oviposition site (and presumably greater inbreeding). Among groups with females that oviposit from the outside of the fig, there is the whole range of male types, from pacifists to fighters. Thus, method of oviposition has little predictive power in terms of male fighting behaviour.

Mating site preferences are also not closely linked to methods of oviposition. 'Externally' ovipositing taxa include species which mate in all three locations, while 'internally' ovipositing species mate either in the galls (agaonines, *Sycophaga*), on the outside of the figs (Sycoecinae) or occasionally in the lumen (some Sycoecinae). The structure of the males in the south-east Asian otitesellines *Eujacobsonia* and *Grasseiana* suggests that they are also lumen-mating species (Boucek, 1988).

3.4 DISCUSSION

In those species where mating sites were documented, mating site and male behaviour seem to be closely linked. Species which mate in galls or on the surface of the figs were either pacifists or aggressors, but not fighters, while species which mate in the lumen were either aggressors or (mainly) fighters. Thus, fighting males were exclusively associated with mating in the lumen. Among higher taxa where gall mating is the norm (Sycophaginae, Agaoninae), fighting males were not recorded, while among the groups which appear to consistently mate in the lumen (Otitesellinae, excluding the *digitata* species group, Sycoryctinae of the tribe Sycoryctini), no pacifists were recorded.

The gall-maters were pacifists, wingless and smaller than their females whereas lumen-maters were typically wingless, larger than con-specific females, and exhibited aggressive or fighting behaviour. Conversely, those males that mate outside the figs were typically winged aggressors or pacifists and smaller than their females. There are exceptions to this general pattern. The wingless aggressor *digitata* morphs of *Otitesella* sp. I appear to be adapted for mating outside figs (chapter 12), and *Phagoblastus* species are winged aggressors with males that either vie for females as they emerge from the ostiole, or wait inside the fig lumen for females as they eclose.

Not only is fig wasp mating site an important determinant of fighting behaviour and male morphology, it is also associated with a change in SSD through an increase in male size. Fig wasps that mate with their immobile females before the females have eclosed from their galls, or those which mate outside the figs are typically smaller than their females, while those that mate in the lumen of the fig are typically larger than conspecific females.

The males of *Drosophila* species which exhibit lekking behaviour are particularly large and exhibit ritualised aggressive behaviour (Ringo, 1976; Spieth, 1974). Such large males are generally believed to be a consequence of sexual selection, as in tephritid flies, where increased size in males has been shown to be an advantage in group displays (Dodson, 1986), where strong sexual selection is associated with such non-monogamous systems, characterised by aggregations of females (Emlen & Oring, 1977).

Gall mating species include gall formers, but also parasitoid species that develop in figs of the subgenus *Sycomorus*. The cavities of these figs are filled with liquid during much of their development. This is often still present when male fig wasps emerge from their galls and begin searching for mates. Interestingly, the males of these species have modified spiracular peritremata that are believed to act as respiratory siphons and temporary air stores (Compton & McLaren, 1989). Thus the increased occurrence of mating in galls in *Sycomorus* figs may be linked to the presence of this liquid, which is much less abundant in most figs of the subgenus *Urostigma*. *Sycoscapter* males in the figs of *F. sycomorus* appear to be exceptional, in that they are fighters, but it is likely that they emerge at a later stage in the figs' development, after the pacifist gall-mating males, at a time when there is little or no fluid in the fig lumen. This may also explain why *Philotrypesis pilosa* (Murray, 1987), from *F. hispida* is a gall mater, unlike the congeneric species observed in this study, in that it develops in a fig species belonging to section *Sycocarpus*, which like the subgenus *Sycomorus* possesses species whose figs are also characterised by large amounts of fluid in the fig lumen during development. *P. pilosa* also appears to be exceptional in that it is a species with Type V males that fight, and yet mates inside the galls.

In fig wasps, the three potential mating sites provide contrasting functional levels of aggregation of females. In gall mating species the females are distributed over the inside of the fig and each one is mated separately in its own gall, often after a lengthy period of searching and chewing through the wall of the gall. Aggregation of females is reduced in species which mate on the outside of the figs simply because of the greater space that is available. The females emerge from the fig and are either encountered as they exit the fig or elsewhere. It is thus only the females of species which emerge from the galls and mate in the lumen that are aggregated and readily accessible to males. Consequently the opportunity for mate monopolization by males is greatest in lumen mating species.

In various insects larger males show different mating behaviour to that of smaller males, mating in groups whilst the smaller males pursue 'alternative' mating behaviour (Austad, 1984; Dominey, 1984). Such male behaviourial dimorphisms have been reported in some New World *Aepocerus* fig wasps. The larger winged males of one species vie aggressively for access to females as the latter emerge from the syconia, while smaller males are passive and mate with the females elsewhere on the trees (Bronstein, 1991). Like *Aepocerus*, *Sycophila* species also have maculated wings and mate outside the figs and the movements of the maculated wings of these species appears to be used in threat displays in addition to courtship (personal observations). The size of the maculae on their wings varies greatly, and is most prominent in larger individuals. Whether this is indicative of variation in behaviour similar to that of *Aepocerus* was not established.

4 LARGE MALE ADVANTAGE AND CORRELATES OF DAMAGE IN FIGHTING FIG WASPS

4.1 INTRODUCTION

Darwin (1871) proposed that sexual selection has two components: intersexual selection, normally the choice of males by females, and intra-sexual selection, usually competition between males for mates (Thornhill & Alcock, 1983). The importance of intersexual selection in insects remains a contentious issue because there is little empirical evidence to show that active female choice occurs (Bradbury & Davies, 1987). One of the best documented examples of female choice in insects occurs in the scorpion fly *Hylobittacus apicalis* (Bittacidae) where females prefer males which present them with large prey (Thornhill, 1976, 1980 a, 1980 b). On fig trees, a similar system may be present involving the lygaeid bug *Stilbocoris natalensis*. Males will collect and predigest a fig seed and transfer it to a female partner who copulates while eating the seed. Males without gifts are unsuccessful (Carayon, 1964). In contrast to intersexual selection, intra-sexual selection has often been recorded in insects. In extreme cases males may fight each other, the winner gaining mates, dominance rights or other advantages that favour transmission of its genes (Maynard Smith & Price, 1973).

Among animals in general, cichlid fish, rattlesnakes, fallow deer, oryx (Eibl-Eibesfeldt, 1961), seals (Le Boeuf, 1974) and antelope (Geist, 1966a), all exhibit ritualised aggressive behaviour. An interesting example of ritualised aggression among arthropods occurs in the jumping spider *Myrmarachne plataleoides* (Moffett, 1991). In these contests opponents have the capacity to seriously injure or kill each other, but seldom do so (Enquist & Leimar, 1990). However, lethal fighting occurs in a variety of arthropods, including mites (Cowan, 1984; Dimock, 1983; Potter, 1981; Potter *et al*, 1976), ants (Stuart, 1987), wasp larvae (Harvey & Partridge, 1987), thrips (Crespi, 1986, 1988) and fig wasps (Frank, 1987; Hamilton, 1979; Murray, 1987, 1989, 1990).

Large size is often an advantage in contests between conspecific males (Hughes, 1986). Examples are present among salticid spiders (Wells, 1988), beetles (Brown & Bartalon, 1986; Otronen, 1988; Palmer, 1978), mites (Dimock, 1983; Potter, 1981; Potter *et al*, 1976), flies (Dodson, 1986) and thrips (Crespi, 1986, 1988). Small males may have some compensatory advantages, however, such as a reduced development time and hence earlier emergence (Hurlbutt King, 1987). By emerging early a small male may increase his chances of inseminating virgin females. This is important in groups such as hymenopteran parasitoids, where many females will only mate once (Matthews, 1985). Small males of the scarab beetle *Podischnus agenor* emerge sooner and disperse further than their larger counterparts, thereby reducing the chances that the nest burrows they construct will be stolen from them by larger individuals (Eberhard, 1979, 1980).

Trivers (1972) predicted that the sex which invests less in each offspring will compete for the sex that invests more. In mammals it is the males that compete for females and since size can convey an important advantage in inter-male competition the males are often larger than females. However, there are numerous cases where female mammals are larger than males (Ralls, 1976, 1977). Sexual selection therefore does not necessarily account for all cases of sexual size dimorphism (SSD) (Ralls, 1976). Other factors contributing to SSD include bio-energetic constraints (Downhower, 1976; Woolbright, 1983); foetal or offspring weight (Myers, 1978); allometric growth (Cooper & Vitt, 1989); sexual cannibalism (Elgar, 1991) or intersexual competition giving rise to differential niche utilisation and resource partitioning (Selander, 1966).

Male fig wasps vary greatly in their anatomy and behaviour. In chapter two male fig wasps were classified into six groups: winged type I, wingless type III and VI pacifists, winged type II and wingless type IV aggressors and type V fighters. While pacifists and aggressors may mate either in the galls of the females, the lumen of the fig or outside the fig, fighters were found to typically mate in the lumen of the fig. It was also found that pacifists and aggressors tended to be smaller than their females or equal in size with them, whereas fighters were larger than conspecific females.

Here I examine whether the presence of large males in fig wasp species that fight could be a consequence of sexual selection operating through large males being more successful in fights. The damage incurred by wasps while inside figs was also studied and related to the densities of males and females inside the fig cavity.

Damage levels were also investigated among species which do not fight. This was in order to determine whether fighting was entirely responsible for the damage levels recorded in the fighting species.

4.2 MATERIALS AND METHODS

Males of *Elisabethiella baijnathi* (type VI), *Otitesella uluzi*, *O. sesquianellata*, *Philotrypesis* sp. C (type V morphs) and *Sycoryctes* sp. D were collected from mature figs of *Ficus burtt-davyi* around Grahamstown. Males of *Apocrypta guineensis* and *Ceratosolen capensis* (both type VI) were collected from figs of *F. sur*, also growing in Grahamstown.

4.2.1 Preliminary morphometrics

Body mass of male wasps could not be determined accurately after fights because sections of the body were often missing. The relationship between body mass and various linear measurements was therefore investigated, in order to determine which could be used as indirect measures of body size.

Individual male wasps, showing no signs of physical damage, were dried for three days at 40° C prior to weighing on a Cahn C-31 microbalance. The dead wasps were then measured using a movable hairline ocular micrometer attached to a Nikon compound microscope. Mandible length (taken as a straight line from the outer base to the tip), head width (across the eyes) and pronotum width (across the widest part) were recorded.

4.2.2 Damage levels among males that do not fight

To check whether damage levels in fighting fig wasp species were entirely a consequence of fighting, missing leg segments and antennae were recorded in three species where fighting was not observed. These were the males of *A. guineensis* and *C. capensis* from three *F. sur* figs and *E. baijnathi* from five *F. burtt-davyi* figs. Figs were collected a short time before the wasps emerged from the figs, which was allowed to occur naturally.

4.2.3 Body size and likelihood of injury

A total of 261 mature figs (without exit holes), from three *F. burtt-davyi* crops, were split open as soon as possible after collection. All the eclosed male wasps, both dead and alive, were counted immediately after collection and examined for damage. Damage was scored on a scale from zero for a perfectly intact individual through to five for a decapitated individual (Table 4.1). The length of each male's mandibles was also recorded. To determine whether the incidence of damage was influenced by the densities of females and males I also counted all the female and male wasps in the figs, distinguishing between females that were still in their galls or had eclosed (effectively all the male wasps had eclosed at that time).

Table 4.1 Damage categories recorded in the male fig wasps, arranged in increasing order of severity.

DAMAGE LEVEL	DESCRIPTION OF DAMAGE
0	No damage observed.
1	Antennae damaged with segments missing.
2	Legs with segments missing and antennae with segments missing.
3	Mandibles damaged.
4	Either thorax or abdomen damaged.
5	Head removed.

Table 4.2 Correlations between mass (mg), and mandible length (mm), head width (mm) and pronotum width (mm) in the males of fig wasps from *F. burtt-davyi*.

WASP	MANDIBLE LENGTH			HEAD WIDTH			PRONOTUM WIDTH		
	N	*r*	*P*	N	*r*	*P*	N	*r*	*P*
Otitesella uluzi	28	0.688	***	26	0.670	***	28	0.655	***
O. sesquianellata	29	0.798	***	28	0.776	***	27	0.672	***
Philotrypesis sp. C	28	0.843	***	28	0.934	***	20	0.804	***
Sycoryctes sp. D	25	0.683	***	24	0.609	**	19	0.120	NS

NS = not significant, ** $P < 0.01$, *** $P < 0.001$

4.2.4 Success in fights

F. burtt-davyi figs from different crops to those used above were collected and opened as already described. Fighting between males was observed with a binocular microscope using a fibre optic 'cold' white light. The combatants were collected after each decisive fight, which was considered to be where the loser was either killed, injured or had retreated. The mandible lengths of the combatants were recorded. The duration of some of the fights was also recorded, using a stopwatch.

4.2.5 Emergence times and wasp size

To determine whether smaller individuals emerged before their larger counterparts, figs were collected from an additional tree at the developmental stage when only a proportion of the males had commenced eclosion from their galls. The figs were frozen immediately and subsequently dissected. It was noted whether individual males had emerged or were still inside their galls and they were then dried for three days at 40° C and weighed on a micro-balance.

4.3 RESULTS

4.3.1 Morphometrics

Both mandible length and head width were highly correlated with body mass in all four species (Table 4.2). Pronotum width was also significantly correlated with mass in all the species except for *Sycoryctes* sp. D. Sample sizes vary slightly within species because not all combinations of measurements were made, due to breakage while measuring the wasps. As mandible length had the most consistently strong correlations with mass, and the mandibles were commonly left intact after fights, they were used routinely as the measure of body size.

4.3.2 Damage in non-fighting males

Damage was not only recorded in fig wasps exhibiting fighting behaviour but also in the pacifist species *C. capensis*, *A. guineensis* and *E. baijnathi* (Tables 4.3 & 4.4). Far greater proportions of the *Ceratosolen* and *Apocrypta* individuals were damaged than in the *Elisabethiella* species. This may be related to the contrasting sizes of their host figs: *F. sur* figs are much larger than those of *F. burtt-davyi* and have many more wasps.

A proportion of the male *Ceratosolen* emerged from the figs after producing the exit holes. The frequency of damaged individuals among those collected outside the figs was lower than among those collected inside (Table 4.3). This might be because the males on the outside avoid much of the melee inside the figs as the females emerge. The anatomy of the wasps also influenced the pattern of damage. For example, in *Ceratosolen* the mid legs are reduced and very delicate, as are all the tarsi of *Apocrypta,* and these were the structures most commonly damaged. The more extreme forms of damage, typical of those in the fighting species, were not recorded, although an occasional 'mangled' specimen was present, probably the result of damage caused when the figs were opened.

Table 4.3 Damage levels of male fig wasps in species not observed to exhibit any aggressive behaviour.

WASP	NUMBER OF FIGS		INTACT	TYPES OF DAMAGE					DAMAGE FREQUENCY (%)
				TARSI MISSING	OTHER LEG SEGMENTS MISSING	ANTENNAE DAMAGED	TARSI AND ANTENNAE DAMAGED	LEGS AND ANTENNAE DAMAGED	
Ceratosolen capensis	3	INSIDE FIG	4	13	16	0	9	18	93.33
		OUTSIDE FIG	24	38	13	3	8	12	75.51
Apocrypta guineensis	3	INSIDE FIG	15	29	16	2	7	10	81.01
Elisabethiella baijnathi	5	INSIDE FIG	51	6	0	0	0	0	11.76

Table 4.4 Damage sustained by male fig wasps (fighting species).

WASP	INTACT	TYPES OF DAMAGE					DAMAGE FREQUENCY (%)
		ANTENNAE DAMAGED	LEGS AND ANTENNAE WITH SEGMENTS MISSING	MANDIBLES DAMAGED	EITHER THORAX OR ABDOMEN DAMAGED	HEAD REMOVED	
Otitesella uluzi	141	69	38	13	1	6	47.38
O. sesquianellata	127	92	20	6	4	2	49.40
Philotrypesis sp. C	210	119	83	3	8	6	51.05
Sycoryctes sp. D	773	165	260	18	12	32	38.65

4.3.3 Body size and likelihood of damage

The damage categories that were recognised are described in Table 4.1. The extent of damage was often severe. This included broken mandibles, punctured heads and severed abdomens, but most frequently involved severed legs and antennae (Table 4.4). Given the results presented in Table 4.3, only the major damage categories can be confidently linked to fighting between the males. Nonetheless, in *F. burtt-davyi* figs 'background' damage levels due to other factors were relatively small (Table 4.3).

The frequencies of the five damage categories differed significantly between species (Chi-square $_{[12]}$ = 1359.65, $P < 0.001$) suggesting that methods of fighting, or at least their effects, varied between the different species. Damage among living wasps was found to be much less common than among dead individuals, most of which had been damaged (Table 4.5).

The average mandible lengths of living (at the time of collection) and dead males of *O. sesquianellata* and *Philotrypesis* sp. C were significantly different, with the mandibles of living wasps larger than those of the wasps which had died. The mandible sizes of living and dead *O. uluzi* and *Sycoryctes* sp. D males were not significantly different (Table 4.6).

4.3.4 Damage in relation to wasp densities

Most *F. burtt-davyi* figs contained fewer than three emerged males of each species, but higher densities of *Sycoryctes* sp. D were often present (Table 4.7). The average numbers of emerged males and

Table 4.5 The frequencies of damage in dead and living male fig wasps.

WASP	DEAD	ALIVE	CHI-SQUARE$_{[1]}$	*P*
Otitesella uluzi				
damaged	111	16	32.18	***
not damaged	13	128		
O. sesquianellata				
damaged	112	12	27.29	***
not damaged	14	113		
Philotrypesis sp. C				
damaged	197	22	94.83	***
not damaged	23	187		
Sycoryctes sp. D				
damaged	355	132	340.574	***
not damaged	45	728		

*** $P < 0.001$

Table 4.6 Comparisons of the mandible lengths of dead and living male fig wasps.

WASP	LIVING			DEAD			T-TEST	*P*
	MANDIBLE LENGTH (mm)			MANDIBLE LENGTH (mm)				
	N	MEAN ± SD	RANGE	N	MEAN ± SD	RANGE		
Otitesella uluzi	180	0.460 ± 0.050	0.27-0.53	53	0.440 ± 0.050	0.26-0.55	-1.79	NS
O. sesquianellata	150	0.426 ± 0.046	0.27-0.51	41	0.390 ± 0.058	0.23-0.52	-4.12	***
Philotrypesis sp. C	209	0.278 ± 0.054	0.14-0.51	99	0.262 ± 0.047	0.15-0.39	-2.55	*
Sycoryctes sp. D	910	0.283 ± 0.034	0.11-0.47	252	0.282 ± 0.033	0.13-0.40	-0.29	NS

NS = not significant, * $P < 0.05$, *** $P < 0.001$

females and the sex ratios are given in Table 4.8. *Sycoryctes* averaged over six males per fig, whereas the other three species had an average of between one and two males. Sex ratios within the fig cavities (where mating takes place) were highly male biased (Table 4.8). However, at the time of collection (which was before the exit tunnels had been chewed) between 16 and 25 percent of all the emerged males were already dead and between 13 and 27 percent of the males had been damaged (Table 4.9).

In all four species the proportion of damaged males (including both dead and living individuals) was positively correlated (Spearman's *r*) with both the number of females that had emerged into the cavities and the total number of conspecific wasps present (Table 4.10 and see Figure 4.1). In *O. sesquianellata* and *Philotrypesis* sp. C, but not *O. uluzi* and *Sycoryctes* sp. D, the proportion of damaged males was also positively correlated with the number of males (Table 4.10). The significant correlations are in part generated by a relatively large number of figs which contained no damaged males in combination with few emerged females (for example see Figure 4.2).

Sex ratios were negatively correlated with the proportion of damaged males in three of the species (Table 4.10, see Figure 4.3). That is, in figs with a relatively more males, damage was reduced. *Sycoryctes* sp. D, was exceptional, with a positive correlation between sex ratio and damage levels. This may be related in some way to the far higher male frequencies recorded in this species (Table 4.8).

Table 4.7 The range in numbers of emerged male fig wasps in the cavities of *F. burtt-davyi* figs.

NUMBERS OF EMERGED MALES	FREQUENCY							
	0	1	2	3	4	5	6	> 6
Otitesella uluzi	14	21	24	12	6	2	1	2
O. sesquianellata	30	43	23	9	6	3	3	1
Philotrypesis sp. C	34	51	33	11	12	6	2	4
Sycoryctes sp. D	16	19	20	15	11	12	9	62

Table 4.8 The numbers of males and female fig wasps in the cavities of the figs. Figs with no emerged males were excluded for calculations of sex ratios (males/(males + females)).

WASPS		FEMALES EMERGED		MALES EMERGED		SEX RATIO (EMERGED WASPS ONLY)	
	N FIGS	MEAN ± SD	RANGE	MEAN ± SD	RANGE	N FIGS	MEAN
Otitesella uluzi	82	1.13 ± 1.85	0-7	2.00 ± 1.8	0-12	68	0.74
O. sesquianellata	118	0.80 ± 1.34	0-5	1.55 ± 1.63	0-10	93	0.75
Philotrypesis sp. C	153	1.58 ± 2.42	0-16	1.76 ± 1.69	0-8	119	0.69
Sycoryctes sp. D	164	1.42 ± 2.69	0-19	6.40 ± 5.90	0-35	154	0.80

Table 4.9 Dead and damaged males inside figs collected prior to the construction of the emergence tunnels. The figures for damage include both dead and living individuals.

WASP	N FIGS	TOTAL NUMBER OF MALE WASPS	% DEAD	% DAMAGED
Otitesella uluzi	68	164	19	22
O. sesquianellata	93	183	16	13
Philotrypesis sp. C	119	269	21	19
Sycoryctes sp. D	155	1050	25	27

Table 4.10 The relationships (Spearman's r) between the proportion of damaged male fig wasps and the densities of males and females in the figs. Only wasps that had emerged into the fig cavities are considered.

WASP	N FIGS OCCUPIED	EMERGED FEMALES		EMERGED MALES		MALES AND FEMALES		SEX RATIO	
		r	P	r	P	r	P	r	P
Otitesella uluzi	68	0.390	***	0.178	NS	0.370	**	-0.250	*
O. sesquianellata	93	0.350	***	0.260	*	0.410	***	-0.260	*
Philotrypesis sp. C	119	0.505	***	0.570	***	0.600	***	-0.350	***
Sycoryctes sp. D	155	0.330	***	0.044	NS	0.194	*	0.330	*

NS = not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

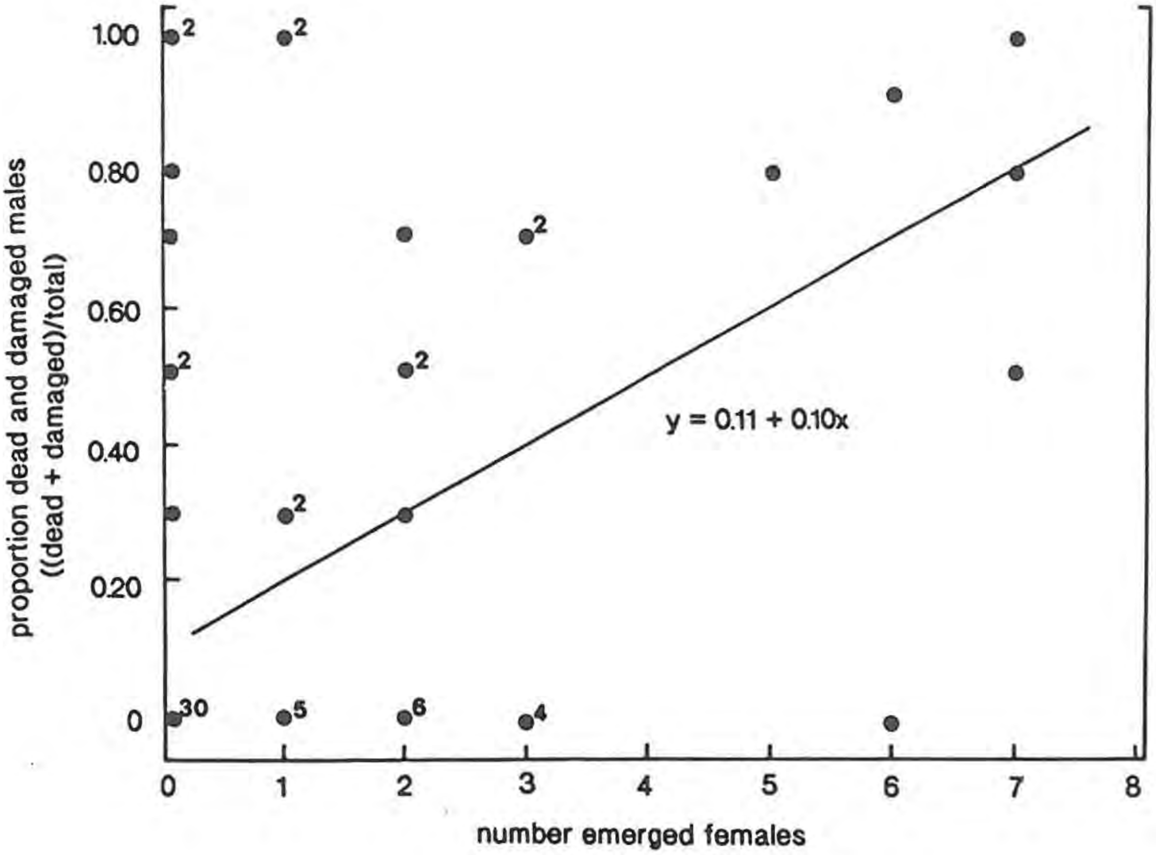


Figure 4.1 The relationship between the proportion of damaged *Otitesella uluzi* males and the number of females in the fig cavity.

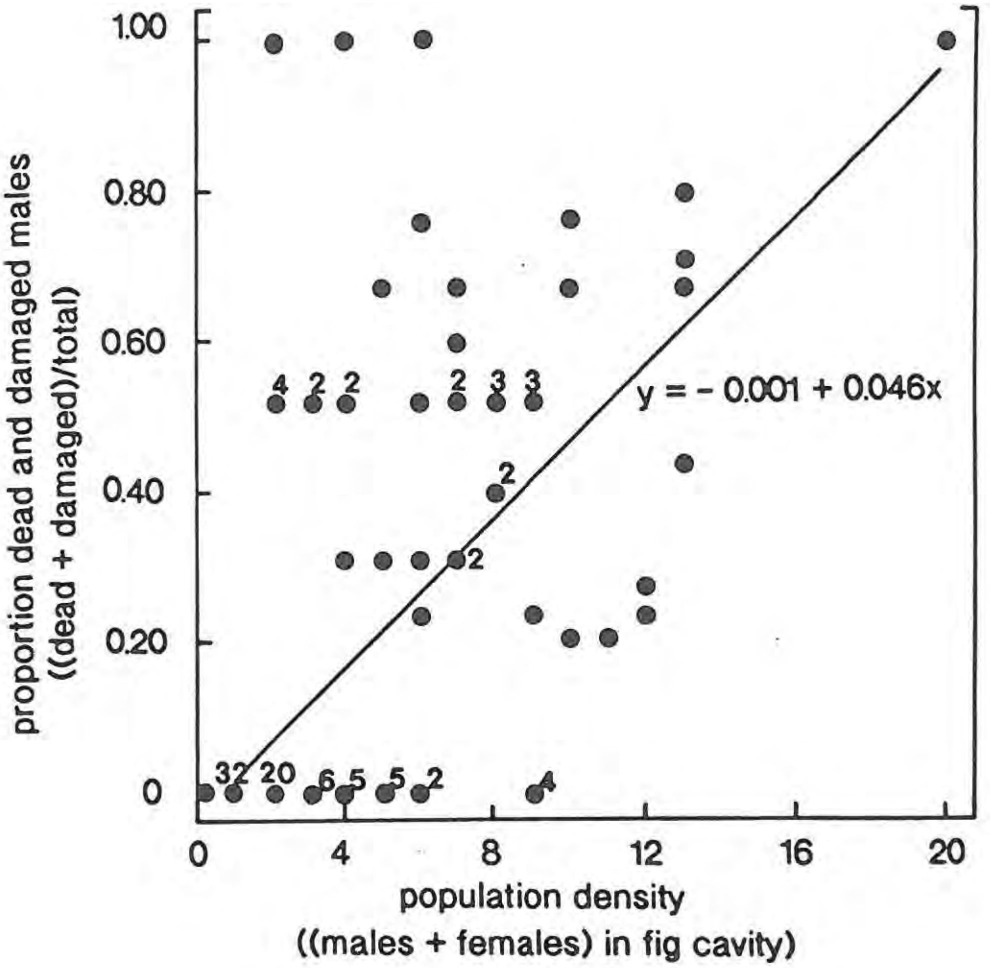


Figure 4.2 The relationship between the proportion of damaged *Philotrypesis* sp. C males and the density of conspecific wasps in the fig cavity.

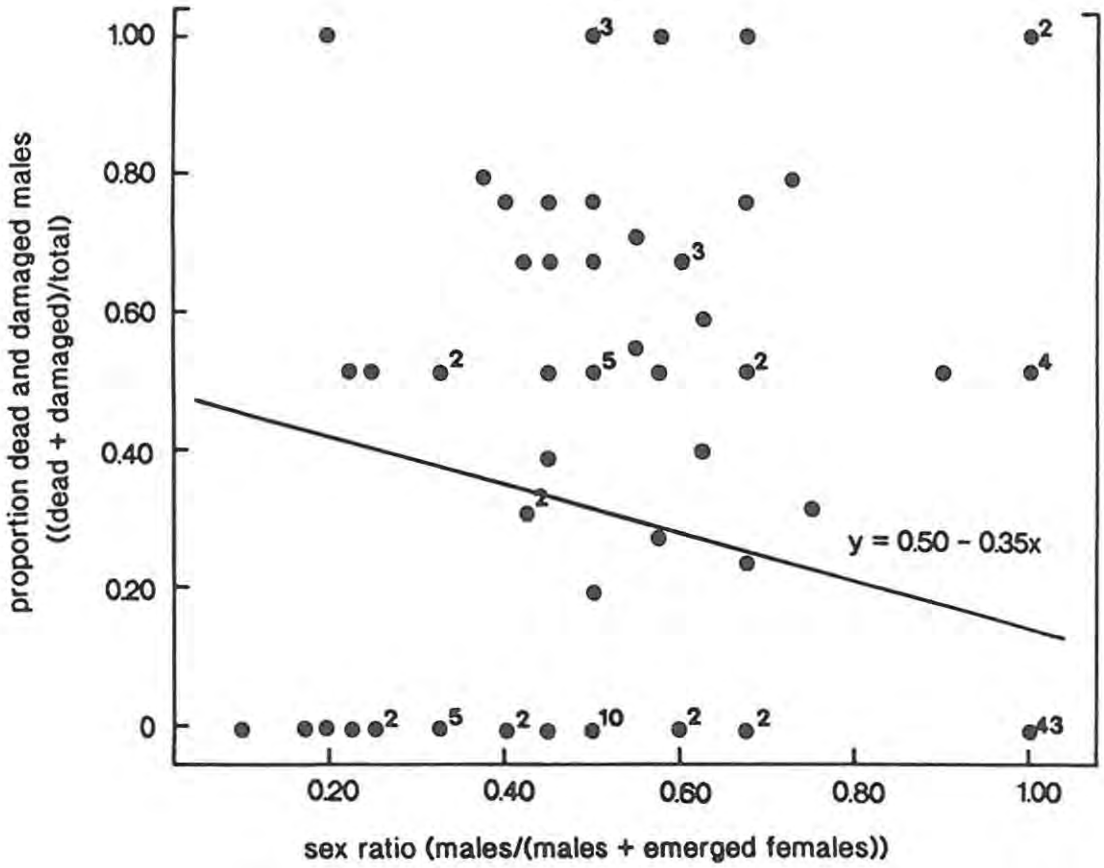


Figure 4.3 The relationship between the proportion of damaged *Philotrypesis* sp. C males and the sex ratio of wasps in the fig cavity.

4.3.5 Fighting behaviour and success in fights

Fighting behaviour in the four species was rather similar (chapter two). Upon encountering each other the male fig wasps either ignored each other and continued moving, or stood still, or walked around while facing each other, with their antennae moving. One of the males might then retreat immediately after a brief altercation, during which both males lunged and attempted to bite the legs, antennae and gasters of their opponents. Often the males would get a grip on each others' heads and a "tug-of-war" ensued. The stronger male often succeeded in lifting the other off the substrate, shaking his opponent and continuing to bite him. Fighting continued until the losing male stopped retaliating, retreated or was dead. The brief altercations consisted of lunges and strikes, where the contestants did not get a grip on each other. After such encounters the smaller males often retreated into a gall and were then cautious about subsequently re-entering the fig lumen.

Unfortunately I was unable to combine behaviourial observations with data on size-related damage in *O. uluzi*. In the other species, the average duration of fights ranged from 15 to 27 seconds (Table 4.11). The winners of decisive fights were on average larger than the losers (Table 4.12) and larger males were more likely to win fights, but did not always do so (Table 4.13).

The shortest fights occurred between opponents with the greatest size difference, but as the size difference between the combatants

Table 4.11 The duration of fights between males of three fig wasp species.

WASP	N FIGHTS	DURATION (SECONDS)	
		MEAN ± SD	RANGE
Otitesella sesquianellata	28	18.19 ± 13.58	1.01-50.52
Philotrypesis sp. C	17	27.15 ± 20.05	1.23-73.55
Sycoryctes sp. D	22	15.13 ± 16.04	2.01-66.48

Table 4.12 The mandible sizes of winners and losers in fights.

WASP	N CONTESTS	MANDIBLE SIZE OF WINNER (mm)		MANDIBLE SIZE OF LOSER (mm)		T- TEST	*P*
		MEAN ± SD	RANGE	MEAN ± SD	RANGE		
Otitesella sesquianellata	43	0.460 ± 0.027	0.40-0.53	0.433 ± 0.028	0.37 - 0.48	-3.78	***
Philotrypesis sp. C	30	0.312 ± 0.057	0.15-0.41	0.256 ± 0.051	0.08 - 0.33	-3.83	***
Sycoryctes sp. D	35	0.300 ± 0.040	0.24-0.44	0.270 ± 0.055	0.14 - 0.44	-2.35	***

*** $P < 0.001$

Table 4.13 The success of fighting male fig wasps in relation to their size.

WASP	N FIGHTS OBSERVED	RELATIVE SIZES OF FIGHT WINNERS		$\text{CHI-SQUARE}_{[1]}$	*P*
		LARGER	SMALLER		
Otitesella sesquianellata	43	31	12	4.45	*
Philotrypesis sp. C	30	27	3	11.43	***
Sycoryctes sp. D	35	26	9	5.19	*

* $P < 0.05$, *** $P < 0.0001$

decreased, the fights become more intense and prolonged (Figures 4.4 a, b & c).

Damage levels were not linearly correlated with wasp size, except in *O. sesquianellata* where larger males had less damage (Table 4.14). Because the fights of short duration were between individuals with the greatest size difference, the chances of injury in these fights was likely to be lower than that in prolonged fights between individuals of similar size. Damage levels amongst small males and large males might therefore be expected to be lower than those in intermediate sized males, because the former were most likely to be involved in highly unevenly matched fights. In order to examine whether damage levels were higher among medium-sized individuals, the males were divided into three groups. This was done by dividing the wasps into equally numerous sub-populations with no overlap in body size. Damage levels were then compared between the groups. There were no significant differences in damage levels between small, medium and large sized individuals in any of the species, although average damage levels in medium sized *O. sesquianellata* were about twice as high as in the other groups (Table 4.15).

4.3.6 Emergence and wasp size

There was no evidence that small males may gain an advantage by developing more quickly and emerging into the fig lumen before the larger males (Table 4.16). In most species there was no difference in the average sizes of the two wasp categories, the

Table 4.14 Correlations between male size and damage levels.

WASP	NUMBER OF WASPS	r	*P*
Otitesella uluzi	233	-0.04	NS
Otitesella sesquianellata	191	-0.18	**
Philotrypesis sp. C	338	0.017	NS
Sycoryctes sp. D	1162	-0.02	NS

NS = not significant, ** $P < 0.01$

Table 4.15 Comparisons of damage scores between groups of individuals ranked by mandible size.

WASP	N WASPS	MANDIBLE CLASS SIZE (mm)	DAMAGE SCORE	MANDIBLE CLASS SIZE			
			MEAN ± SD	MEDIUM		LARGE	
				MANN-WHITNEY U	*P*	MANN-WHITNEY U	*P*
Otitesella uluzi	73	small (0.27-0.47)	0.36 ± 1.15	1516.00	NS	1214.50	NS
	40	medium (> 0.47-0.50)	0.26 ± 0.80	-		641.00	NS
	32	large (> 0.50)	0.34 ± 1.23	-		-	
O. sesquianellata	52	small (0.26-0.42)	0.19 ± 0.82	988.00	NS	840.00	NS
	40	medium (> 0.42-0.45)	0.38 ± 1.10	-		675.50	NS
	31	large (> 0.45)	0.17 ± 0.89	-		-	
Philotrypesis sp. C	69	small (0.14-0.25)	0.13 ± 0.34	1968.00	NS	2137.50	NS
	54	medium (> 0.25-0.29)	0.07 ± 0.26	-		158.00	NS
	62	large (> 0.29)	0.19 ± 0.69	-		-	
Sycoryctes sp. D	330	small (0.12-0.29)	0.18 ± 0.58	60566.00	NS	24078.50	NS
	380	medium (>0.29-0.31)	0.27 ± 0.77	-		28683.00	NS
	150	large (> 0.31)	0.29 ± 0.85	-		-	

NS = not significant

Table 4.16 A comparison of the weights of male fig wasps that were still in their galls with those which had emerged into the fig cavity.

WASP	NOT EMERGED		ECLOSED		T-TEST	*P*
	MASS (mg)		MASS (mg)			
	N	MEAN ± SD	N	MEAN ± SD		
O. uluzi	9	0.064 ± 0.026	29	0.082 ± 0.015	-2.59	*
O. sesquianellata	26	0.046 ± 0.011	31	0.044 ± 0.007	0.91	NS
Philotrypesis sp. C	6	0.043 ± 0.016	7	0.067 ± 0.029	-1.74	NS
Sycoryctes sp. D	12	0.045 ± 0.011	28	0.042 ± 0.008	1.01	NS

NS = not significant, * $P < 0.05$

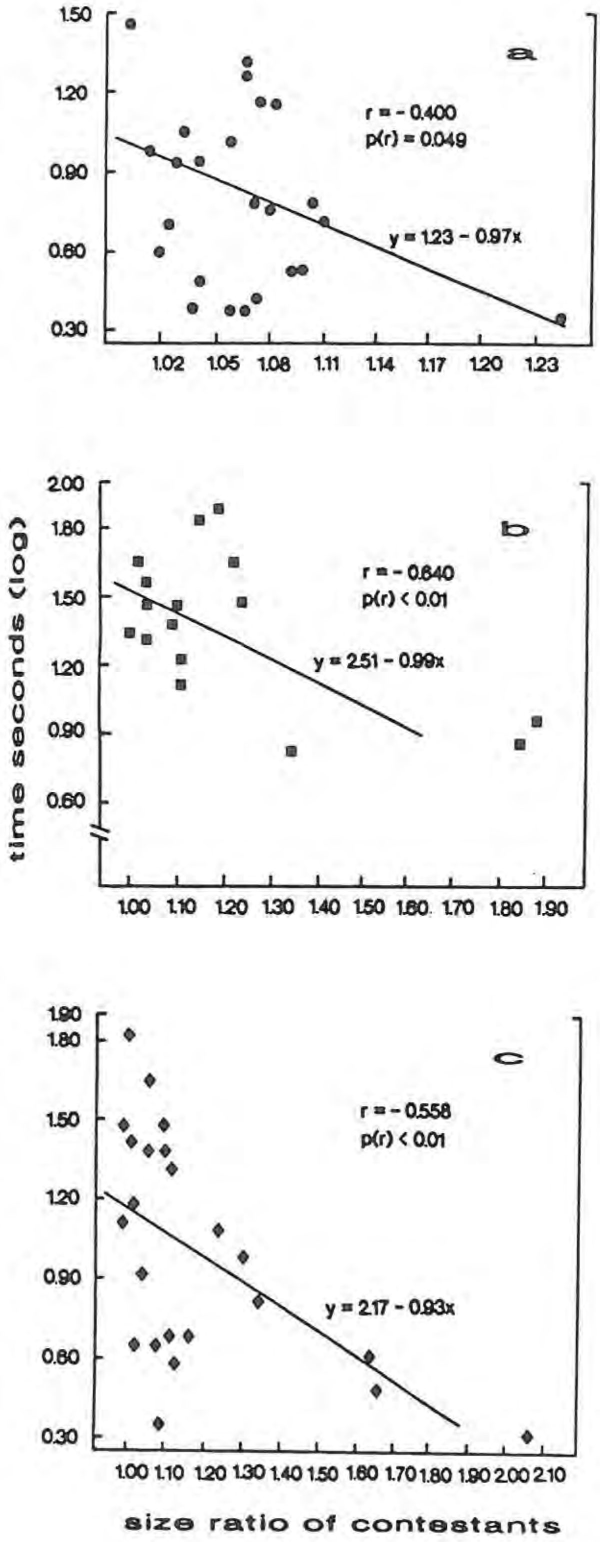


Figure 4.4 The relationship between fight duration and the size ratio of contestants in fights a) *Otitesella sesquianellata*, b) *Philotrypesis* sp. C and c) *Sycoryctes* sp. D.

exception being the males *O. uluzi*, where the males in the lumen were significantly larger, not smaller, than those still in their galls.

4.4 DISCUSSION

Game theory (Austad, 1989; Hughes, 1986; Maynard Smith, 1979; Maynard Smith & Price, 1973) views individuals in conflict situations as contesting for fitness-related resources (benefits) that may result in a loss of some fitness (cost) to both contestants. Theoretical models (Hammerstein, 1981; Maynard Smith & Parker, 1976) have focused on asymmetries between contestants, such as the size of individuals and their weapons. Game theory predicts that if contestants differ in fighting ability, this asymmetry, if perceived by both contestants, should be used to settle the contest quickly. Size is often a good indicator of fighting ability (Verrell, 1986) leading to the predictions that the larger of the two contestants should win and second that contest cost should increase with increasing similarity in the size of the opponents. Contest cost is defined in terms of duration and consequent loss of mating opportunity, energy expenditure and risk of injury or death (Austad, 1983; Verrell, 1986). Murray (1987) noted that severe injuries were rarely associated with fights of short duration, but in fights of long duration either one or both participants were severely injured. The results presented here on fig wasps are consistent with game theory predictions in that the relative size of the opponents was a good predictor of contest outcome, with larger individuals being more likely to win fights, and contest cost (measured as time spent fighting) increasing as the size of the opponents became more similar. Damage, also a measure of contest cost, was less clearly linked to asymmetry in contestant size.

Demonstrations of mating advantage due to male size in the absence of inter-male competition are rare (Simmons, 1988), but include a field cricket where larger males are more 'sexually competent' than their smaller counterparts and *Drosophila* species where larger males mate more often (Santos *et al*, 1988). The observed advantage of large size during fighting in fig wasps is likely to be translated into a reproductive advantage, as has been shown in fungus beetles (Conner, 1988), elephant seals (Le Boeuf, 1974), atlantic salmon (Jarvi, 1990), a bee *Centris pallida* (Alcock *et al*, 1977, Alcock, 1979 a, 1979 b) and stick insects (Sivinski, 1978). While I have not confirmed that there is any increased mating opportunity for large male fig wasps this is very likely to be the case. Fighting can result in debilitating or even fatal injuries, especially among losers, and these make future matings unlikely or impossible. In addition, individuals that have lost a fight are often nervous and hide away, further reducing their opportunities for successful mating. Murray (1987) similarly noted that in *P. pilosa* injured males retreated into galls and that large males easily dominated smaller males. Thus the advantage gained by large males in fights may well provide the selection pressure which has resulted in these male fig wasps being on average larger than their con-specific females. This is in contrast to species where males do not fight, and are smaller than or equal in size with their females.

Sexual size dimorphism in polymorphic species, such as *Philotrypesis* sp. C, is also consistent with this pattern. The aggressor, type IV and alate, type I males are both smaller than their females and the fighting type V morph is larger than the female (chapter three). Neither the alate nor smaller males of *Philotrypesis* were seen to fight and may represent 'alternative means of obtaining mates' *sensu* Austad (1984) and Dominey (1984). Their alternative behaviour appears to be 'logical' given that small flightless males would lose fights, but raises the question of why apterous males of other species do not show similar variation.

In other insects, there are situations where small male size is advantageous (Marshall, 1988). Small males may be more mobile and may also have a reduced development time and hence earlier emergence (Hurlbutt King, 1987) which may increase their chance of inseminating females (Matthews, 1985). The results presented here, however, provide no evidence that small individuals of fighting fig wasps develop more quickly and emerge before larger males. There might be an advantage to small size in wingless pacifist fig wasps that are gall maters, if it makes access to galls containing conspecific females easier, but even this could be negated by their smaller mandibles finding it harder to chew through galls. These possibilities were not investigated.

Murray (1987) used a model of contest competition (Murray & Gerrard, 1985) to look at fighting in the fig wasp *Philotrypesis pilosa* in terms of costs (death and injury) and benefits (mating opportunities). Although the observations described in this chapter were not designed to test Murray and Gerrard's predictions, some of the results do concur with those of Murray's, where it was shown that the extent of damage increased with increasing densities of females that had emerged from their galls. This may be due to fights being directly associated with mating opportunities. Murray (1987) distinguished between intense fights of longer duration associated with mating opportunities and those that were less intense, of shorter duration and not associated with mating opportunities. Such distinctions were not made here, but the results did show that in two of the species the proportion of damaged males increased with the density of males in the fig lumen and for all species the proportion of damaged males was positively correlated with population density. These results are not unexpected, in that as the number of males and the population density increases so does the frequency of encounter between males, resulting in more fights and the damage they cause. More unexpected were the correlations, for all species, of damage with numbers of eclosed females and sex ratios. The former may be an indication that severe fights are more likely to develop when females are nearby, as observed by Murray (1987).

The proportion of damaged males may also increase with population density because of increased 'background' damage, not incurred from fighting. Such non-fighting related damage seems to be especially prevalent in large figs where hundreds or even thousands of individuals can be crawling around in a confined space. The problem of damage produced by factors other than fighting means that only the more extreme injuries can be assumed to be fight related, unless their cause is actually viewed by an observer. Fortunately, however, 'background' damage levels seem to be low in *F. burtt-davyi* where most of the observations were carried out. 'Background' damage also does not negate the other patterns that were detected because they would not explain the significant differences in the mandible sizes of dead and living males and the large male advantage in fights. Moreover, a difference in damage levels between the *religiosa* and *digitata* males of *Otitesella* sp. I was observed, and this is associated with differences in fighting behaviour (chapter 12).

Because small males tend to avoid fights (chapter two) and large males win fights, losers of fights will often be in the intermediate size range. If intermediate sized individuals are more likely to be killed or injured and body size has a non-zero heritability (Arthur, 1984; cited in McLachlan and Neems, 1989) then this disruptive selection could help explain the evolution of male dimorphism (Eberhard, 1982; Gadgil, 1972; Gadgil & Taylor, 1975; Gross, 1985; Hamilton, 1979). However, there was no evidence to suggest that this process was occurring in the fighting fig wasps looked at here.

5 IS GALL SIZE LINKED TO ADULT BODY SIZE IN MALE FIG WASPS ?

5.1 INTRODUCTION

In parasitic wasps a positive correlation between host size and adult body size has been demonstrated for numerous solitary species, where only one wasp larva develops per host. Examples include *Roptrocerus xylophagorum* (Torymidae, Samson, 1984), *Hyposoter exiguae* (Ichneumonidae, Jowyk & Smilowitz, 1978), *Lariophagus distinguendus* (Pteromalidae, Charnov *et al*, 1981) and *Trichogramma evanescens* (Trichogrammatidae, Salt, 1940). A positive correlation between host size and wasp size has also been demonstrated in some gregarious wasps, where both the number and size of the progeny increases in larger hosts. Examples are *Caraphractus cinctus* (Mymaridae, Jackson, 1968), two *Aphytis* species (Aphelinidae, Opp & Luck, 1986), *Coccygomimus turionella* (Ichneumonidae, Sandlan, 1979), *Nasonia vitripennis* (Pteromalidae, Wylie, 1976) and *Trichogramma semifumatum* (Trichogrammatidae, Taylor & Stern, 1971). Where two differently sized host species are attacked this can result in a bimodal size distribution in the parasitoid population, as in *Telenomus ashmeadi* (Proctotrupidae) and *Opius melleus* (Braconidae, Salt, 1941). Thus in parasitoid hymenopterans adult body size seems to be dependent on the amount of food available to the larvae. If food is restricted then small individuals emerge, while if the resources available are totally inadequate then the parasite dies, or develops into an abnormal runt (Salt, 1940).

Unlike most other chalcids, the majority of fig wasps are phytophagous and develop in galls formed in the female flowers of *Ficus* species. Groups apparently consisting exclusively of such gallers include the Agaoninae, Epichrysomallinae, Otitesellinae, Sycoecinae and Sycophaginae. A thousand or more individual agaonines may emerge from a single fig (C. Zachariades, personal communication), where each larva developed inside its own separate gall. Galls produced by *Otitesella* species develop extremely rapidly after oviposition, suggesting that ovipositing females, and not just the wasp larvae, can have a major influence in the eventual size of the galled ovules.

Not all fig wasps are gallers. There are also parasitoid/inquiline fig wasps, with larvae that develop in the same galls as other fig wasps, and eventually kill them. Presumably these fig wasps are unable to gall the fig flowers themselves, an ability which seems to be linked to the size of the acid glands in the adult female (Abdurahiman & Joseph, 1978). In at least some fig wasp parasitoids, their body size is related to the size of the galls where they developed. *Apocrypta guineensis*, recorded from the large galls of *Apocryptophagus* species in *F. sur*, for example, are far larger than conspecifics which have developed at the expense of pollinator larvae (C. Zachariades, personal communication). Parasitoid fig wasps are also generally solitary, although two *A. guineensis* males sometimes emerge from *Apocryptophagus* galls (C. Zachariades, personal communication).

Unlike the situation with many other plant galls (for examples, see Darlington, 1975), fig wasps eventually occupy almost the entire galls in which they develop. Gall size is therefore potentially a determinant of the size of the adult fig wasps that eclose from them. Nutrients available to the wasps may not necessarily be linked to gall size given that galls act as nutrient 'sinks', but the maximum dimensions of the wasps are clearly set by the dimensions of the cavity in the gall. Via control of gall size, ovipositing wasps, or their progeny, may therefore be able to influence body size, and hence fighting ability of the males (chapter 4) and the fecundity of the females, which is linked in some species to body size (Nefdt, 1989).

In *F. burtt-davyi* the pollinator *E. baijnathi* and two *Otitesella* species are gallers (Van Noort & Compton, personal communication), while *Sycoryctes* sp. D and *Philotrypesis* sp. C are parasitoids/inquilines. Here I describe the relationship between gall size and adult mass in these fig wasps and discuss the results in the light of the relationship between wasp size and reproductive fitness.

5.2 MATERIALS AND METHODS

Almost mature *F. burtt-davyi* figs, without exit holes and with fig wasp pupae/adults still inside their galls, were collected from four trees in the vicinity of Grahamstown. The fig wasps were extracted from their galls, identified and weighed using a Cahn - 31 microbalance after being dried for three days at 40° C. Because the galls were not spherical, both length and breadth were measured, and used to estimate gall volume, the measure of gall size that was employed. Length and breadth measures were inserted into the equation for calculating the volume of a spheroid, 4/3pi x length x breadth^2 (Smith, 1966).

5.3 RESULTS

In the fig wasp species examined there were no differences in the means and variances of gall sizes of the sexes, except in *Sycoryctes* sp. D where male gall size was more variable than female gall size in one collection (Levene-F = 12.77, $P < 0.001$) (Table 5.1). Data for males and females were therefore combined when testing for differences in gall size between trees and fig wasp species. Differences in gall sizes between collections on different trees were detected (Table 5.2) and for this reason each collection was analyzed separately.

O. sesquianellata galls were consistently larger than those of *E. baijnathi*, *Philotrypesis* sp. C and *Sycoryctes* sp. D, while the gall sizes of the latter three species generally did not differ significantly (Table 5.3). Exceptions were the galls of *Philotrypesis* sp. C and *Sycoryctes* sp. D in Tree 1, where the latter were significantly larger (Table 5.3). *O. sesquianellata* individuals from the galls were heavier than those of *E. baijnathi*, *Philotrypesis* sp. C and *Sycoryctes* sp. D.

Table 5.1 Comparisons of the gall sizes of conspecific male and female fig wasps. *Otitesella sesquianellata* and *Sycoryctes* sp. D were absent from Tree 3.

FIG WASP	TREE	SEX	GALL SIZE (mm^3)			T-TEST *P*
			N	MEAN ± SD	RANGE	
Elisabethiella baijnathi	1	♂	31	3.31 ± 0.81	1.80-5.13	-0.96 NS
		♀	144	3.45 ± 0.71	2.18-7.09	
	2	♂	11	3.97 ± 0.78	2.79-5.38	0.53 NS
		♀	77	3.83 ± 0.81	2.40-5.82	
	3	♂	2	3.33 ± 0.09	3.26-3.39	-1.12 NS
		♀	53	3.89 ± 0.71	2.77-5.70	
	4	♂	7	2.19 ± 0.61	1.65-3.26	-0.53 NS
		♀	354	2.31 ± 0.61	1.25-6.44	
Otitesella sesquianellata	1	♂	65	4.90 ± 1.23	2.59-8.00	1.17 NS
		♀	133	4.69 ± 1.19	2.52-9.83	
	2	♂	14	4.45 ± 1.29	2.72-6.59	-1.80 NS
		♀	25	5.19 ± 1.17	3.44-8.31	
	4	♂	46	3.35 ± 1.01	1.89-5.83	-2.00 NS
		♀	55	3.74 ± 0.91	1.94-5.97	
Philotrypesis sp. C	1	♂	10	3.40 ± 0.64	2.75-4.89	1.18 NS
		♀	35	3.18 ± 0.49	3.18-4.40	
	2	♂	3	3.18 ± 0.45	2.70-3.58	-1.33 NS
		♀	21	3.89 ± 0.89	2.64-6.14	
	3	♂	2	4.01 ± 0.15	3.90-4.11	4.28 NS
		♀	2	3.55 ± 0.05	3.49-3.57	
	4	♂	19	2.44 ± 0.72	1.43-4.33	0.22 NS
		♀	40	2.40 ± 0.66	1.05-3.82	
Sycoryctes sp. D	1	♂	12	3.69 ± 0.48	2.98-4.37	0.75 NS
		♀	43	3.54 ± 0.61	2.45-5.46	
	2	♂	7	3.66 ± 0.77	2.61-4.72	-0.68 NS
		♀	17	3.93 ± 0.90	2.73-5.97	
	4	♂	33	2.40 ± 0.92	1.038-5.07	1.31 NS
		♀	153	2.24 ± 0.58	1.17-4.61	

NS = not significant

Table 5.2 ANOVA of gall volume (mm^3) between the three collections from *Ficus burtt-davyi* where all four fig wasps were recorded.

FIG WASP	F	DF	*P*
Elisabethiella baijnathi	276.00	2, 621	***
Otitesella sesquianellata	40.69	2, 335	***
Philotrypesis sp. C	41.41	2, 130	***
Sycoryctes sp. D	123.93	2, 262	***

*** $P < 0.001$

Table 5.3 Comparisons of gall sizes between pairs of fig wasp species from *Ficus burtt-davyi*.

FIG WASP	GALL SIZE (mm^3)			*Otitesella sesquianellata*		*Philotrypesis* sp. C		*Sycoryctes* sp. D	
	N	MEAN ± SD	RANGE	MANN -WHITNEY U	*P*	MANN-WHITNEY U	*P*	MANN-WHITNEY U	*P*
TREE 1									
Elisabethiella baijnathi	175	3.43 ± 0.73	1.80-7.09	4444.50	***	349.50	NS	2982.50	NS
Otitesella sesquianellata	198	4.76 ± 1.20	2.53-9.83	-		6818.00	***	7849.50	***
Philotrypesis sp. C	47	3.22 ± 0.53	2.52-4.89	-		-		646.00	**
Sycoryctes sp. D	55	3.58 ± 0.59	2.45-5.46	-		-		-	
TREE 2									
Elisabethiella baijnathi	88	3.85 ± 0.80	2.40-5.82	552.00	***	1090.50	NS	841.50	NS
Otitesella sesquianellata	39	4.93 ± 1.25	2.72-8.32	-		784.00	***	584.00	***
Philotrypesis sp. C	27	3.77 ± 0.90	2.09-6.14	-		-		28.50	NS
Sycoryctes sp. D	24	3.85 ± 0.86	2.61-5.96	-		-		-	
TREE 4									
Elisabethiella baijnathi	361	2.30 ± 0.61	1.25-6.45	3146.00	***	5977.00	NS	19721.50	NS
Otitesella sesquianellata	101	3.57 ± 0.98	1.89-5.97	-		4604.00	***	13665.00	***
Philotrypesis sp. C	59	2.41 ± 0.68	1.05-4.33	-		-		5425.50	NS
Sycoryctes sp. D	186	2.27 ± 0.65	1.03-5.07	-		-		-	

NS = not significant, ** $P < 0.01$, *** $P < 0.001$

There was no difference between the weights of *Philotrypesis* sp. C and *Sycoryctes* sp. D individuals from the galls, but they were heavier than those of *E. baijnathi* (Table 5.4). This is surprising given that the former are parasitoids of *E. baijnathi*. Frequency distributions of the gall sizes from a representative collection (Tree 4) are given in Figure 5.1.

On an individual basis, fig wasp mass was weakly correlated with gall volume when data for all the species were combined (n = 1145, $r = 0.09$ and $P = 0.0035$), this was also the case in two collections of *O. sesquianellata* and one of *E. baijnathi* (Table 5.5), but not in the remaining collections nor with the other species (Table 5.5). Too few winged *Philotrypesis* males were available in the collections to make any between-morph analyses possible.

5.4 DISCUSSION

Gall size was found to be related to adult mass for fig wasp species from *F. burtt-davyi*, in as far as *O. sesquianellata*, which produces significantly larger galls than *E. baijnathi*, is a larger species. Similarly, in figs of *F. sur* very large galls are produced by certain *Apocryptophagus* species, and Epichrysomallinae fig wasps also produce galls that are far larger than those of the pollinators (personal observations). Given the poor correlations that were obtained, the relationship between gall size and the mass of wasps is nonetheless clearly at best a weak one. How variation in gall size is achieved among fig wasps is unknown. Gall size

Table 5.4 Comparisons of dry mass between pairs of fig wasp species from *Ficus burtt-davyi*.

FIG WASP	MASS (mg)			*Otitesella sesquianellata*		*Philotrypesis* sp. C		*Sycoryctes* sp. D	
	N	MEAN ± SD	RANGE	MANN -WHITNEY U	*P*	MANN-WHITNEY U	*P*	MANN-WHITNEY U	*P*
TREE 1									
Elisabethiella baijnathi	143	0.028 ± 0.007	0.011-0.050	1662.50	***	1303.00	***	1891.50	***
Otitesella sesquianellata	188	0.048 ± 0.012	0.018-0.080	-		6427.00	***	8024.00	***
Philotrypesis sp. C	41	0.035 ± 0.007	0.020-0.048	-		-		1094.00	NS
Sycoryctes sp. D	51	0.034 ± 0.008	0.011-0.053	-		-		-	
TREE 2									
Elisabethiella baijnathi	73	0.027 ± 0.010	0.011-0.074	172.50	***	480.50	***	430.50	**
Otitesella sesquianellata	36	0.049 ± 0.011	0.023-0.073	-		810.50	***	646.50	***
Philotrypesis sp. C	27	0.035 ± 0.009	0.017-0.049	-		-		318.50	NS
Sycoryctes sp. D	20	0.032 ± 0.007	0.018-0.044	-		-		-	
TREE 4									
Elisabethiella baijnathi	224	0.030 ± 0.007	0.013-0.057	1301.00	***	3410.00	***	10922.50	***
Otitesella sesquianellata	96	0.049 ± 0.011	0.024-0.078	-		4729.50	***	14063.50	***
Philotrypesis sp. C	58	0.036 ± 0.008	0.014-0.050	-		-		5482.50	NS
Sycoryctes sp. D	166	0.035 ± 0.007	0.016-0.074	-		-		-	

NS = not significant, *** $P < 0.001$

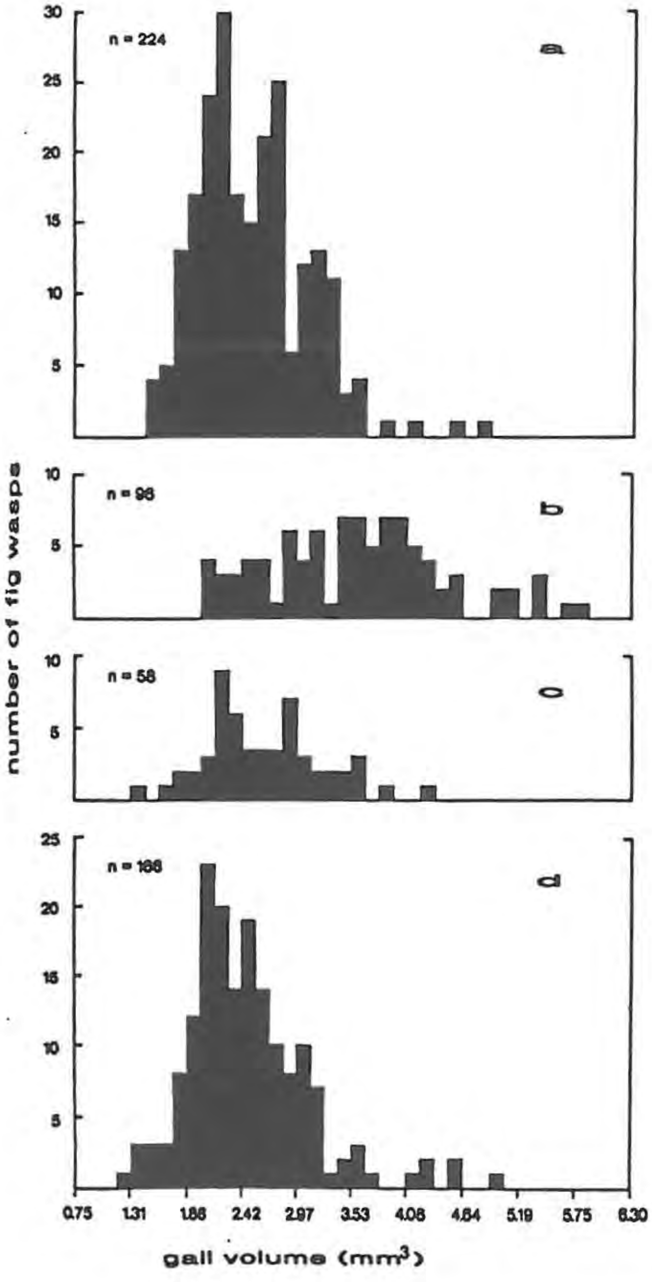


Figure 5.1 Frequency histograms of gall size for a) *Elisabethiella baijnathi*, b) *Otitesella sesquianellata*, c) *Philotrypesis* sp. C and d) *Sycoryctes* sp. D.

Table 5.5 Correlations of gall size (mm^3) with the dry mass (mg) of the fig wasps they contained.

FIG WASP	N	r	P
TREE 1			
Elisabethiella baijnathi	143	0.197	*
Otitesella sesquianellata	188	0.338	***
Philotrypesis sp. C	41	0.224	NS
Sycoryctes sp. D	51	0.133	NS
TREE 2			
Elisabethiella baijnathi	73	-0.08	NS
Otitesella sesquianellata	36	0.487	**
Philotrypesis sp. C	27	0.210	NS
Sycoryctes sp. D	20	0.369	NS
TREE 4			
E. baijnathi	224	-0.021	NS
O. sesquianellata	96	0.172	NS
Philotrypesis sp. C	58	0.235	NS
Sycoryctes sp. D	166	0.114	NS

NS = not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

variation in the golden rod gall fly *Eurosta solidaginis* (Tephritidae) is influenced by genetic variation among flies (Weis & Abrahamson, 1986) and in willows, gall size also varies between different clones of the plant (Clancy & Price, 1989).

Larger individual insects of both sexes may have increased fitness over smaller individuals. However, the slope of the relationship between increasing body size and fitness may not be the same for the two sexes. Usually it is the female which gains proportionally greater fitness from a given increase in body size (Charnov *et al*, 1981, Van Den Assem *et al*, 1989). Consequently, it has been argued that if a searching female parasitoid has a range of host sizes in which to distribute her solitary male and female progeny, she will optimise her oviposition if she lays male eggs in relatively small hosts and females in relatively large ones. Such selective oviposition has been recorded in *L. distinguendus* (Charnov *et al*, 1981). Similarly, in gregarious parasitoids, a more male biased sex ratio is predicted in smaller hosts. This happens in two *Extenterus* species (Ichneumonidae) where the sex ratio of wasps emerging from male hosts is less female biased than that of wasps emerging from the larger female hosts (Lyons, 1977).

Increased size generally conveys a reproductive advantage in female insects because larger females tend to have a greater number of eggs (Opp & Luck, 1986; Waage & Ng, 1984). This has been confirmed in the fig wasp *E. baijnathi* (Nefdt, 1989). Larger individuals may also live longer than their smaller counterparts, as shown in *L. distinguendus* (Charnov *et al*, 1981) and *Trichogramma evanescens* (Waage & Ng, 1984). In most chalcids an increase in a male's size may have little impact on its reproductive success, which probably explains why male chalcids are generally smaller than females (Gauld & Fitton, 1987; Hurlbutt, 1987; Van den Assem *et al*, 1989).

The range of gall sizes of the galler *E. baijnathi* overlapped very closely with those of the two parasitoids *Sycoryctes* sp. D and *Philotrypesis* sp. C, whereas some of the galls produced by *O. sesquianellata* were much larger than those of the other fig wasps. The correspondence in gall size between the parasitoids and *E. baijnathi* suggests that *Philotrypesis* sp. C and *Sycoryctes* sp. D mainly parasitize this species, as there was no evidence of these species emerging from any galls larger than those of *E. baijnathi*. However, these parasitoids have previously been reared from figs containing only *Otitesella* species (Compton, personal communication) suggesting that these species can act as alternative hosts to the pollinator *E. baijnathi*. The potential for the parasitoids to utilize larger galls nonetheless generally seems to be ignored in *F. burtt-davyi,* despite the possible benefits via increased body size. However, I have shown (chapter 3) that in some fig wasp species males are not smaller than their female counterparts. In species with fighting males, the males are on average larger than their females, while in species where the males are not fighters they are smaller or similar sized. This may be a consequence of sexual selection, in that larger males tend to win fights, and this is presumed to increase their chances of mating (chapter 4). Selection for larger body size may therefore be operating in both males and females in some fig wasps. However, costs of larger body size can also be envisaged. In female agaonines, very large individuals may be at a disadvantage because they find it more difficult to penetrate the fig ostiole. Similarly large body size could reduce the mobility of male wasps in the confined space inside of figs. Silby *et al* (1991) have discussed the basis of stabilising selection in another group of insects - bruchid beetles.

Little is known about the factors that determine adult wasp size in phytophagous gall wasps (Cynipidae, Askew, 1988) or fig wasps, but the quality and quantity of nutrition is likely to be critical (Weis *et al*, 1988). Many fig wasp galls enlarge very quickly, implying that the adult females at least initiate the galling process. The females of galling fig wasp species may therefore have the ability to vary the sizes of the galls where their larvae develop. This might have been expected to result in a greater development of outsized males among gallers compared with parasitoids, but as shown in chapter 3, no clear link between life history and SSD was detected. Parasitoids, in contrast, can only vary the resources available for their progeny through either the timing of their oviposition, when they kill their hosts, by selecting hosts in large galls or becoming inquilines. Joseph and Abdurahiman (1987) argued that the variability in resources available for larvae might account for the unisexual variation and polymorphism observed in some parasitoid fig wasp species.

The cecidomyid fly *Ficiomyia perarticulata* galls the ovules of *F. citrifolia* (Roskam & Nadel, 1990) in Florida. Males and females develop in galls which differ both in morphology and size. This is not the case in the fig wasps that were examined, where external appearances and gall sizes were similar. Gall size is therefore not manipulated in relation to the sex of fig wasp progeny. This together with the weak correlation between the size of the galls and the adults they produce, makes it unlikely that gall size, per se, is the factor responsible for determining SSD in fig wasps. Gall size would also seem to be an unlikely determinant of morph differentiation, but this was not confirmed.

6 SEX RATIOS OF FIG WASPS

6.1 INTRODUCTION

Fisher, in 1930, suggested that frequency dependent selection would produce a 1:1 sex ratio in an outbreeding population at equilibrium. His reasoning was that whenever population sex ratios deviated from equality, selection would favour the rarer sex. In other words, if a female produced male offspring in a predominantly female population then she would eventually have more grandchildren than if she had produced female offspring under the same circumstances. This is because male progeny would be assured of increased mating opportunities. A female would continue to benefit by producing exclusively male progeny until such a time as males outnumbered females in the population.

In nature, sex ratios are not always 1:1. Rarely, they can be heavily biased towards males as, for example, in the bushbaby *Galago crassicaudatus* (Galagidae) (Clark, 1978). More commonly, however, sex ratios are female biased, as in numerous parasitic wasps (Herre, 1987; King & Skinner, 1991; Waage, 1982; Werren, 1983; Wylie, 1976).

Hamilton (1967) described unusual conditions that would favour such female biased sex ratios. He reasoned that under conditions where female progeny only have the opportunity to mate with their brothers, a female should produce just enough sons to mate with all her daughters. Outbred populations are expected to have an optimal sex ratio approaching 1:1, while intermediate levels of sib-mating favour intermediate sex ratios. Other ecological features conducive to female biased sex ratios are localised, restricted broods of siblings, the ability of females to store sperm, and immobile males restricted to their development sites, with only mated females dispersing (Hamilton, 1967). Many of the examples Hamilton (1967) used were parasitic hymenopterans which, being haplodiploid and mostly arrhenotokous, are potentially able to control their sex ratios by control of fertilisation (Crozier, 1977).

Sex ratios could be genetically fixed within a species, or vary in response to local breeding conditions. Some parasitic wasps, for example *Nasonia vitripennis* (Werren, 1980) and pollinating fig wasps (Agaoninae) have been shown to accurately adjust their sex ratios according to the presence of other ovipositing females, in line with the predictions of local mate competition theory (Frank, 1985; Herre, 1985b; Nefdt, 1989). Evidence exists that other parasitic wasps, for example the pteromalid *Muscidifurax zaraptor* (Wylie, 1979); a trichogrammatid *Trichogramma evanescens* (Waage & Lane, 1984); the scelionids *Telenomus remus* (van Welzen & Waage, 1987) and *T. heliothides* (Strand, 1988) and the braconid *Asobara persimilis* (Owen, 1983) may also be able to adjust their sex ratios. Similarly, wasps such as the ichneumonid, *Coccygomimus turionella* (Sandlan, 1979) and the scelionid *Gryon japonicum* (Noda & Hirose, 1989) are able to adjust their sex ratios according to host quality, for example size, in accordance with certain fitness maximization predictions (Charnov, *et al*, 1981).

The lifestyle of fig wasps epitomizes the conditions described by Hamilton (1967) that should favour female biased sex ratios. In pollinating fig wasps and most other 'internally' ovipositing species the female enters only one fig to oviposit, and dies there. Consequently the entire brood of the female is restricted to a single fig, and she may be the only ovipositing female present. Under these circumstances mating occurs only between siblings. Other fig wasps, for example species of *Apocrypta*, *Otitesella*, *Philotrypesis* and *Sycoryctes* oviposit from the outside, through the wall of the fig and move from fig to fig to oviposit. Consequently each fig is likely to contain the offspring of several females, unless the population densities are low, and the incidence of sib-mating in these species is likely to be lower than that of internally ovipositing species. Less female biased sex ratios would therefore be predicted (Hamilton, 1979).

While the sex ratios of a few pollinating fig wasps have been studied (Frank, 1985b; Herre, 1985; 1987, Nefdt, 1989) it has not been shown whether 'externally' ovipositing fig wasps do have higher sex ratios than 'internally' ovipositing ones. Here I describe the sex ratios of some of the fig wasps associated with three fig tree species and relate them to the oviposition methods of the wasps. In species with polymorphic males I also examine differences in sex ratios between figs where both male forms are present and others without winged males.

Hamilton (1979) also suggested that there was a link between inbreeding and the presence or absence of fighting ability in male fig wasps. More inbred species were expected to be less likely to display fighting behaviour. Given that more inbred species are also expected to have more female biased sex ratios, then a comparison of the sex ratios of species with fighting males and pacifist males can be used as an indirect test of Hamilton's predictions of the importance of inbreeding for the development of male fighting behaviour. In other words, are species with fighting males characterised by less female biased sex ratios than species with pacifist males?

6.2 MATERIALS AND METHODS

Mature figs without wasp exit holes were collected from several trees of *F. burtt-davyi*, *F. ingens* and *F. sur* growing around Grahamstown. Once collected, figs were placed individually in netting covered vials and left until most of the fig wasps had emerged from the figs and died. The wasps were stored in a freezer for subsequent counting and identification.

Both sexes of most of the fig wasp species could be easily distinguished from each other. However, the *Apocryptophagus* and *Sycophaga* species from *F. sur* had to be excluded from the analyses, because the males of these species could not be separated.

Sex ratios were calculated as (males/(males + females)) or ((1 + males)/(males + females)): so that higher sex ratios are indicative of higher proportions of males. Wasp population densities were calculated in two ways: either excluding or including figs where a particular species was entirely absent. The latter values are likely to be irrelevant for species that mate inside the figs, but not for species where some males search for mates outside of the figs.

6.3 RESULTS

6.3.1 Sex ratios and population densities within figs and crops

The average sex ratios of individual figs within crops and population densities of the wasps are given in Table 6.1 and summarised in Table 6.2. The sex ratios from individual crops ranged from as low as 0.10 in *Platyscapa soraria* to 0.85 in *Otitesella uluzi*. Average population densities ranged from two wasps per fig in *O. sesquianellata* to 830 wasps for *Ceratosolen capensis* (Table 6.1). These values only include figs occupied by a species and densities are considerably lower if all figs in a crop are included (Table 6.1). Population densities on different crops varied significantly in all the wasp species (Table 6.3).

Cumulative sex ratios over the crop as a whole were significantly female biased in eight species, and significantly male biased in two species, and for any species cumulative sex ratios were the same within crops (Tables 6.4, 6.5 & 6.6). However, there was often extremely large variation in sex ratios between crops,

Table 6.1 Sex ratios and population densities of wasps used in this study.

HOST *FICUS*/ FIGWASP SPECIES	N FIGS	N OCCUPIED FIGS	SEX RATIO	WASP DENSITIES	
				OCCUPIED FIGS	ALL FIGS
				MEAN ± SD	MEAN ± SD
F. burtt-davyi					
Elisabethiella baijnathi					
1	100	96	0.14	34.69 ± 16.86	33.30 ± 17.87
2	100	95	0.19	14.46 ± 10.95	13.73 ± 11.12
3	70	52	0.26	4.67 ± 5.62	3.47 ± 5.25
4	52	45	0.23	3.91 ± 2.31	3.38 ± 2.53
5	31	25	0.15	3.40 ± 2.35	2.80 ± 2.52
6	57	47	0.16	17.76 ± 14.43	14.64 ± 14.74
7	39	39	0.14	39.54 ± 25.92	39.54 ± 25.92
8	66	66	0.16	50.37 ± 23.77	50.37 ± 23.77
Otitesella uluzi					
1	100	13	0.46	4.38 ± 7.25	0.56 ± 2.92
2	100	69	0.53	6.11 ± 4.81	4.21 ± 4.89
3	70	21	0.33	2.57 ± 3.48	0.77 ± 2.22
6	57	9	0.14	3.56 ± 2.56	0.56 ± 1.60
7	39	15	0.57	2.73 ± 1.90	1.05 ± 1.76
8	66	43	0.44	5.11 ± 5.08	3.32 ± 4.75
Otitesella sesquianellata					
1	100	45	0.43	6.31 ± 6.44	2.83 ± 5.30
2	100	71	0.44	4.89 ± 2.97	3.47 ± 3.34
3	70	59	0.47	4.36 ± 3.30	3.67 ± 3.42
4	52	48	0.29	4.14 ± 2.85	3.82 ± 2.96
5	31	19	0.41	2.10 ± 1.15	1.28 ± 1.36
6	57	50	0.48	12.60 ± 7.32	11.05 ± 8.01
7	39	24	0.50	7.00 ± 5.53	4.30 ± 5.51
8	66	31	0.45	6.45 ± 5.98	3.02 ± 5.23
Philotrypesis sp. C					
1	100	66	0.42	5.93 ± 6.07	3.91 ± 5.67
2	100	85	0.45	8.30 ± 6.12	7.05 ± 6.38
3	70	67	0.45	15.29 ± 7.53	14.63 ± 7.99
4	52	25	0.19	1.84 ± 1.10	0.90 ± 1.20
5	31	16	0.27	1.69 ± 1.08	0.80 ± 1.13
6	57	44	0.42	7.70 ± 7.53	5.94 ± 7.36
7	39	33	0.38	7.30 ± 6.50	6.17 ± 6.49
8	66	53	0.52	6.15 ± 4.27	4.93 ± 4.54

Table 6.1 *continued*

HOST *FICUS*/ FIGWASP SPECIES	N FIGS	N OCCUPIED FIGS	SEX RATIO	WASP DENSITIES	
				OCCUPIED FIGS	ALL FIGS
				MEAN ± SD	MEAN ± SD
Sycoryctes sp. D					
1	100	94	0.45	25.28 ±14.17	23.76 ± 15.00
2	100	74	0.36	10.81 ± 10.30	7.99 ± 10.05
3	70	54	0.47	5.98 ± 5.88	4.61 ± 5.74
4	52	23	0.22	2.30 ± 1.49	1.01 ± 1.51
35	31	13	0.27	1.92 ± 1.38	0.80 ± 1.30
6	57	50	0.38	20.48 ± 16.18	8.28 ± 16.55
7	39	36	0.39	16.39 ± 13.33	15.13 ± 13.53
8	66	18	0.33	4.94 ± 3.57	1.35 ± 2.87
F. ingens					
Platyscapa soraria					
1	16	13	0.15	34.08 ± 27.90	27.68 ± 28.48
2	36	17	0.16	12.70 ± 9.08	5.90 ± 8.89
3	21	3	0.07	20.67 ± 26.65	2.95 ± 11.22
4	27	27	0.11	45.44 ± 22.17	45.44 ± 22.17
5	6	6	0.10	68.17 ± 20.04	68.17 ± 20.04
6	5	5	0.02	11.80 ± 5.31	11.80 ± 10.68
7	4	4	0.13	10.00 ± 10.68	10.00 ± 10.68
8	5	4	0.10	28.50 ± 17.31	22.80 ± 19.68
9	11	11	0.11	105.27 ± 41.90	105.27 ± 41.90
Otitesella sp. I					
1	16	16	0.40	28.88 ± 13.94	28.88 ± 13.94
2	36	24	0.54	38.04 ± 16.97	24.67 ± 22.87
3	21	21	0.56	19.57 ± 9.53	19.57 ± 9.53
4	27	25	0.66	25.28 ± 16.97	23.40 ± 17.65
5	6	6	0.57	22.00 ± 16.49	22.00 ± 16.49
6	5	5	0.77	17.60 ± 4.61	17.60 ± 4.61
7	4	4	0.45	28.25 ± 13.30	28.25 ± 13.30
8	5	5	0.75	15.60 ± 12.11	15.60 ± 12.11
9	11	10	0.35	38.10 ± 17.97	34.64 ± 20.55
Philotrypesis sp. H					
1	16	12	0.38	11.08 ± 8.88	8.31 ± 0.075
2	36	20	0.64	14.80 ± 9.67	8.22 ± 10.31
3	21	21	0.67	26.09 ± 17.95	26.09 ± 17.95
6	5	5	0.54	23.60 ± 4.09	23.60 ± 4.09
7	4	4	0.71	5.00 ± 4.69	5.00 ± 4.69

Table 6.1 *continued*

HOST *FICUS*/ FIGWASP SPECIES	N FIGS	N OCCUPIED FIGS	SEX RATIO	WASP DENSITIES	
				OCCUPIED FIGS	ALL FIGS
				MEAN ± SD	MEAN ± SD
F. sur					
Ceratosolen capensis					
1	10	9	0.33	5.77 ± 2.86	5.19 ± 3.25
2	10	10	0.24	367.00 ± 176.47	367.00 ± 176.47
3	10	10	0.31	830.40 ± 282.44	830.40 ± 282.44
4	24	24	0.16	215.29 ± 163.50	215.29 ± 163.50
5	8	8	0.19	265.00 ± 235.46	265.00 ± 235.46
6	10	9	0.23	36.00 ± 28.84	32.40 ± 29.47
7	6	6	0.65	49.83 ± 44.95	49.83 ± 44.95
8	26	25	0.38	169.52 ± 160.93	163.00 ± 161.15
9	6	6	0.22	113.67 ± 83.53	113.67 ± 83.53
Apocrypta guineensis					
1	10	10	0.36	35.40 ± 15.22	35.40 ± 15.22
2	10	10	0.40	132.50 ± 107.38	132.50 ± 107.38
3	10	10	0.49	40.00 ± 34.84	40.00 ± 34.84
4	24	23	0.51	109.30 ± 87.15	104.75 ± 88.11
5	8	8	0.51	185.87 ± 63.69	185.87 ± 63.69
6	10	8	0.58	44.75 ± 48.11	35.80 ± 46.44
7	6	8	0.54	76.83 ± 54.76	76.83 ± 54.76
8	26	25	0.59	85.36 ± 46.47	82.07 ± 48.51
9	6	6	0.65	230.33 ± 82.38	230.33 ± 82.38

Table 6.2 Summary of the fig collections and the sex ratios of the wasps they contained.

FICUS AND WASPS	CROPS WITH WASPS	N OCCUPIED FIGS	TOTAL NUMBER OF WASPS	SEX RATIO	DENSITY/FIG (occupied figs only)
					MEAN ± SD
F. burtt-davyi (8 crops, 515 figs)					
Elisabethiella baijnathi	8	465	10914	0.18	23.47 ± 22.59
Otitesella uluzi	6	175	826	0.46	4.86 ± 4.83
Otitesella sesquianellata	8	347	2124	0.43	6.12 ± 5.59
Philotrypesis sp. C	8	389	3100	0.42	7.97 ± 7.12
Sycoryctes sp. D	8	362	5282	0.39	14.59 ± 14.17
F. ingens (9 crops, 131 figs)					
Platyscapa soraria	9	90	3728	0.12	41.42 ± 36.78
Otitesella sp. I	9	116	3210	0.55	27.00 ± 16.50
Philotrypesis sp. H	5	68	1129	0.58	16.60 ± 14.23
F. sur (9 crops, 110 figs)					
Ceratosolen capensis	9	106	24856	0.26	232.30 ± 268.47
Apocrypta guineensis	9	107	10415	0.54	98.25 ± 82.41

Table 6.3 ANOVA for fig wasp population densities between crops (occupied figs only).

FICUS AND WASPS	ANOVA	*P*
F. burtt-davyi		
Elisabethiella baijnathi	$F_{[7,457]} = 72.69$	***
Otitesella uluzi	$F_{[5,164]} = 2.77$	*
Otitesella sesquianellata	$F_{[7,339]} = 17.86$	***
Philotrypesis sp. C	$F_{[7,381]} = 21.87$	***
Sycoryctes sp. D	$F_{[7,354]} = 26.45$	***
F. ingens		
Platyscapa soraria	$F_{[8,81]} = 16.50$	***
Otitesella sp. I	$F_{[8,109]} = 3.81$	***
Philotrypesis sp. H	$F_{[4,57]} = 4.62$	**
F. sur		
Ceratosolen capensis	$F_{[8,98]} = 22.74$	***
Apocrypta guineensis	$F_{[8,97]} = 8.02$	***

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Table 6.4 Total numbers of male and female wasps in each collection from *F. burtt-davyi*. Chi-square were used to test whether the sex ratios differed from equality. Some species were absent from certain crops.

FIG WASP	COLLECTION NUMBER	N FIGS	TOTAL NUMBER ♂	TOTAL NUMBER ♀	CHI-SQUARE	P	
						♀ BIASED	♂ BIASED
Elisabethiella baijnathi							
	1	96	421	2909	8579.52	***	
	2	95	269	1105	280.26	***	
	3	52	54	189	40.70	***	
	4	45	32	144	39.65	***	
	5	25	11	76	28.33	***	
	6	47	127	708	230.07	***	
	7	39	235	2217	957.44	***	
	8	66	590	2735	772.31	***	
TOTAL			1739	10083	3363.50	***	
HETEROGENEITY$_{[7]}$					7564.80	***	
Otitesella uluzi							
	1	13	20	37	2.61	NS	
	2	69	195	226	1.14	NS	
	3	21	24	30	0.33	NS	
	6	9	4	28	10.47	***	
	7	15	20	21	0.01	NS	
	8	43	67	153	17.47	***	
TOTAL			330	495	16.68	***	
HETEROGENEITY$_{[5]}$					15.34	**	

Table 6.4 *continued*

FIG WASP	COLLECTION NUMBER	N FIGS	TOTAL NUMBER ♂	TOTAL NUMBER ♀	CHI-SQUARE	P	
						♀ BIASED	♂ BIASED
Otitesella sesquianellata							
	1	45	129	155	1.19	NS	
	2	71	150	197	4.25	*	
	3	59	128	138	0.18	NS	
	4	48	66	133	15.23	***	
	5	19	16	24	0.80	NS	
	6	50	294	336	1.40	NS	
	7	24	81	87	0.10	NS	
	8	31	76	124	5.84	*	
TOTAL			940	1194	15.17	***	
HETEROGENEITY$_{[7]}$					13.83	*	
Philotrypesis sp. C							
	1	66	144	248	14.04	***	
	2	85	294	411	9.78	**	
	3	67	451	573	7.29	**	
	4	25	11	35	6.71	**	
	5	16	6	5	4.94	*	
	6	44	124	21	12.46	***	
	7	33	93	215	6.37	*	
	8	53	146	148	1.78	NS	
TOTAL			1269	1831	51.36	***	
HETEROGENEITY$_{[7]}$					5.10	NS	

Table 6.4 *continued*

FIG WASP	COLLECTION NUMBER	N FIGS	TOTAL NUMBER ♂	TOTAL NUMBER ♀	CHI-SQUARE	*P*	
						♀ BIASED	♂ BIASED
Sycoryctes sp. D							
	1	94	1053	1324	15.50	***	
	2	74	279	521	37.45	***	
	3	54	154	169	0.34	NS	
	4	23	11	42	9.99	**	
	5	13	7	18	2.59	NS	
	6	50	372	652	39.01	***	
	7	36	200	390	31.40	***	
	8	18	21	68	13.40	***	
TOTAL			2097	3184	113.08	***	
HETEROGENEITY$_{[7]}$					36.61	***	

NS = not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Table 6.5 Total numbers of male and female wasps in each collection from *F. ingens*. Chi-square were used to test whether the sex ratios differed from equality. One species was absent from certain crops.

WASP	COLLECTION NUMBER	N FIGS	TOTAL NUMBER ♂	TOTAL NUMBER ♀	CHI-SQUARE	*P*	
						♀ BIASED	♂ BIASED
Platyscapa soraria							
	1	13	47	396	162.84	***	
	2	17	26	190	72.74	***	
	3	3	3	59	31.77	***	
	4	27	122	1105	345.24	***	
	5	6	34	375	172.17	***	
	6	5	2	57	32.87	*	
	7	4	4	36	15.24	***	
	8	4	13	101	39.91	***	
	9	11	130	1028	409.80	***	
TOTAL			381	3347	1401.69	***	
HETEROGENEITY$_{[8]}$					119.11	***	
Otitesella sp. I							
	1	16	194	268	5.96	*	
	2	24	482	431	1.43	NS	
	3	21	232	179	3.44	NS	
	4	25	408	224	27.36		***
	5	6	81	51	3.45	NS	
	6	5	68	20	14.14		***
	7	4	51	62	0.53	NS	
	8	5	54	24	5.99		*
	9	10	140	241	13.39	***	

Table 6.5 *continued*

WASP	COLLECTION NUMBER	N FIGS	TOTAL NUMBER ♂	TOTAL NUMBER ♀	CHI-SQUARE	*P*	
						♀ BIASED	♂ BIASED
TOTAL			1710	1500	6.87		**
HETEROGENEITY$_{[8]}$					141.81		***
Philotrypesis sp. H							
	1	12	53	80	2.78	NS	
	2	20	183	113	8.39		**
	3	21	399	149	60.15		***
	6	5	62	56	0.15	NS	
	7	4	10	10	-	-	
TOTAL			707	408	40.84		***
HETEROGENEITY$_{[4]}$					30.63		***

NS = not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Table 6.6 Total numbers of male and female wasps in each collection from *F. sur*. Chi-square were used to test whether the sex ratios differed from equality.

WASP	COLLECTION NUMBER	N FIGS	TOTAL NUMBER OF MALES	TOTAL NUMBER OF FEMALES	CHI-SQUARE	*P*	
						♀ BIASED	♂ BIASED
Ceratosolen capensis							
	1	9	17	35	3.21	NS	
	2	10	865	2805	551.26	***	
	3	10	2637	5667	571.83	***	
	4	24	1084	4083	950.45	***	
	5	8	418	236	25.82		***
	6	9	83	241	40.96	***	
	7	56	94	205	21.37	***	
	8	25	1542	2696	160.08	***	
	9	6	163	519	99.70	***	
TOTAL			6903	16487	2049.54	***	
HETEROGENEITY$_{[8]}$					275.44	***	
Apocrypta guineensis							
	1	9	124	230	16.23	***	
	2	10	580	745	10.32	***	
	3	10	183	217	1.44	NS	
	4	22	1211	1303	1.69	NS	
	5	8	753	734	0.12	NS	
	6	7	140	218	8.59	**	
	7	6	259	202	3.54	NS	
	8	25	1171	963	10.16		***
	9	6	886	496	56.15		***
TOTAL			5307	5108	1.90	NS	
HETEROGENEITY$_{[8]}$					106.34	***	

NS = not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

sometimes with reversals in the frequencies of the sexes.The population sex ratios varied significantly between crops in most, but not all of the wasp species (Tables 6.4 - 6.7). The sex ratios were significantly negatively correlated with differences in the population densities between individual figs in all the species except *C. capensis* and *A. guineensis* (Table 6.8). Thus there was a general tendency for relatively fewer males to be present in figs containing numerous individuals.

6.3.2 Sex ratios, ovipositional method and fighting behaviour in males

Sex ratios of the ten wasp species were significantly different (ANOVA, $F_{[9,\ 2213]} = 65.52$, $P < 0.001$). The two pollinating species *E. baijnathi* and *C. capensis* had similar sex ratios, as did *Sycoryctes* sp. D and *Otitesella* sp. I, while those for the remaining species were all different from each other and from those of other wasps (Scheffe's range test, all $P < 0.01$). Overall sex ratios for the three species of 'internally' ovipositing fig wasps ranged from 0.12 to 0.26 compared to a range from 0.39 to 0.58 among the 'externally' ovipositing species (Table 6.9).

Comparisons of the average sex ratios of species with pacifist or fighting males (Table 6.10) highlights the low sex ratios of the three pollinators (all with pacifist males). However, *A. guineensis* which also has pacifist males, but had a sex ratio approximating unity, which is typical of the species with fighting males. *A. guineensis* was also exceptional in being the only 'externally' ovipositing species with males that do not fight.

Table 6.7 ANOVA of sex ratios between crops.

FICUS AND WASP	ANOVA	*P*
F. burtt-davyi		
Elisabethiella baijnathi	$F_{[7, 457]} = 27.18$	***
Otitesella uluzi	$F_{[7, 167]} = 1.57$	NS
Otitesella sesquianellata	$F_{[7, 339]} = 2.20$	*
Philotrypesis sp. C	$F_{[7, 381]} = 4.50$	***
Sycoryctes sp. D	$F_{[7, 354]} = 7.65$	***
F. ingens		
Platyscapa soraria	$F_{[8, 81]} = 1.34$	NS
Otitesella sp. I	$F_{[8, 107]} = 8.11$	***
Philotrypesis sp. H	$F_{[4, 59]} = 8.59$	***
F. sur		
Ceratosolen capensis	$F_{[8, 98]} = 4.45$	***
Apocrypta guineensis	$F_{[8, 97]} = 8.97$	NS

NS = not significant, * $P < 0.05$, *** $P < 0.001$

Table 6.8 Correlations of sex ratios with population densities within individual figs.

FIG TREE FIG WASP SPECIES	N FIGS	*r*	*P*
F. burtt-davyi			
Elisabethiella baijnathi	465	-0.43	***
Otitesella uluzi	175	-0.57	***
Otitesella sesquianellata	347	-0.44	***
Philotrypesis sp. C	389	-0.54	***
Sycoryctes sp. D	362	-0.45	***
F. ingens			
Platyscapa soraria	90	-0.34	**
Otitesella sp. I	116	-0.31	**
Philotrypesis sp. H	68	-0.30	*
F. sur			
Ceratosolen capensis	106	-0.09	NS
Apocrypta guineensis	107	-0.09	NS

NS = not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Table 6.9 Comparisons of the sex ratios of 'internal' and 'external' ovipositing fig wasps.

INTERNAL OVIPOSITORS		EXTERNAL OVIPOSITORS	
WASP	MEAN SEX RATIO	WASP	MEAN SEX RATIO
Elisabethiella baijnathi	0.18[1]	*Otitesella uluzi*	0.46[1]
Platyscapa soraria	0.12[1]	*Otitesella sesquianellata*	0.43[1]
Ceratosolen capensis	0.26[1]	*Philotrypesis* sp. C	0.42[1]
		Sycoryctes sp. D	0.39[1]
		Otitesella sp. I	0.55[2]
		Philotrypesis sp. H	0.58[2]
		Apocrypta guineensis	0.48
RANGE	0.12-0.26	RANGE	0.39-0.58

[1] overall crop sex ratios significantly female biased (Tables 6.4, 6.5 & 6.6)
[2] overall crop sex ratios significantly male biased (Tables 6.4, 6.5 & 6.6)

Table 6.10 Sex ratios of fig wasps with pacifist and fighting males.

PACIFISTS		FIGHTERS	
WASP	MEAN SEX RATIO	WASP	MEAN SEX RATIO
Elisabethiella baijnathi	0.18[1]	*Otitesella uluzi*	0.46[1]
Platyscapa soraria	0.12[1]	*Otitesella sesquianellata*	0.43[1]
Ceratosolen capensis	0.26[1]	*Philotrypesis* sp. C	0.42[1]
Apocrypta guineensis	0.48	*Sycoryctes* sp. D	0.39[1]
		Otitesella sp. I	0.55[2]
		Philotrypesis sp. H	0.58[2]
RANGE	0.12-0.48	RANGE	0.39-0.58

[1] overall crop sex ratios significantly female biased (Tables 6.4, 6.5 & 6.6)
[2] overall crop sex ratios significantly male biased (Tables 6.4, 6.5 & 6.6)

6.3.3 Sex ratios and polymorphism

Philotrypesis sp. C was the only fig wasp with both flightless and winged males. The average sex ratio of this species in individual figs containing winged males and flightless males was 0.489 (n = 82 figs), which was the same as that in populations where only flightless males were present (sex ratio = 0.490, n = 252 figs, ANOVA $F_{[1, 332]} = 0.00$, $P = 0.95$). The average sex ratio in figs with only winged males was 0.530 (n = 16) and was also the same as that in figs where only flightless males were present (ANOVA $F_{[1, 266]} = 0.42$, $P = 0.52$).

6.4 DISCUSSION

How fig wasps are able to adjust their sex ratios in relation to density is not well understood. Sex ratio adjustment could take place in response to the presence of other ovipositing females via physical interference between ovipositing adults, as for example in *Muscidifurax zaraptor* (Pteromalidae) (Wylie, 1979) or recognition of contact traces of other wasps as in the host-egg marking of *Telenomus remus* (Scelionidae) (van Welzen & Waage, 1987). Mechanisms which may result in changes in sex ratios include sex-limited infections (Werren *et al*, 1986), superparasitism combined with differential mortality of the sexes or indirect food competition for food resources (Flanders, 1969; Suzuki *et al*, 1984; Wellings *et al*, 1986). Different sized clutches in combination with fixed ovipositional sequences of male and female eggs can also account for differences in observed sex ratios, as in *Trichogramma evanescens* (Trichogrammatidae) Waage & Lane (1984). Many scelionids lay males first (Waage, 1982), but *Gryon japonicum*

(Scelionidae) lays a male in the second host egg of every patch it encounters (Waage, 1982). Other variations include that seen in *Trichogramma chilonis* (Trichogrammatidae), which lays one male in every eight eggs (Suzuki, *et al*, 1984) and *Dinarmus vagabundus* (Pteromalidae) where the female eggs are laid first and male eggs last (Rojas-Rousse *et al*, 1988).

Sex ratio adjustment in relation to the number of foundresses present has been confirmed experimentally in two of the species studied here - *E. baijnathi* and *C. capensis* (Nefdt, 1989). A possible mechanism for sex ratio adjustment in these species was proposed - that they lay male eggs first, and that when increasing numbers of foundresses are present the number of eggs that each lays declines, causing the sex ratio to increase. In this study, evidence for sex ratio adjustment in the form of density related changes in sex ratios was detected in several species including those which oviposit from the outside of the fig, but not in *C. capensis*.

The failure to detect adjustment in *C. capensis* and *A. guineensis* was not the result of a lack of variation in population densities, which differed significantly between crops. However, Nefdt (1989) counted foundress numbers and their progeny, excluding parasitoids/inquilines while I only counted the numbers of progeny. Consequently his results were obtained under more controlled conditions. Possible explanations for not detecting sex ratio adjustment in *C. capensis* include misleading estimates of wasp density due to high levels of parasitism by *A. guineensis* or that the sex ratios were modified by the presence of *Sycophaga cyclostigma* (which was present in all the collections). This is also an 'internally' ovipositing species and if Nefdt's hypothesis is correct, then figs shared with *Sycophaga* would be expected to produce less female biased sex-ratios for a given number of *C. capensis* foundresses. Unfortunately, the inability to identify the males of *Sycophaga* prevents confirmation of this using the current data.

In *Philotrypesis* sp. C, which has both flightless and winged males, there was no difference in sex ratios between populations in figs containing females and both kinds of male, and those with only flightless males. This is perhaps surprising, given the complex interactions between density, morph ratios and sex ratios in this species (chapter 8).

Sex ratio reflects breeding structure (Hamilton, 1967) and the results support Hamilton's (1979) prediction that, because they are likely to be inbred, 'internally' ovipositing fig wasp species should have strongly female biased sex ratios, while the sex ratios of 'externally' ovipositing species should be closer to parity. Hamilton (1979) also suggested that 'internal' ovipositors were less likely to have fighting males than 'external' ovipositors because within each fig their males are on average less related. The three agaonid species examined agree with these predictions, but not *A. guineensis*, which is an 'external' ovipositor, with males that did not fight, and with an overall sex ratio that was close to 1:1. Thus, *A. guineensis* does not conform to Hamilton's predictions concerning its male behaviour, but does in terms of its sex ratio, which is that expected of an out-breeding species. However, as I have shown (chapter 2) mating site is an important determinant of fighting behaviour and the gall mating behaviour of this species may well explain why its males do not fight even though they are relatively outbred. Nonetheless, data for 'internally' ovipositing species other than agaonines are required before any firm conclusions can be made on the links between the method of oviposition, sex ratio and male morphology and behaviour.

7 VIRGINITY AND SPERM DEPLETION IN FIG WASPS

7.1 INTRODUCTION

Fig wasps, like most hymenopterans, are believed to be arrhenotokous and haplodiploid (Crozier, 1977). That is, mated female fig wasps may lay either unfertilized eggs that will develop into males or fertilised eggs that develop into females. Unmated females can only produce male offspring.

Local mate competition (LMC) theory predicts that in highly inbred populations, with high levels of sib-mating, as exemplified by some fig wasps, a female should produce fewer sons than daughters (Hamilton, 1967). Strongly female-biased sex ratios are thus expected in many fig wasps (see chapter 6). In situations where only one foundress female is present the sex ratio of her progeny will be determined by the number of female progeny each son can mate with; a female should lay just enough sons to allow for the fertilization of all her daughters. The limits of the optimal sex ratio should therefore be determined by the rates of sperm depletion among her sons. Several studies have shown that sex ratio adjustment in relation to foundress density does occur in agaonid fig wasps (Frank, 1985b, Herre, 1985, 1987, Nefdt, 1989). However, females that are unmated (constrained females *sensu* Hardy and Godfray, 1990) can only produce male progeny. It has been speculated that the presence of such constrained females in populations should select for mated females to produce even more female biased sex ratios than selected for by LMC (Godfray, 1988; Hardy & Godfray, 1990). While sex ratio manipulation has been studied in numerous fig wasps, little is known about levels of unmatedness in their populations, that is the percentage of virgin females that are present (Godfray, 1988; Hardy & Godfray, 1990).

Hardy and Godfray (1990) provide a summary of methods that can be used to determine matedness in hymenopteran parasitoids. Indirect methods of determining whether or not females in wild populations are mated require considerable time and effort. These include catching wild females, allowing oviposition in the laboratory and raising the offspring. Any resultant broods consisting entirely of males are indicative of unmatedness. Alternatively, the numbers of all male or all female broods in nature provide an estimate of the numbers of mothers that were not mated and the numbers of offspring that will probably not be mated if mating only occurs at and around emergence sites, because once they have left their emergence sites it is unlikely that they will be mated with elsewhere. Direct methods to determine matedness include dissection of the wasps to confirm the presence of sperm in the spermathecae. However, most parasitoids are very small, which makes this method difficult. Furthermore, in cases where females and males disperse away from their emergence sites before mating, females must be obtained while ovipositing and not at the time of emergence. Where mating takes place at the time of emergence, as in some fig wasps, this is not crucial.

Fig wasps have three primary mating sites, in the female's gall, the lumen of the fig and outside the fig, either on its surface or elsewhere. The males of both gall and lumen-mating species are typically wingless (chapter three). This means that once the females of these species have emerged unmated from their galls or from the figs, they will remain so, unless the species is polymorphic with a second male form that mates outside the figs (Hamilton, 1979, see also chapters eight & 12). If there is a small number of individuals in a fig then there may be a greater chance of the females escaping from a fig unmated than if there is a high number of individuals in a fig (Hamilton, 1979).

Here I describe the levels of matedness in the females of some fig wasp species associated with *F. burtt-davyi*. Matedness was estimated both prior to wasp emergence from the figs and after emergence. I also determined whether males in fig lumens still had sperm in their seminal vesicles or whether multiple matings had resulted in sperm depletion. These data address the related questions of how many virgin fig wasps are produced, and whether this is due to females being 'missed' by males or is a consequence of male sperm 'exhaustion'.

7.2 MATERIALS AND METHODS

Mature figs, without exit holes, were collected from four *F. burtt-davyi* trees in the Grahamstown area. All the female and male fig wasps that had already emerged into the fig lumen were examined for sperm-filled spermathecae or sperm-depleted seminal vesicles respectively. All wasps, both emerged and those still in their galls, were counted, but non-emerged females were not examined for matedness because they may not have had access to males. Female fig wasps were also caught on 'sticky' traps. The traps were 21cm X 30cm sheets of clear plastic sprayed with pruning sealant. These were placed in the trees when wasps were emerging from figs. The numbers of all female broods inside individual figs provided a third, indirect, measure of matedness levels prior to the wasps' emergence.

7.2.1 Determination of matedness and sperm depletion

Freshly collected, live female fig wasps were placed in a drop of water and squashed between two glass microscope slides. Using a compound microscope the spermathecae were then examined to see if they contained any sperm. Darkly coloured fig wasps, for example the *Otitesella* species, needed to be positioned carefully so that when the wasps were squashed, the spermathecae were displaced away from the gaster. Determination of whether male fig wasps still contained sperm in their seminal vesicles was achieved in the same way. If sperm were present within the spermathecae or seminal vesicles they were moving and easy to see.

7.3 RESULTS

A total of 439 figs were collected from the four *F. burtt-davyi* trees. The numbers of fig wasps they contained are given in Table 7.1. Five species of fig wasps were present in each collection. Overall sex ratios were significantly female biased in all the species except *Otitesella uluzi* (Table 7.2). However, within a species, the sex ratio often differed markedly between individual crops, in many cases not differing significantly from a 1:1 ratio (chapter six).

The total numbers of males in a fig was significantly positively correlated with the number of conspecific females in all the wasp species (Table 7.3). Consistently, the number of females in a fig was significantly negatively correlated with the sex ratio, so the proportion of males present decreased with the number of females (Table 7.4).

The numbers of males and females that had emerged into the fig cavities are given in Table 7.5. Comparisons of the numbers of females and males within the fig cavity, contrary to the comparisons between total numbers of wasps in a fig, show that either equivalent numbers of males and females were present or that the populations were male biased (Table 7.6). This is not surprising since female wasps often tend to emerge at a later stage than their males, just before the exit hole is chewed. Considerable heterogeneity in the sex ratios between crops was again evident.

7.3.1 Matedness

The percentage of males and females that occurred in figs lacking the opposite sex was generally low, with the exception of one small

Table 7.1 The numbers of male and female fig wasps collected from *Ficus burtt-davyi*.

FIG WASP	COLLECTION	NUMBER OF FIGS WITH WASPS	MALES		FEMALES		SEX RATIO
			MEAN ± SD	RANGE	MEAN ± SD	RANGE	
Elisabethiella baijnathi	1	94	3.19 ± 3.67	0-21	10.91 ± 8.02	0-40	0.20
	2	97	4.70 ± 3.20	0-19	29.86 ± 15.12	0-76	0.14
	3	19	8.20 ± 9.72	1-34	38.40 ± 16.91	0-67	0.15
	4	20	6.40 ± 5.25	1-21	38.15 ± 26.99	6-125	0.15
Otitesella uluzi	1	70	2.68 ± 2.39	0-17	2.97 ± 2.90	0-14	0.50
	2	14	1.64 ± 2.23	0-8	2.71 ± 5.18	0-20	0.50
	3	12	1.58 ± 1.16	0-4	3.00 ± 3.40	0-8	0.41
	4	12	1.50 ± 0.90	1-4	1.66 ± 2.05	0-7	0.60
Otitesella sesquianellata	1	71	2.14 ± 1.58	0-7	2.77 ± 2.07	0-8	0.46
	2	43	2.95 ± 3.40	0-14	3.55 ± 3.67	0-16	0.42
	3	14	2.64 ± 2.34	0-8	5.85 ± 5.92	0-17	0.40
	4	8	2.25 ± 1.48	1-5	3.12 ± 1.88	0-6	0.43
Philotrypesis sp. C	1	85	3.43 ± 2.75	0-12	4.71 ± 3.87	0-19	0.46
	2	66	1.95 ± 1.56	0-6	3.63 ± 3.85	0-24	0.42
	3	16	3.76 ± 2.65	1-11	4.23 ± 3.03	0-11	0.32
	4	16	3.00 ± 3.69	0-15	5.00 ± 4.63	1-19	0.32
Sycoryctes sp. D	1	77	3.63 ± 3.71	0-22	7.06 ± 7.01	0-31	0.36
	2	93	11.22 ± 6.64	0-41	13.90 ± 8.35	0-44	0.44
	3	4	1.50 ± 1.00	1-3	1.75 ± 1.25	0-3	0.54
	4	18	5.63 ± 5.25	0-19	8.68 ± 7.82	1-25	0.43

Table 7.2 Comparisons of the total numbers of males and females with tests for deviations from a 50:50 sex ratio.

WASP	COLLECTION	TOTAL NUMBER OF MALES	TOTAL NUMBER OF FEMALES	CHI-SQUARE[1]	*P*
Elisabethiella baijnathi	1	303	1026	216.95	***
	2	437	2896	981.97	***
	3	156	730	207.73	***
	4	128	763	259.29	***
TOTAL		1024	5415	2396.84	***
HETEROGENEITY[3]				730.90	***
Otitesella uluzi	1	188	208	0.505	NS
	2	23	38	1.88	NS
	3	19	36	2.71	NS
	4	18	20	0.05	NS
TOTAL		248	302	2.65	NS
HETEROGENEITY[3]				2.49	NS
Otitesella sesquianellata	1	152	197	2.91	NS
	2	127	153	1.20	NS
	3	37	82	8.85	***
	4	18	25	0.58	NS
TOTAL		334	457	9.64	***
HETEROGENEITY[3]				3.90	NS
Philotrypesis sp. C	1	292	400	8.47	***
	2	129	240	17.10	***
	3	60	68	0.25	NS
	4	48	80	4.06	*

Table 7.2 *continued*

WASP	COLLECTION	TOTAL NUMBER OF MALES	TOTAL NUMBER OF FEMALES	CHI-SQUARE[1]	*P*
Elisabethiella baijnathi	1	303	1026	216.95	***
TOTAL		529	788	25.70	***
HETEROGENEITY[3]				4.18	NS
Sycoryctes sp. D	1	280	544	43.40	***
	2	1043	1293	13.41	***
	3	6	7	0.039	NS
	4	101	156	5.96	*
TOTAL		1430	2000	43.38	***
HETEROGENEITY[3]				19.42	***

NS = not significant, * $P < 0.05$, *** $P < 0.001$

Table 7.3 Correlations between the number of males and the number of females in each fig (four crops combined).

WASP	TOTAL NUMBER OF FIGS	*r*	*P*
Elisabethiella baijnathi	232	0.54	***
Otitesella uluzi	106	0.50	***
Otitesella sesquianellata	140	0.40	***
Philotrypesis sp. C	186	0.42	***
Sycoryctes sp. D	193	0.52	***

*** $P < 0.001$

Table 7.4 Correlations between the sex ratio and the number of females in each fig (four crops combined).

WASP	TOTAL NUMBER OF FIGS	*r*	*P*
Elisabethiella baijnathi	232	-0.25	***
Otitesella uluzi	106	-0.50	***
Otitesella sesquianellata	140	-0.22	***
Philotrypesis sp. C	186	-0.24	***
Sycoryctes sp. D	193	-0.26	***

*** $P < 0.001$

Table 7.5 The numbers of fig wasps that had emerged from their galls into the fig cavities.

WASP	COLLECTION	N FIGS WITH EMERGED WASPS	TOTAL NUMBER OF EMERGED MALES		TOTAL NUMBER OF EMERGED FEMALES		SEX RATIO OF EMERGED WASPS
			MEAN ± SD	RANGE	MEAN ± SD	RANGE	
Elisabethiella baijnathi	1	72	2.75 ± 2.48	0-13	4.91 ± 6.08	0-21	0.49
	2	92	3.93 ± 2.49	0-13	1.01 ± 1.88	0-11	0.84
	3	10	4.60 ± 2.76	1-10	1.60 ± 3.78	0-12	0.89
	4	20	5.45 ± 4.32	1-17	1.50 ± 5.53	0-24	0.91
Otitesella uluzi	1	61	2.36 ± 1.80	0-12	1.43 ± 2.02	0-7	0.73
	2	9	2.22 ± 1.56	0-5	0.67 ± 1.12	0-3	0.81
	3	9	1.11 ± 0.60	0-2	1.89 ± 2.03	0-5	0.52
	4	7	1.29 ± 0.49	1-2	0	-	-
Otitesella sesquianellata	1	56	1.67 ± 1.13	0-5	1.21 ± 1.50	0-5	0.68
	2	37	2.43 ± 2.05	0-10	0.73 ± 1.33	0-5	0.85
	3	9	1.33 ± 0.87	0-3	0.78 ± 1.30	0-4	0.72
	4	5	1.20 ± 0.45	1-2	0.60 ± 1.34	0-3	0.88
Philotrypesis sp. C	1	67	2.69 ± 1.82	1-8	2.78 ± 2.98	0-16	0.63
	2	51	1.73 ± 1.02	1-5	1.09 ± 1.49	0-5	0.76
	3	13	1.62 ± 0.77	1-3	1.30 ± 1.49	0-4	0.69
	4	9	1.89 ± 2.08	0-6	0.67 ± 0.87	0-2	0.73
Sycoryctes sp. D	1	68	2.68 ± 2.17	0-12	2.26 ± 3.64	0-19	0.63
	2	86	10.10 ± 5.90	1-35	0.92 ± 1.55	0-8	0.94
	3	3	1.00	1	0.33 ± 0.58	0-1	0.83
	4	14	3.29 ± 2.43	1-10	0.36 ± 0.85	0-3	0.90

Table 7.6 Comparisons of the total numbers of males and females within the fig cavities with tests for deviations from a 50:50 sex ratio.

WASP	COLLECTION	TOTAL NUMBER IN FIG CAVITY		CHI-SQUARE$_{[1]}$	*P*
		MALES	FEMALES		
Elisabethiella baijnathi	1	198	354	22.49	***
	2	362	93	82.21	***
	3	46	16	7.70	***
	4	109	30	11.14	***
TOTAL		715	493	20.57	***
HETEROGENEITY$_{[3]}$				102.97	***
Otitesella uluzi	1	144	87	7.16	***
	2	20	6	4.06	*
	3	10	17	0.94	NS
	4	9	0	6.10	*
TOTAL		183	110	9.25	***
HETEROGENEITY$_{[3]}$				9.01	*
Otitesella sesquianellata	1	94	68	2.09	NS
	2	90	27	18.35	***
	3	12	7	0.69	NS
	4	6	3	0.53	NS
TOTAL		202	105	15.74	***
HETEROGENEITY$_{[3]}$				5.92	NS
Philotrypesis sp. C	1	180	186	0.05	NS
	2	88	56	3.60	NS
	3	21	17	0.21	NS
	4	17	6	2.84	NS
TOTAL		306	265	1.48	NS
HETEROGENEITY$_{[3]}$				5.21	NS
Sycoryctes sp. D	1	183	154	1.25	NS
	2	869	79	398.32	***
	3	3	1	0.53	NS
	4	46	5	19.77	***
TOTAL		1101	239	309.25	***
HETEROGENEITY$_{[3]}$				309.25	***

NS = not significant, * $P < 0.05$, *** $P < 0.001$

collection of *O. uluzi*, where over 34% of the wasps were in single sex figs (Table 7.7). The numbers for *Philotrypesis* males include only wingless individuals. No winged males were recorded from single sex figs in these collections.

Based on direct examinations, the numbers of mated and unmated females that had emerged into the fig cavities are given in Table 7.8. The percentage of unmated females in a collection ranged from 1.80% for *Sycoryctes* sp. D to 33.33% for *O. sesquianellata*, while the average levels of unmatedness from all the collections ranged from 4.20% for *E. baijnathi* to 26.77% for *Sycoryctes* sp. D (Table 7.8).

The proportion of mated females in the fig cavity was generally not correlated with either the number of males to have emerged (Table 7.9), with the sex ratio of wasps in the cavity (Table 7.10) or the total sex ratio for all the wasps in each fig (Table 7.11). *E. baijnathi* was exceptional, with levels of matedness increasing with the proportion of males in the population (Tables 7.10 & 7.11). Unlike the other species present, *E. baijnathi* is a gall mater and the mating activities of this species are likely to have been nearer to completion than those of the lumen mating species. *E. baijnathi* also had the most female-biased sex ratios, so males were probably never over-abundant.

When figs with only one male emerged into the fig cavity are examined, most of the females to have emerged had nonetheless been successfully mated (Table 7.12). None of the male fig wasps

Table 7.7 The numbers of figs containing single-sex populations including all wasps in figs, not just those that have eclosed.

WASP	COLLECTION	NUMBER OF FIGS WITH MALES ONLY	NUMBER OF MALES UNMATED	% OF MALES UNMATED	NUMBER OF FIGS WITH FEMALES ONLY	NUMBERS OF FEMALES UNMATED	% OF FEMALES UNMATED
Elisabethiella baijnathi							
	1	0	0	0	20	150	14.61
	2	1	2	0.004	4	49	1.69
	3	0	0	0	0	0	0
	4	0	0	0	0	0	0
	TOTAL	1	2	0.004	24	199	19.40
Otitesella uluzi							
	1	15	24	12.76	6	9	4.32
	2	5	8	34.78	5	13	34.21
	3	0	0	0	4	7	19.44
	4	0	0	0	0	0	0
	TOTAL		32	12.90	15	29	26.36
Otitesella sesquianellata							
	1	10	15	9.80	10	22	11.16
	2	4	6	4.70	9	19	12.41
	3	0	0	0	2	9	10.91
	4	0	0	0	0	0	0
	TOTAL	14	21	6.28	21	50	10.94
Philotrypesis sp. C							
	1	11	11	3.76	7	10	0.25
	2	7	7	5.40	10	18	0.75
	3	0	0	0	0	0	0
	4	0	0	0	3	4	5.00

Table 7.7 *continued*

WASP	COLLECTION	NUMBER OF FIGS WITH MALES ONLY	NUMBER OF MALES UNMATED	% OF MALES UNMATED	NUMBER OF FIGS WITH FEMALES ONLY	NUMBERS OF FEMALES UNMATED	% OF FEMALES UNMATED
	TOTAL	18	18	3.40	20	32	4.60
Sycoryctes sp. D							
	1	3	7	2.50	8	12	2.20
	2	3	9	0.008	3	30	2.30
	3	0	0	0	0	0	0
	4	0	0	0	1	1	0.60
	TOTAL	6	16	1.11	12	43	2.15

Table 7.8 Numbers of unmated and mated females in the cavities.

WASP	COLLECTION	N WASPS	MATED FEMALES PER FIG		N WASPS	UNMATED FEMALES PER FIG		% FEMALES UNMATED
			MEAN ± SD	RANGE		MEAN ± SD	RANGE	
Elisabethiella baijnathi	1	283	3.93 ± 5.94	0-44	12	0.16 ± 0.47	0-2	3.38
	2	79	0.86 ± 1.52	0-55	5	0.05 ± 0.34	0-3	5.38
	3	7	0.74 ± 2.35	0-10	1	0.11 ± 0.46	0-2	6.25
	4	27	1.35 ± 4.69	0-21	3	0.15 ± 0.67	0-3	10.00
	TOTAL	396	2.04	0-55	21	0.12	0-3	4.20
Otitesella uluzi	1	60	0.98 ± 1.63	0-7	9	0.14 ± 0.43	0-2	10.34
	2	4	0.43 ± 0.94	0-3	0	0		0
	3	12	1.33 ± 1.97	0-5	0	0		0
	4	0	0	0	0	0		0
	TOTAL	76	0.88	0-7	9	0.10	0-2	8.18
Otitesella sesquianellata	1	46	0.83 ± 1.33	0-5	3	0.05 ± 0.28	0-2	4.41
	2	21	0.58 ± 1.19	0-5	1	0.04 ± 0.21	0-1	3.70
	3	3	0.35 ± 1.08	0-4	0	0		0
	4	1	0.16 ± 0.35	0-2	1	0.25 ± 0.70	0-2	33.33
	TOTAL	71	0.66	0-5	5	0.05	0-2	4.76
Philotrypesis sp. C	1	124	1.85 ± 2.69	0-16	11	0.17 ± 0.49	0-3	5.11
	2	42	0.82 ± 1.38	0-5	0	0		0
	3	20	1.5 ± 2.47	0-9	1	0.06 ± 0.25	0-1	5.88
	4	3	0.31 ± 0.70	0-2	0	0		0

Table 7.8 *continued*

WASP	COLLECTION	N WASPS	MATED FEMALES PER FIG		N WASPS	UNMATED FEMALES PER FIG		% FEMALES UNMATED
			MEAN ± SD	RANGE		MEAN ± SD	RANGE	
	TOTAL	189	1.35	0-16	12	0.09	0-3	4.54
Sycoryctes sp. D	1	110	1.62 ± 2.82	0-15	44	0.65 ± 1.36	0-6	28.57
	2	60	0.70 ± 1.16	0-9	11	0.13 ± 0.57	0-4	13.92
	3	1	0.25 ± 0.50	0-1	0	0		0
	4	2	0.17 ± 0.38	0-10	9	0.67 ± 2.37	0-10	1.80
	TOTAL	173	1.01	0-15	64	0.37	0-10	26.77

Table 7.9 Correlations of the proportion of emerged females that had mated and the number of emerged males in the figs.

WASP	NUMBER OF FIGS WITH EMERGED MALES AND FEMALES	*r*	*P*
Elisabethiella baijnathi	95	-0.02	NS
Otitesella uluzi	40	-0.24	NS
Otitesella sesquianellata	44	-0.05	NS
Philotrypesis sp. C	82	-0.11	NS
Sycoryctes sp. D	85	0.02	NS

NS = not significant

Table 7.10 Correlations of the proportion of emerged females that had mated and the sex ratio, of the wasps inside fig cavities.

WASP	NUMBER OF FIGS WITH EMERGED MALES AND FEMALES	*r*	*P*
Elisabethiella baijnathi	95	0.20	*
Otitesella uluzi	40	-0.25	NS
Otitesella sesquianellata	44	0.03	NS
Philotrypesis sp. C	82	0.02	NS
Sycoryctes sp. D	85	0.11	NS

NS = not significant, * $P < 0.05$

Table 7.11 Correlations of the proportion of females that had mated and the sex ratio of all wasps in a fig.

WASP	NUMBER OF FIGS	*r*	*P*
Elisabethiella baijnathi	225	0.49	***
Otitesella uluzi	78	-0.14	NS
Otitesella sesquianellata	123	0.14	NS
Philotrypesis sp. C	165	-0.01	NS
Sycoryctes sp. D	178	0.04	NS

NS = not significant, *** $P < 0.001$

Table 7.12 The numbers of mated and unmated females that had emerged in figs with only one emerged male.

WASP	NUMBER OF FIGS WITH ONLY ONE EMERGED MALE	NUMBER OF FEMALES MATED		NUMBER OF FEMALES NOT MATED		% MATED
		MEAN ± SD	RANGE	MEAN ± SD	RANGE	
Elisabethiella baijnathi	36	2.45 ± 4.59	0-21	0.17 ± 0.50	0-2	94
Otitesella uluzi	32	0.55 ± 1.20	0-5	0.03 ± 0.18	0-1	95
Otitesella sesquianellata	51	0.43 ± 0.85	0-4	0.02 ± 0.14	0-1	96
Philotrypesis sp. C	63	0.73 ± 1.38	0-7	0.02 ± 0.13	0-1	98
Sycoryctes sp. D	25	0.72 ± 1.27	0-6	0.04 ± 1.10	0-5	95

examined had empty seminal vesicles. This demonstrated that *E. baijnathi* males can mate with at least 21 females without sperm exhaustion. Equivalent minimum values for mating competency for *O. uluzi*, *O. sesquianellata*, *Philotrypesis* sp. C and *Sycoryctes* sp. D are 5, 4, 7 and 6 females respectively.

Estimates of matedness among wasps that had emerged from figs and were caught on sticky traps ranged from 75% to 93% (Table 7.13). One exceptional collection of *O. sesquianellata* had only one in four females mated, but the sample size was very low. The overall values were comparable to the estimates based on matedness inside the figs and the percentage of females occurring in male-free figs (Table 7.14).

7.4 DISCUSSION

The one indirect and two direct methods that were employed in this study gave only slightly different estimates of matedness (Table 7.14). The highest matedness estimates were generally based on the numbers of females in male-free figs, which is to be expected, given that some females sharing figs with males are nonetheless likely to be unmated. Some of the unmated females in the fig cavities would have had a chance to mate after the time that the samples were collected. This matedness estimate was therefore expected to be lower than those obtained from the sticky traps. This was not always the case, however, which raises the possibility that unmated females may not disperse from their natal figs as rapidly as mated females, thus lowering the average matedness levels among the wasps in the trees.

Table 7.13 The proportions of unmated females among the fig wasps caught on sticky traps. Although recorded inside the figs no *Otitesella uluzi* were collected on the traps.

WASP	COLLECTION	NUMBER OF FIG WASPS EXAMINED	% MATED
Elisabethiella baijnathi	1	20	100.00
	2	20	95.00
	3	23	82.00
	4	5	80.00
	total	68	89.25
Otitesella sesquianellata	1	1	100.00
	2	6	100.00
	3	4	25.00
	4	0	-
	total	11	75.00
Philotrypesis sp. C	1	11	100.00
	2	12	91.60
	3	16	81.00
	4	22	100.00
	total	61	93.15
Sycoryctes sp. D	1	20	95.00
	2	15	60.00
	3	7	85.00
	4	9	100.00
	total	51	85.00

Table 7.14 Comparisons of the three female matedness estimates (as the percentage of females mated).

WASP	FEMALES NOT IN MALE-FREE FIGS	DISSECTION	STICKY TRAPS
Elisabethiella baijnathi	96	96	89
Otitesella uluzi	86	92	-
Otitesella sesquianellata	91	95	75
Philotrypesis sp. C	98	95	93
Sycoryctes sp. D	99	73	85

The presence of any unmated females in a hymenopteran population should lead to selection on mated females to bias their optimal sex ratio towards daughters (Godfray & Grafen, 1988). Godfray (1988) examined virginity in several species of fig wasps and had results similar to those presented here, in that he found that the proportions of unmated females were generally low. Hardy and Godfray (1990) subsequently reviewed the literature on levels of unmatedness and found this to be true for haplodiploid hymenopterans in general.

Hamilton (1979) studied several Neotropical species of fig wasp and found that rarer fig wasps had winged males whereas common species had wingless males. He further suggested that species with dimorphic males should be less common than species with wingless males, but more common than those with winged males. He therefore linked wingedness with the likelihood of being mated, because in rare species there would be selection on males to retain the ability to search for mates outside of their natal figs. Although the number of wasps within occupied figs is significantly correlated with the proportion of figs occupied for some fig wasps, for example *Philotrypesis* sp. C (see Figure 7.1) and (Table 7.15), matedness levels in the species studied here did not vary between the most common and least common species. This may be because of the aggregated nature of oviposition, so that even uncommon species are sufficiently aggregated in the figs where they

Table 7.15 The relationship between the average number of wasps per occupied fig and the proportion of figs in a crop that were occupied. Pollinators effectively occupied all the figs and are therefore not included.

WASP	N CROPS	*r*	*P*
Otitesella uluzi	5	0.64	NS
Otitesella sesquianellata	8	0.15	NS
Philotrypesis sp. C	8	0.90	**
Sycoryctes sp. D	8	0.84	**
Otitesella sp. I	8	-0.70	*
Philotrypesis sp. H	4	0.26	NS
Apocrypta guineensis	9	0.37	NS

NS = not significant, * $P < 0.05$, ** $P < 0.01$

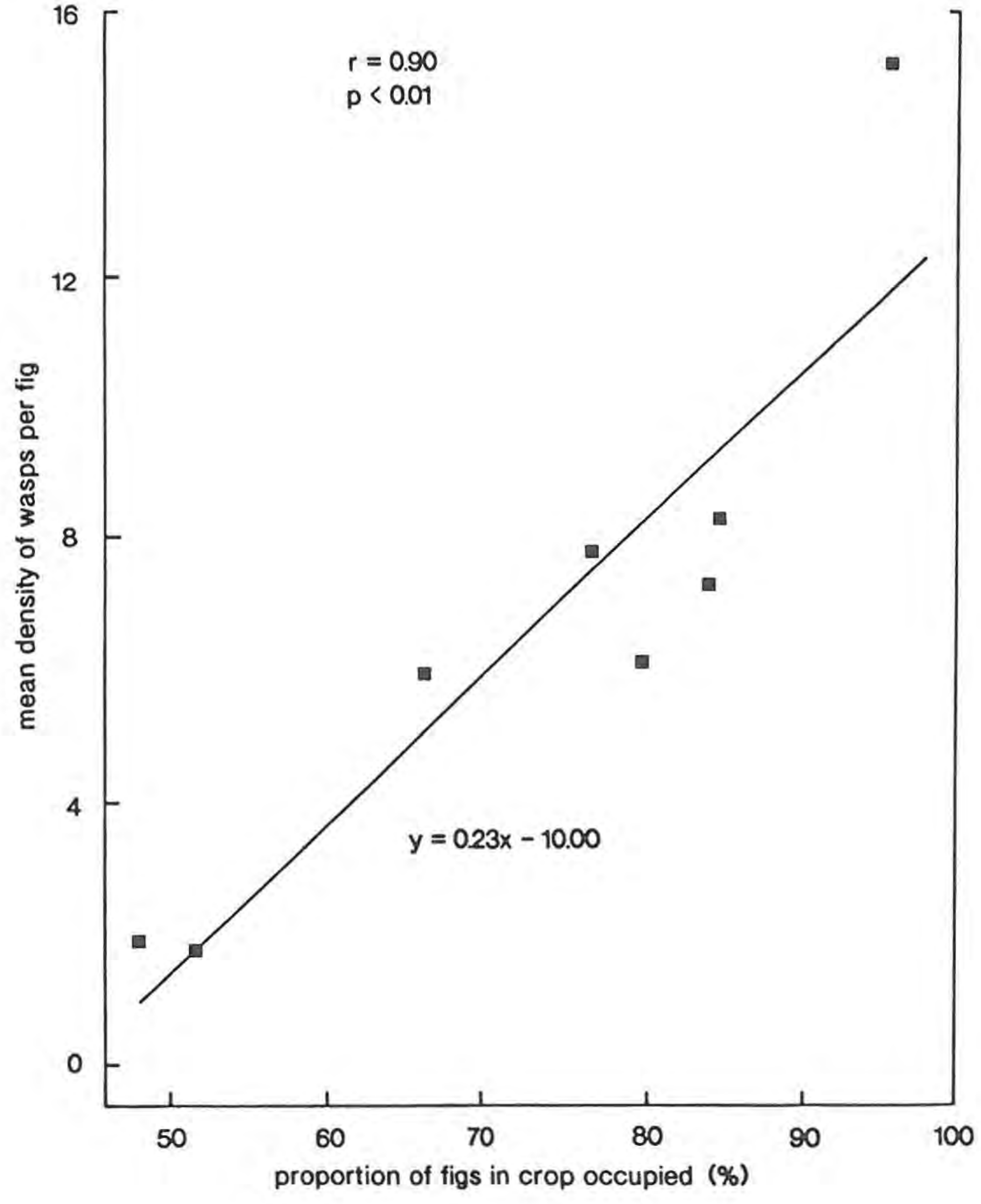


Figure 7.1 The relationship between the average number of *Philotrypesis* sp. C wasps in a fig and the proportion of figs in a crop occupied by that species.

occur so that mating is ensured (see chapter 8, Table 8.1). Wasp densities per fig are nonetheless sometimes higher in crops where a large proportion of figs are occupied (Table 7.15 and, for example Figure 7.1). Godfray (1988) nonetheless found that an *Apocrypta* species, contrary to the other fig wasps he studied with wingless males, showed an unexpectedly high level of unmatedness (23%). This species was apparently a specialist parasitoid of a relatively uncommon *Apocryptophagus* species. He suggested that winged males would have been expected in such a relatively rare parasitoid. However, *Apocrypta* males are clearly phylogenetically constrained from possessing wings, which cannot re-evolve. Perhaps high levels of unmatedness can be seen as a potential 'cost' of specialising on a single, sometimes rare, host in this genus where most species may be polyphagous, as in *A. guineensis*, from *F. sur* (Compton & Robertson, 1990).

8 THE RELATIONSHIP BETWEEN MALE ANATOMY AND DENSITY IN FIG WASP SPECIES

8.1 INTRODUCTION

Dispersal polymorphisms may be linked to the sex of individuals, or may occur in individuals of the same sex. Variation in flight ability is the most frequently recorded form of dispersal polymorphism, involving short- and long- winged individuals (for example in gerrids (Brinkhurst, 1958, 1963; Zera *et al*, 1983) and fulgorids (Denno, 1976) or winged and wingless ones (a sciarid fly *Plastosciara perniciosa* (Stefan, 1973), several aphids (Dixon, 1968), the thrip *Hoplothrips pedicularis* (Crespi, 1986), *Melittobia* wasps (Eulophidae) (Freeman & Ittyeipe, 1982; Schmeider, 1933) and beetles of the genus *Ptinellodes* (Ptinellidae) (Dybas, 1978; Taylor, 1981)). Less obvious dimorphisms related to dispersal ability can also occur, as in the discrete short and long distance flying forms in some cicadellids (Rose, 1972) and reproductives of the ant *Formica exsecta* (Fortelius *et al*, 1987). These non sex-linked dimorphisms are usually related to variation in habitat quality, stability and dispersal (Southwood, 1962). In fulgorids and delphacids, higher quality habitats support a greater proportion of winged individuals than lower quality habitats. This is because winged individuals are more mobile and therefore better able to locate and reach more favourable habitats (Denno, 1976; Denno *et al* 1980). Equivalent variation has also been observed inter-specifically in *Gerris* species (Brinkhurst, 1958).

Sexual dimorphism for dispersal ability is present in mutillid, bethylid and tiphiid wasps, where only the females are winged (Brothers, 1989; Evans, 1969), and in strepsipterans where only females are flightless (Kirkpatrick, 1937). Such sex-linked dimorphism is associated with differences in life style between the sexes. Only the wingless females of mutillid wasps burrow in the soil searching for hosts to parasitize (Evans, 1969) and male strepsipterans need to be able to fly if they are to find the females, which usually live within their hosts (Kirkpatrick, 1937).

Variation in dispersal ability may also be evident within only one of the sexes. Males of a *Trichogramma* species are either apterous or alate, while females consistently have wings (Salt, 1939). Similarly, only females of the acarid mite *Siteroptes* exhibit dimorphism in structures specialized for riding on insects (Moser & Cross, 1975). Variation in dispersal ability among members of one of the sexes is also present in fig wasps. Because of the life cycle of fig wasps (chapter 1), the females are always winged. In contrast, male structure is much more variable and several species are polymorphic, with both alate and apterous males (chapter 2).

Morphology in male fig wasps is linked to their mating sites (chapter 3). Winged males typically mate outside the figs whereas wingless males mate inside figs, either in the cavity of the fig or in the galls where the females developed. The wingless *digitata* males of some *Otitesella* species provide an exception to this pattern (chapter 11). Hamilton (1979) argued that if fig wasps are rare, and the males wingless, then sons and daughters would often be alone in figs and die unmated. However, when fig wasps are common, males are likely to find females to mate with in their natal figs and females are likely to be mated before they leave the figs. In such situations wingless males would be at an advantage over winged individuals. Thus, in uncommon fig wasp species Hamilton predicted that the males would be winged while in common species they would be wingless. Species with two forms of males were predicted to occur at intermediate or fluctuating densities. Based on optimization assumptions, Hamilton also suggested that winged males in a polymorphic species might be more common at low population densities while the wingless forms would predominate at higher population densities.

The fig wasp fauna associated with *F. burtt-davyi* includes species with wingless, winged and polymorphic males. This chapter examines whether this range in the dispersal ability of the males is related to the abundance of the species, as predicted by Hamilton. Morph ratios at differing densities in the polymorphic *Philotrypesis* sp. C are also compared in order to determine whether they are fixed, or potentially adaptive to local conditions.

8.2 MATERIALS AND METHODS

Mature figs, without exit holes, were collected from eight *F. burtt-davyi* trees in the Grahamstown vicinity. Each fig was placed individually in a netting covered vial. Once fig wasps had emerged they were kept frozen for subsequent identification and counting. Wasp abundance was then related to male morphology of each species. The relationship between density and morph ratios in *Philotrypesis* sp. C was also examined.

8.3 RESULTS

The wasp species present in the figs were *Elisabethiella baijnathi*, *Otitesella uluzi*, *O. sesquianellata* and *Sycoryctes* sp. D (all with flightless males), *Philotrypesis* sp. C (with both winged and flightless males) and *Phagoblastus* sp. B (with only winged males). The mean overall densities of the wasps, and densities where only occupied figs are considered, are given in Table 8.1. Although *Phagoblastus* sp. B was the least common species, being found in only 24 of the 515 figs, the density of these wasps per occupied fig was comparable to that of *Otitesella uluzi*, *O. sesquianellata* and *Philotrypesis* sp. C, all of which were found in at least five times as many figs (Table 8.1). Thus density estimates at a crop level do not necessarily reflect local densities, in those figs that are being occupied.

The proportion of figs that contained *Philotrypesis* sp. C ranged from 66% to 95% in different collections. Average densities in occupied figs and sex ratios of this species are given in Tables 8.2 and 8.3.

Table 8.1 Average densities of wasps in *F. burtt-davyi* figs. A total of 515 figs were sampled. Mean densities do not include crops where the species were entirely absent.

WASPS	N CROPS	N FIGS OCCUPIED	DENSITY PER FIG	DENSITY (PER OCCUPIED FIG)	
			MEAN	MEAN ± SD	RANGE (ACROSS CROPS)
SPECIES WITH FLIGHTLESS MALES					
Elisabethiella baijnathi	8	349	15.90	23.47 ± 22.59	3.40-50.37
Otitesella uluzi	6	127	1.17	4.75 ± 4.80	3.73-6.11
Otitesella sesquianellata	8	289	3.43	6.12 ± 5.58	2.10-12.60
Sycoryctes sp. D	8	310	8.78	14.59 ± 14.17	1.92-25.28
SPECIES WITH WINGED AND FLIGHTLESS MALES					
Philotrypesis sp. C	8	334	5.17	7.97 ± 7.12	1.69-15.29
SPECIES WITH WINGED MALES					
Phagoblastus sp. B	6	24	0.31	6.70 ± 5.38	1.50-9.33

Table 8.2 *Philotrypesis* sp. C sex ratios and densities in occupied figs.

CROP	N OCCUPIED FIGS	TOTAL NUMBERS			SEX RATIO
		FEMALES	WINGED MALES	FLIGHTLESS MALES	MEAN
1	66	248	5	143	0.42
2	85	411	13	281	0.45
3	67	573	31	421	0.45
4	25	35	1	10	0.19
5	16	21	3	3	0.27
6	44	58	13	111	0.42
7	33	148	6	87	0.38
8	53	180	23	123	0.52
TOTAL	389	1574	85	1179	0.49

Table 8.3 The numbers of *Philotrypesis* sp. C males and females in figs of *F. burtt-davyi*. Densities relate to occupied figs only

CROP	N FIGS IN CROP	N FIGS OCCUPIED	DENSITY OF FEMALES	DENSITY OF WINGED MALES	DENSITY OF FLIGHTLESS MALES	TOTAL WASP DENSITY
			MEAN ± SD	MEAN ± SD	MEAN ± SD	MEAN ± SD
1	100	66	3.76 ± 4.51	0.08 ± 0.27	2.10 ± 2.25	5.94 ± 6.07
2	100	85	4.84 ± 4.03	0.15 ± 0.39	3.31 ± 2.73	8.30 ± 6.12
3	70	67	8.55 ± 4.99	0.46 ± 0.68	6.28 ± 3.47	15.30 ± 7.53
4	52	25	1.40 ± 1.00	0.04 ± 0.20	0.40 ± 0.64	1.83 ± 1.10
5	31	16	1.31 ± 1.14	0.19 ± 0.40	0.18 ± 0.40	1.69 ± 1.07
6	57	44	4.89 ± 5.18	0.30 ± 0.46	2.52 ± 2.57	7.70 ± 7.53
7	39	33	4.48 ± 4.23	0.18 ± 0.39	2.63 ± 2.78	7.30 ± 6.45
8	66	53	3.40 ± 2.93	0.43 ± 0.77	2.32 ± 1.73	6.15 ± 4.27

Wasp densities and sex ratios differed significantly between crops (Table 8.4). Flightless males strongly outnumbered winged males, which made up only 3% of the total population (Table 8.2). A maximum of three winged males was recorded from any one fig, compared with 17 wingless males and 24 females (Figure 8.1). Of the 389 figs where *Philotrypesis* sp. C was recorded, 90 contained only a single sex (Figure 8.2). Flightless males were absent from only 71 (18%) of the figs, whereas the rarer winged morph was absent from 79% (Figure 8.2). Not surprisingly, the combination of flightless males with females was that most frequently encountered within the figs (Figure 8.3). 14% of the figs contained only females, while flightless males were 'stranded' without potential mates in 8% of the figs and winged males were the only inhabitants in 1.28%. When the numbers of wasps inside the figs are considered, only 4.9% of the total were recorded from single sex figs (Figure 8.4). 5% of all the females were found in figs without males and 4.4% of the flightless males were 'stranded'. When different crops are compared, those containing higher densities of wasps had relatively fewer females in male-free figs (Figure 8.5).

Sex ratios were not significantly correlated with population densities in individual figs (r = -0.05, P = 0.36, n = 389). However, the proportion of winged males within the figs was negatively correlated with the total numbers of males per fig (Figure 8.6a) and total *Philotrypesis* density per fig (Figure 8.6b). The change in morph frequencies with density is also illustrated by the frequency histograms of winged and wingless males in the figs

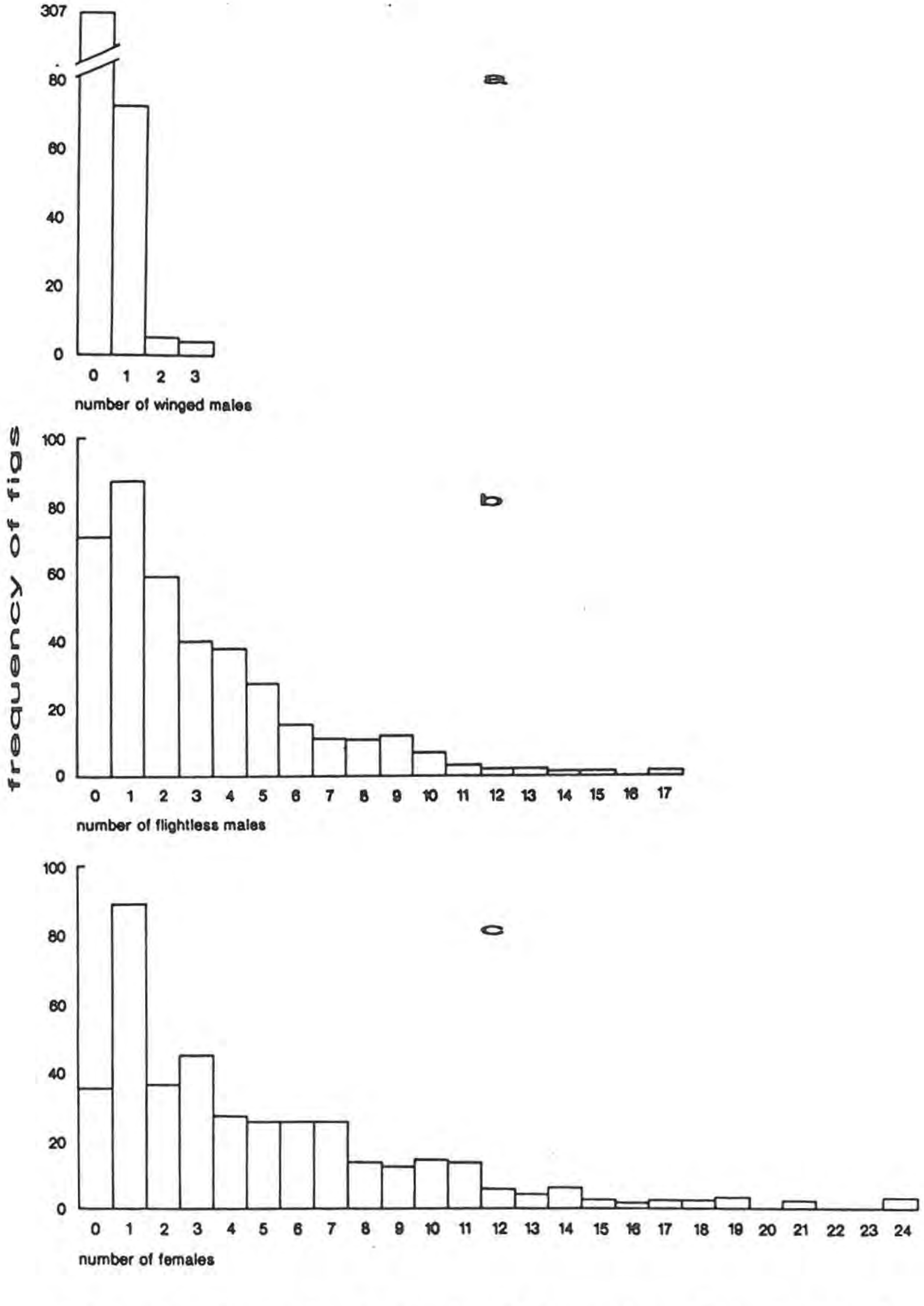


Figure 8.1 Frequencies of figs with *Philotrypesis* sp. C a) winged males, b) wingless males and c) females.

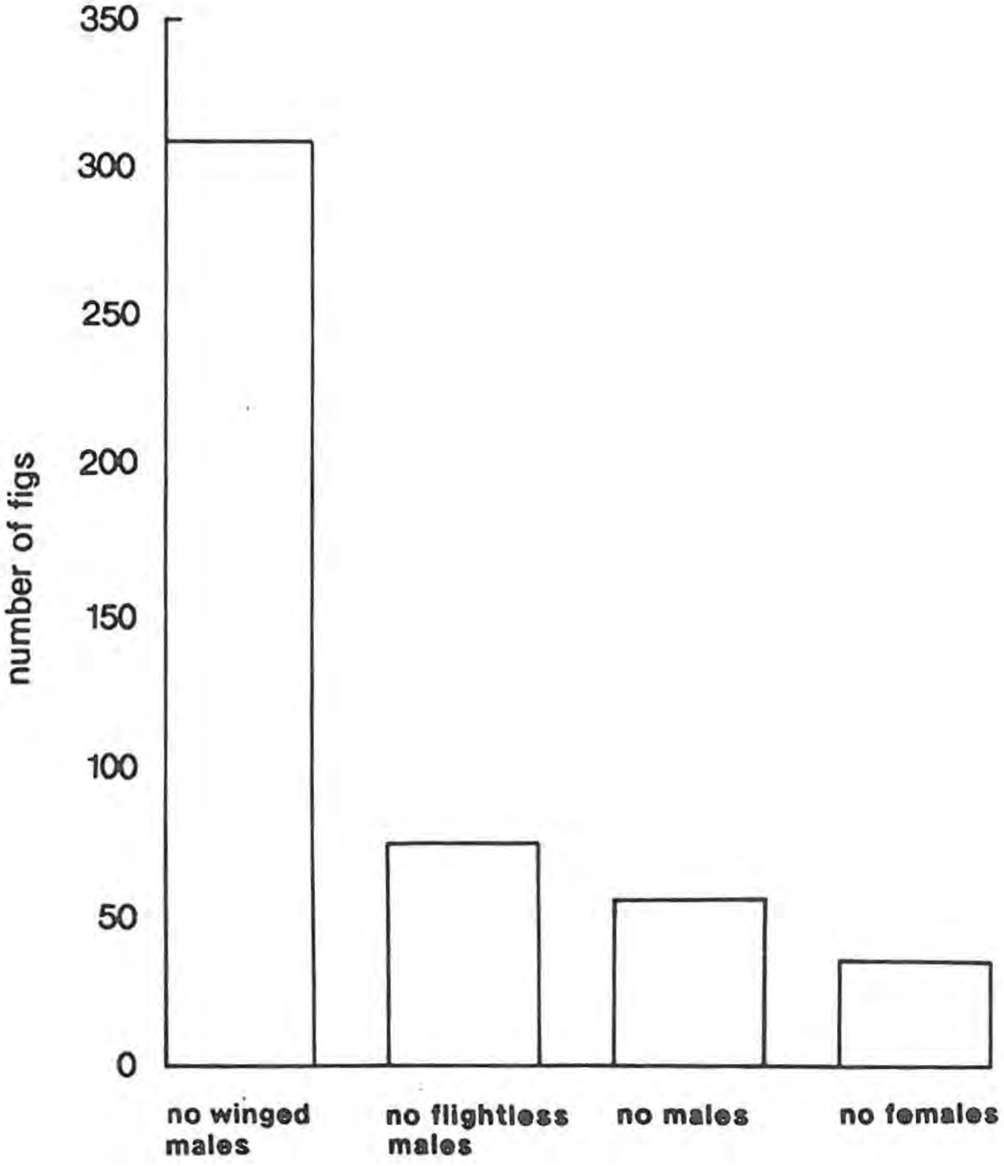


Figure 8.2 Frequencies of figs with no *Philotrypesis* sp. C males, winged males, wingless males or females.

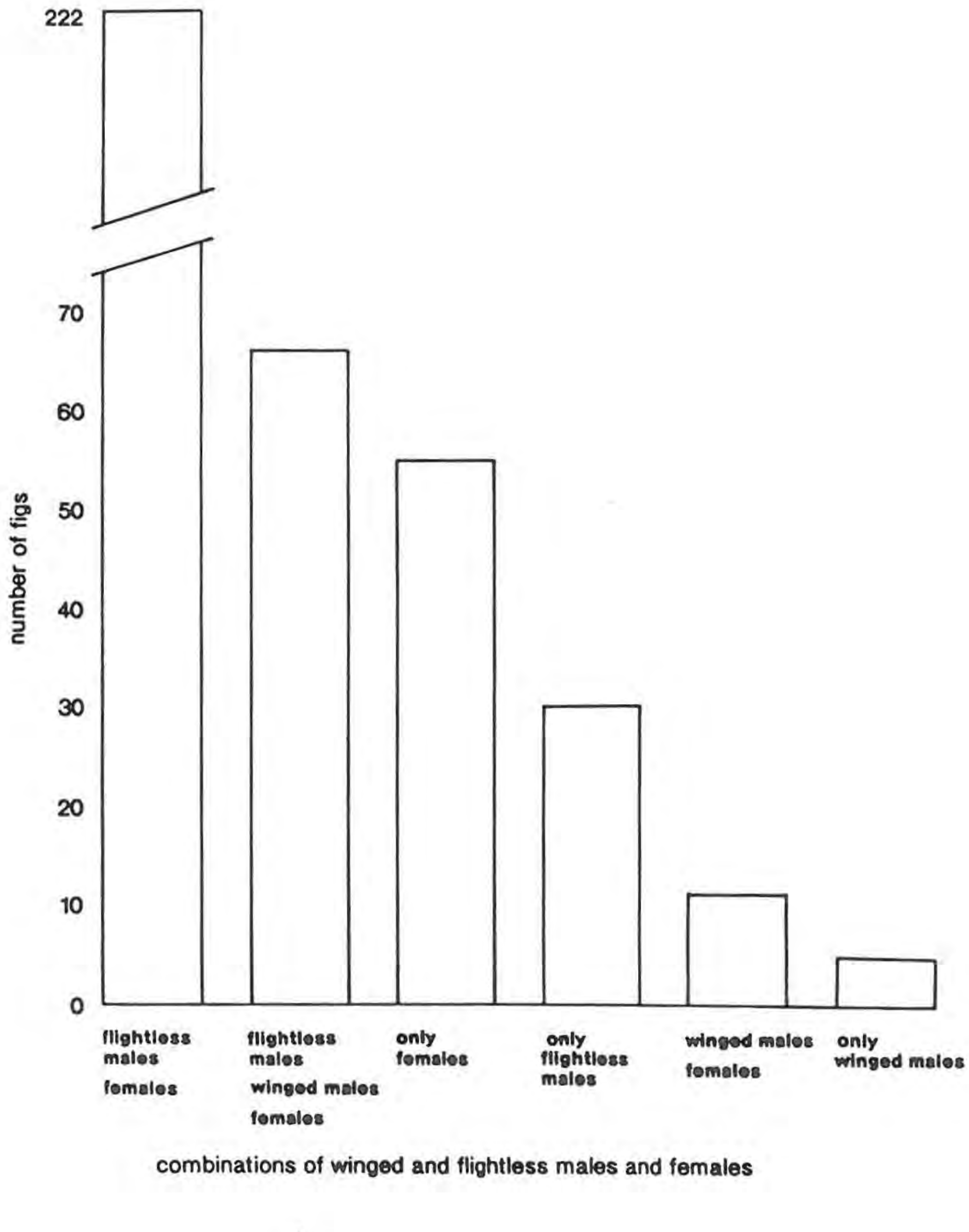


Figure 8.3 Frequencies of figs with combinations of *Philotrypesis* sp. C winged and wingless males and females.

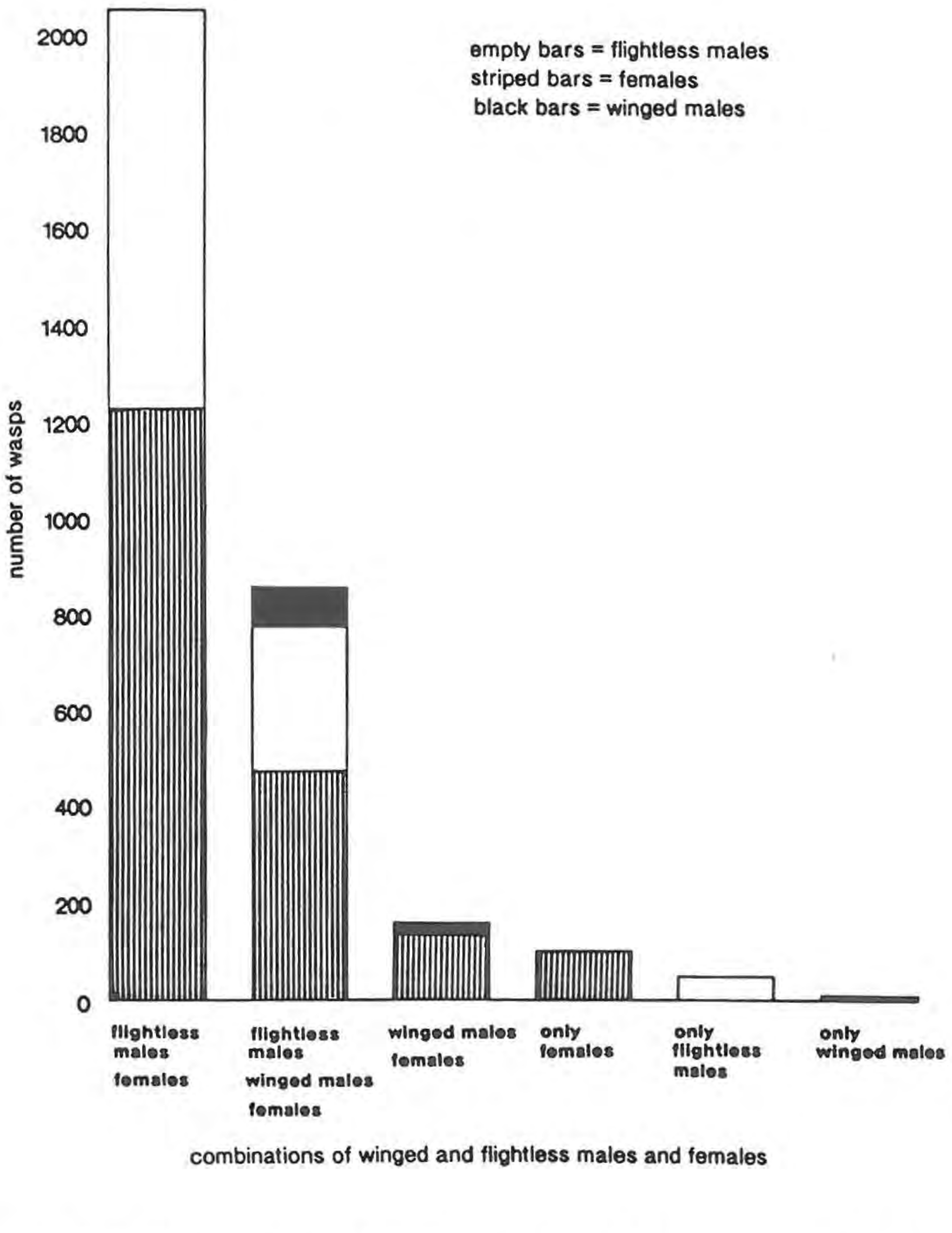


Figure 8.4 The numbers of *Philotrypesis* sp. C, winged and wingless males and females occurring together in figs. There were no figs with both winged and wingless males, but no females.

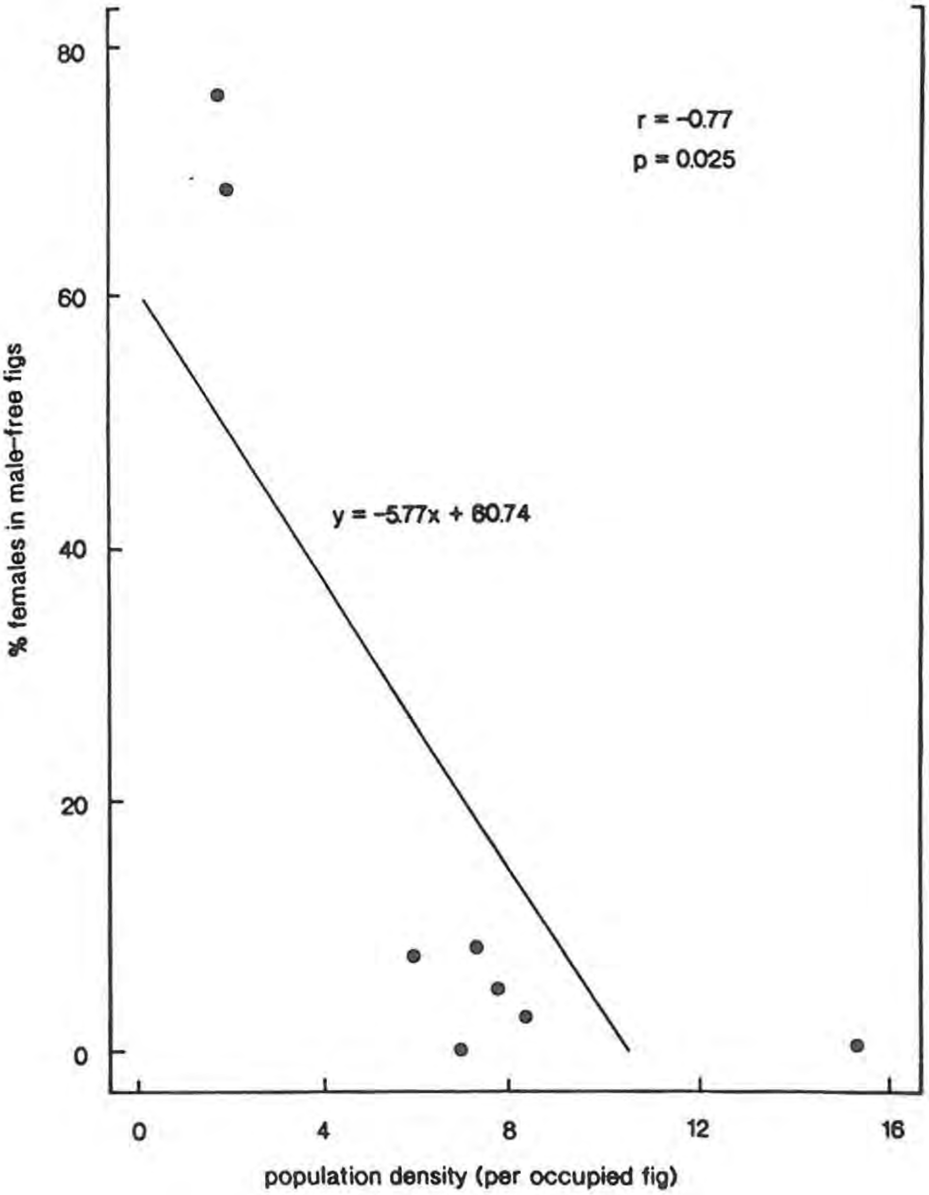


Figure 8.5 The relationship between the percentage of *Philotrypesis* sp. C females in male-free figs and the average population density in figs.

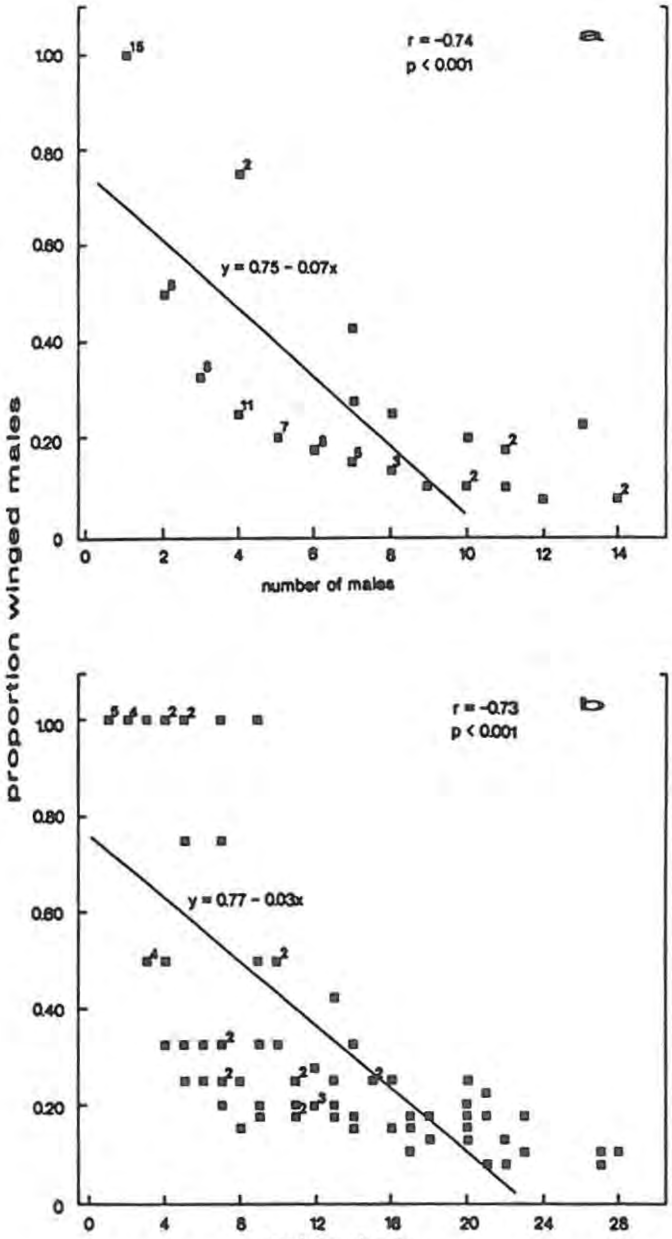


Figure 8.6 The relationship between the proportion of *Philotrypesis* sp. C alate males in a fig and a) total number of males and b) population density in each fig.

(Figure 8.1). 73 of the 82 figs with winged males in them had only one such male, and at most three were present. This contrasts with the frequency distribution of wingless males, where many of the figs contained more than three individuals (Table 8.5). Thus when high densities of males were present in a fig, this was a consequence of the large numbers of the flightless morph.

When average morph ratios in different crops are compared with wasp densities, there is a significant negative correlation between the proportion of winged males and wasp density. In other words, crops with high densities of wasps had a reduced proportion of winged males (Figure 8.7). This is the same pattern observed when individual figs are considered (Figure 8.6). There was also a significant negative correlation between the proportion of winged males and mean sex ratios (r = -0.86, $P < 0.01$, n = 8) due to low density crops tending to have more female biased sex ratios (r = 0.66, P = 0.07, n = 8).

8.4 DISCUSSION

Philotrypesis sp. C, as a species with both alate and flightless males, was expected to occur at lower population densities in figs of *F. burtt-davyi* than the fig wasp species that had exclusively wingless males (*O. uluzi*, *O. sesquianellata*, *E. baijnathi* and *Sycoryctes* sp. D), but at higher densities than the species with winged males. In a number of fig wasps, including *Philotrypesis* sp. C, occupation of a small number of figs within a crop is also associated with a reduced density per occupied fig (chapter 7). Nonetheless, the pattern predicted by Hamilton (1979) was not

Table 8.4 ANOVA comparing the mean densities per occupied fig and sex ratios in *Philotrypesis* sp. C populations from eight *F. burtt-davyi* trees.

CHARACTERISTIC	F-VALUE$_{[7,381]}$	P
TOTAL *PHILOTRYPESIS*	21.87	***
MALES	26.36	***
FLIGHTLESS MALES	24.78	***
WINGED MALES	5.08	***
FEMALES	13.30	***
SEX RATIO	4.87	***

*** $P < 0.001$

Table 8.5 Frequencies of winged and flightless *Philotrypesis* sp. C males in 389 figs of *F. burtt-davyi*.

	NUMBER OF MALES					CHI-SQUARE$_{[4]}$	P
	0	1	2	3	> 3		
WINGED MALES	307	73	5	4	0	165.65	***
FLIGHTLESS MALES	35	85	36	45	88		

*** $P < 0.001$

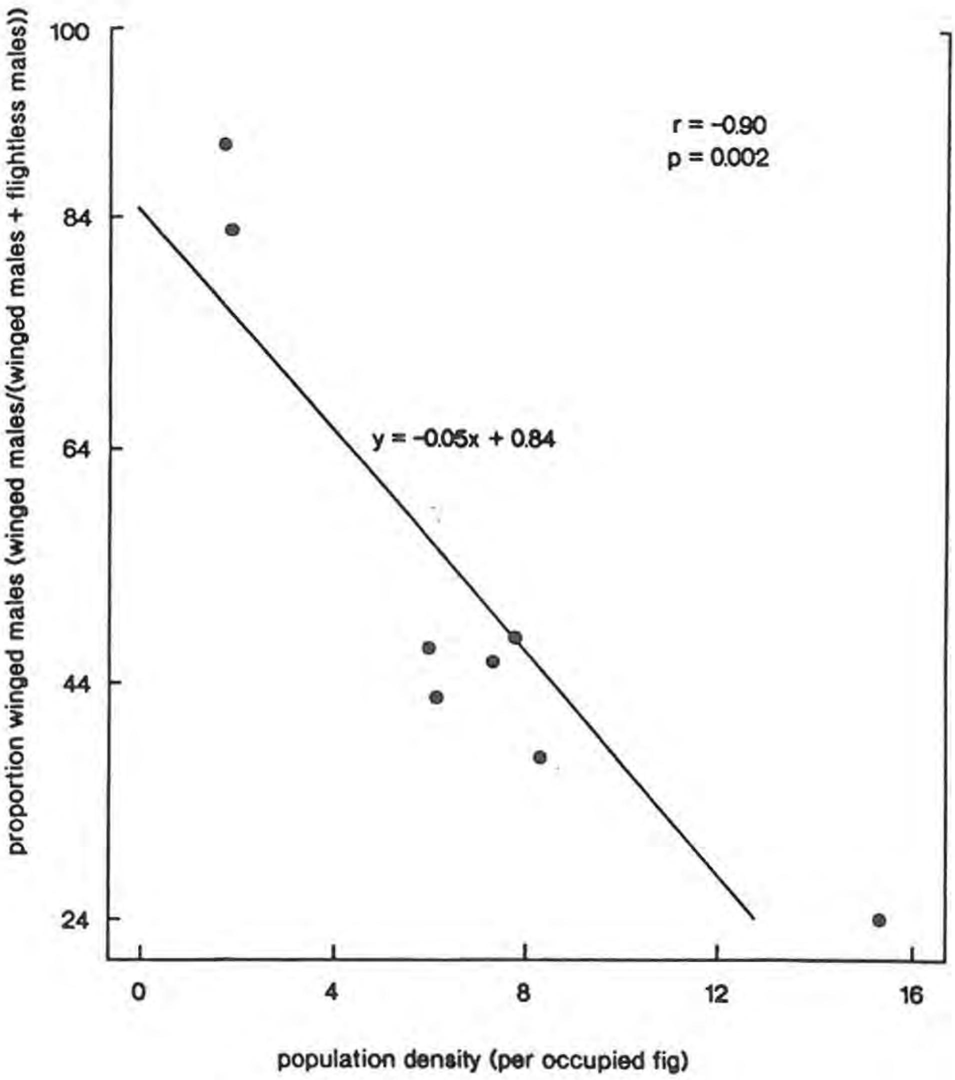


Figure 8.7 The relationship between the proportion of winged *Philotrypesis* sp. C males and wasp densities in eight crops.

evident in the *F. burtt-davyi* crops that were examined, with population densities of *Philotrypesis* sp. C higher than those of two of the species with only flightless males. *Phagoblastus* sp. B, the only species with only winged males, was nonetheless the rarest, as predicted. *Phagoblastus* sp. B occurred in far fewer figs than the other species, but its average population density in the figs that it occupied was not lower than those of some of the species with wingless males. Under such circumstances Hamilton's predictions break down because the reproductive advantage of winged males in rarer species largely falls away. The high density of *Phagoblastus* individuals per occupied fig is presumably a reflection of the 'internal' oviposition behaviour of this species, although females can exit from figs after oviposition (R.J.C. Nefdt, personal communication). Observations from other *Ficus* species on additional polymorphic fig wasps and species with only winged males are required before any firm conclusions may be drawn about the relationship between fig wasp population density and male dispersal morphology.

Some fig wasps do seem to occur at consistently low densities, with few individuals sharing the same figs (personal observations). These include *Acophila* species from *F. ingens* and species of the genus *Watshamiella*. Large fig collections from, for example, *F. sycomorus* may contain just a few females, and no males of *Watshamiella* (Compton *et al*, 1991). As might be expected, given their rarity, both these genera appear to have only winged males (but see chapter 2 for examples of *Watshamiella* species showing wing reduction). However, in the case of some *Watshamiella* species, the possibility of males being redundant, with populations containing only females that are produced by thelytokous parthenogenesis, cannot be ruled out.

Winged male *Philotrypesis* mate outside of the figs, whereas mating by wingless males is mainly restricted to the inside of their natal figs. At low population densities, *Philotrypesis* males and females are more likely to be alone inside figs (see Figure 7.1). Such males, if flightless, will die without mating, but the females and winged males can emerge and mate with individuals from other figs. Thus at low densities winged males may be at a reproductive advantage over wingless males because of their increased vagility (Roff, 1986a). Conversely, at higher wasp densities, wingless males are likely to be sharing figs with females and have the opportunity to monopolize matings, before winged males can encounter the females on the surface of the figs. The importance of mating with females first will depend on factors such as sperm precedence and the willingness of females to mate repeatedly (Thornhill & Alcock, 1983). These remain to be investigated. Nonetheless, the observed variation in morph ratios in relation to wasp density implies that females of *Philotrypesis* sp. C adjust the morph ratios of their male offspring. This is in agreement with Hamilton's (1979) predictions and suggests that there must be a selective advantage in doing so. A similar pattern is seen with the dimorphism in male *Otitesella* sp. I (chapter 11). How ovipositing *Philotrypesis* females can achieve the observed adjustment in morph ratios is another unknown.

9 POLYMORPHISM AND CONTINUOUS VARIATION IN MALE PHILOTRYPESIS

9.1 INTRODUCTION

Differentiation between discrete and continuous variation in insects is not always easy, especially when variation in the relative size of body parts is involved. Bimodality in frequency distributions is a common way of detecting dimorphism, as used for example in studies of the ant *Formica exsecta* (Fortelius *et al*, 1987) and the defender larvae of the encyrtid *Copidosomopsis tantymema* (Cruz, 1981, Cruz *et al*, 1980). Eberhard & Gutierrez (1991) stress that apparent bimodalities can result from collector bias, which often selects for extremes among continuous variables. In determining whether beetles or earwigs are dimorphic for horn or cerci size Eberhard & Gutierrez (1991) make it clear that only if, in the same sample, the frequency distributions of body size are unimodal and horn size are bimodal, can sources of misinterpretation be eliminated.

Complex statistical analyses may be required to detect less apparent dimorphisms involving the relative proportions of body parts (Eberhard & Gutierrez, 1991), but frequency distribution plots and regression analyses can be used in conjunction to detect many dimorphisms. In numerous ant species physical castes among the non-reproductives (workers and soldiers) have been distinguished using plots of morphometric characters, for example head width versus pronotal width (Wilson, 1953). The best fit regression line is typically broken, the break corresponding to the dip in bimodal frequency plots of the same data (Wilson, 1953). Eberhard and Gutierrez (1991) analyzed pairs of morphometrical characters in several species of beetles and earwigs by looking for either discontinuity at a switch point or a change of slope at that point. They considered discontinuity in a regression line as stronger evidence for a dimorphism than a change of slope in that line.

The bimodal frequencies and sigmoidal regressions described above are typically associated with allometric growth. This is where various parts of the body are of different sizes relative to one another according to how large the individual is. Soldier castes, for example, typically have disproportionately large heads and mandibles compared to worker castes. In contrast, isometric or equivalent growth rates among the different body parts are normally associated with continuous, unimodal frequency distribution plots.

Species of the fig wasp genus *Philotrypesis* (Sycoryctinae) include most of the known examples of fig wasps with both flightless and alate males (chapter 2). While this dimorphism is clear-cut, another phenomenon observed frequently in this genus is the occurrence of both large and small flightless males in the same species. Similar size variation has also been mentioned in descriptions of a few other Sycoryctinae, such as *Sycoscapter reticulatis* Wiebes (Wiebes, 1966) and *S. montis* Wiebes (Wiebes, 1971). Grandi (1930) was the first to record extreme variation in the size of *Philotrypesis* males, which was subsequently discussed by Joseph

(1954) and Wiebes (1971). Grandi (1930) concluded that this variation in body size was a feature of all the *Philotrypesis* species he looked at, and that there was a concordant change in the relative sizes of the body parts, the sculpturing of the cuticle and the size of the setae. Table 9.1 lists some of the terms he developed to describe the morphological variation in *Philotrypesis*. It also serves to illustrate the large degree of variation he observed.

Although Grandi (1930) provided a series of names for different sized male *Philotrypesis*, he considered the variation he observed to be continuous. Whether this is always the case, or whether two or more discrete flightless morphs also occur in some species, has not been examined previously. In this chapter I describe the occurrence of *Philotrypesis* species in collections of fig wasps from southern Africa and examine the morphological variation of the males in relation to the taxonomy of their host plants. Because closely related trees are likely to support closely related wasps (Ulenberg, 1985; Wiebes, 1982a) this provides an indication of whether certain lineages have lost the ability to produce the winged males, which is presumably the plesiomorphic condition in the genus. I then examine quantitatively, using frequency histograms and regression analyses, the differences between apparently 'large' and 'small' male forms in two selected *Philotrypesis* species. For comparative purposes, similar analyses were carried out on a species in the genus *Sycoryctes*, where variation in male form is less apparent.

Table 9.1 Some of the terminology developed by Grandi (1930) to describe morphological variation in male *Philotrypesis* (translated from classical italian).

MORPHOLOGICAL CHARACTER	TERM	DEFINITION
male form	heteromorphous	wingless
	hemipterous	half winged
	homomorphous	alate, as in female
wings	macropterous	fully winged
	leptopterous	wings long and threadlike (length greater than 10x width)
	brachypterous	wings long and threadlike (less than 5x long as wide)
	subapterous	alar lamina scarcely distinguishable
body size	eumegetic	large
	epigemetic	medium
	hypomegetic	small/dwarf
mandible size	macrognathous	big
	brachygnathous	small
mandible shape	homodont	teeth all the same
	triodont	three teeth
	heterodont	different sized teeth

9.2 MATERIALS AND METHODS

9.2.1 *Philotrypesis* species in southern African figs

The collection of southern African fig wasps maintained by Dr. S.G. Compton were examined for the presence of *Philotrypesis* species along with the presence of alate and/or flightless males.

9.2.2 Morphometric analysis of large and small males

I examined variation in the flightless males of *P. parca* Wiebes from *F. thonningii*, collected in Grahamstown, eastern Cape and *Philotrypesis* sp. N from *F. verruculosa*, collected at the Kosi Bay camp site, northern Natal. Both species have flightless males which exhibit extreme size variation. *P. parca* also has alate males, but *Philotrypesis* sp. N does not.

The wasps were dried at 40° C for three days and weighed on a Cahn C-31 microbalance. Subsequently the wasps were measured using an ocular-micrometer on a compound microscope. To prevent the specimens from shattering they were placed in water under the coverslips. For each individual, colour, head width (across the eyes), mandible length and prothorax width (across the widest part) were recorded. Similar procedures were adopted with the males of *Sycoryctes remus* from *F. thonningii*.

9.2.3 Statistics

BMDP statistical software was used to perform all the statistics described below. Frequency histograms of mass, head width, mandible length and prothorax width were plotted. Morphometrics were then inter-correlated.

Analysis of co-variance (ANCOVA) is based on two assumptions; firstly that there is a significant regression across the data and second that this regression is a linear relationship (Sokal & Rohlf, 1981). The ANCOVA procedure firstly tests whether there is parallelism of the slopes in the paired groups under examination. If the slopes do not vary significantly it can be assumed that the covariate may be represented by a single regression coefficient. The ANCOVA then proceeds to test for the equality of y-intercepts, using the same single regression coefficient, which is equivalent to testing the differences of the means of the different male forms (Sokal & Rohlf, 1981). Body mass was used as the covariate in this study.

9.3 RESULTS

9.3.1 Occurrence of *Philotrypesis* species in southern Africa

The fig wasp collections that were examined, together with their localities and collectors are listed in Appendix 2. Thirteen *Ficus* species from southern Africa were host to one species of *Philotrypesis* each and *F. stuhlmannii* and *F. trichopoda* to two *Philotrypesis* species each (Table 9.2). Without a taxonomic revision of the genus it is uncertain how many species were represented, but host specificity appears well developed and to date no African *Philotrypesis* species has been recorded from more than one host tree (Boucek *et al*, 1981).

None of the *Philotrypesis* species in the collections had winged males only. *Philotrypesis* from fig species in the sections *Sycidium* and *Urostigma* and subsections *Galoglychia* and *Caulocarpae* had only flightless males present. Thus *Philotrypesis* species with both alate and flightless males were only present in species from the *Galoglychia* subsections *Platyphyllae* and *Chlamydodorae*. Given the large number of collections that were from section *Urostigma*, it seems likely that the ability to produce winged males has been lost among the *Philotrypesis* species associated with that section. The data are insufficient for firm conclusions regarding the other sections.

9.3.2 Abundance of alate and flightless males

Because of the sampling methods that had been employed, precise counts of the relative abundance of alate and flightless in males were not possible. Nonetheless, in collections where alate males were present they were clearly far less common than the flightless males. Furthermore, among these polymorphic *Philotrypesis* species, alate males were found in a smaller proportion of the collections than the flightless ones (Table 9.2).

9.3.3 Morphological variation among flightless *Philotrypesis* males

Not surprisingly, mandible length, head width, prothorax width and mass were strongly and positively inter-correlated in both *Philotrypesis* species and in *Sycoryctes remus* (Table 9.3 and see Figure 9.1). The variation in *S. remus* approximated a (sometimes skewed) normal distribution (Figure 9.2) whereas the frequency distributions of mass, mandible length, head width and prothoracic

Table 9.2 The presence of *Philotrypesis* in collections of *Ficus* species from southern Africa. Two *Philotrypesis* species were recorded from the figs of *F. stuhlmannii* and *F. trichopoda*. No collections with only alate males were recorded.

FICUS SECTIONS SUBSECTIONS AND SPECIES	MALE FREQUENCIES			
	N COLLECTIONS	N WITH *PHILOTRYPESIS*	FLIGHTLESS MALES ONLY	FLIGHTLESS AND ALATE MALES
SYCIDIUM				
F. capreifolia	2	2	2	0
UROSTIGMA				
F. ingens	17	12	12	0
F. c. salicifolia	11	10	10	0
F. verruculosa	8	8	8	0
GALOGLYCHIA				
GALOGLYCHIA				
F. lutea	5	3	3	0
PLATYPHYLLAE				
F. glumosa	23	13	9	4
F. stuhlmannii	10	3	2	1
	10	2	2	0

Table 9.2 *continued*

FICUS SECTIONS SUBSECTIONS AND SPECIES	MALE FREQUENCIES			
	N COLLECTIONS	N WITH *PHILOTRYPESIS*	FLIGHTLESS MALES ONLY	FLIGHTLESS AND ALATE MALES
F. abutilifolia	20	15	15	0
F. trichopoda	13	10	10	0
	13	10	10	0
CHLAMYDODORAE				
F. burtt-davyi	18	18	16	2
F. ilicina	11	10	6	4
F. reflexa	8	1	1	0
F. thonningii	32	22	20	2
CAULOCARPAE				
F. p. polita	4	1	1	0
F. s. sansibarica	5	2	2	0

Table 9.3 Correlations between morphological characters in *Philotrypesis parca*, *Philotrypesis* sp. N and *Sycoryctes remus*.

MORPHOLOGICAL CHARACTER	MASS		MANDIBLE LENGTH		HEAD WIDTH	
	r	*P*	*r*	*P*	*r*	*P*
Philotrypesis parca						
mandible length	0.91	***	-		-	
head width	0.94	***	0.98	***	-	
prothorax width	0.92	***	0.96	***	0.98	***
Philotrypesis sp. N						
mandible length	0.50	***	-		-	
head width	0.80	***	0.59	***	-	
prothorax width	0.67	***	0.57	***	0.66	***
Sycoryctes remus						
mandible length	0.77	***	-		-	
head width	0.83	***	0.83	***	-	
prothorax width	0.90	***	0.82	***	0.85	***

*** $P < 0.001$

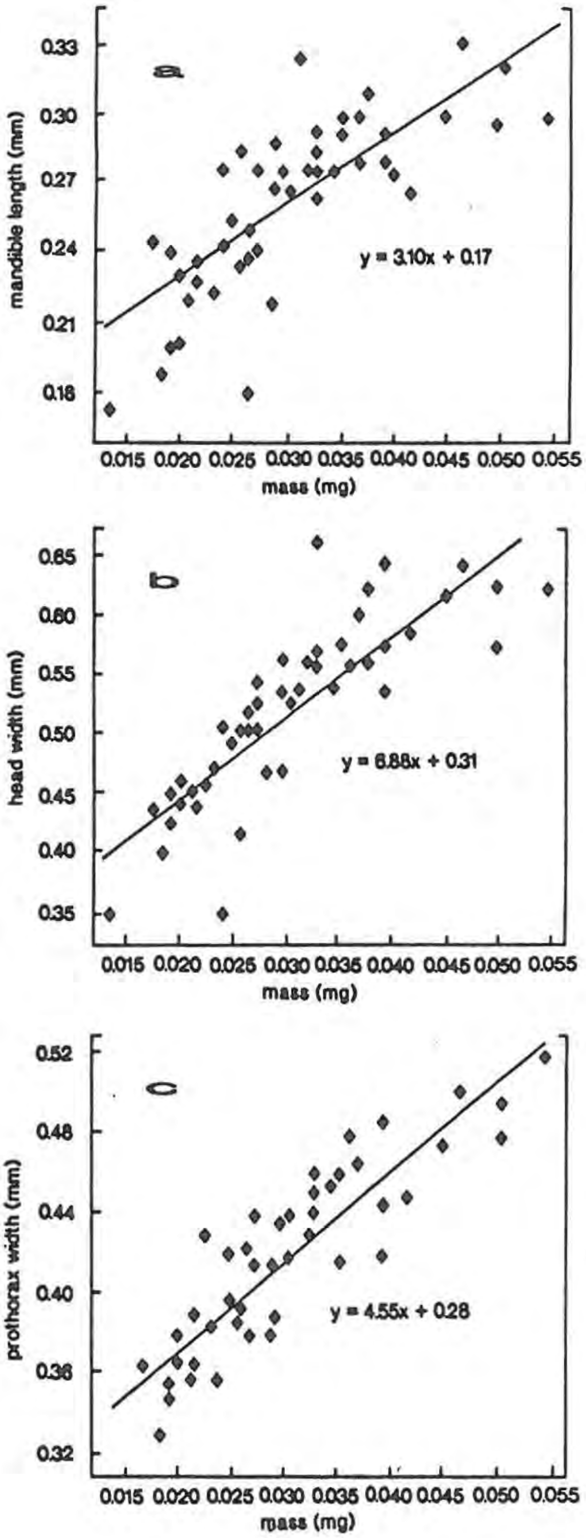


Figure 9.1 Correlations of mass versus morphological characters in *Sycoryctes remus* males; a) mandible length, b) head width and c) prothorax width.

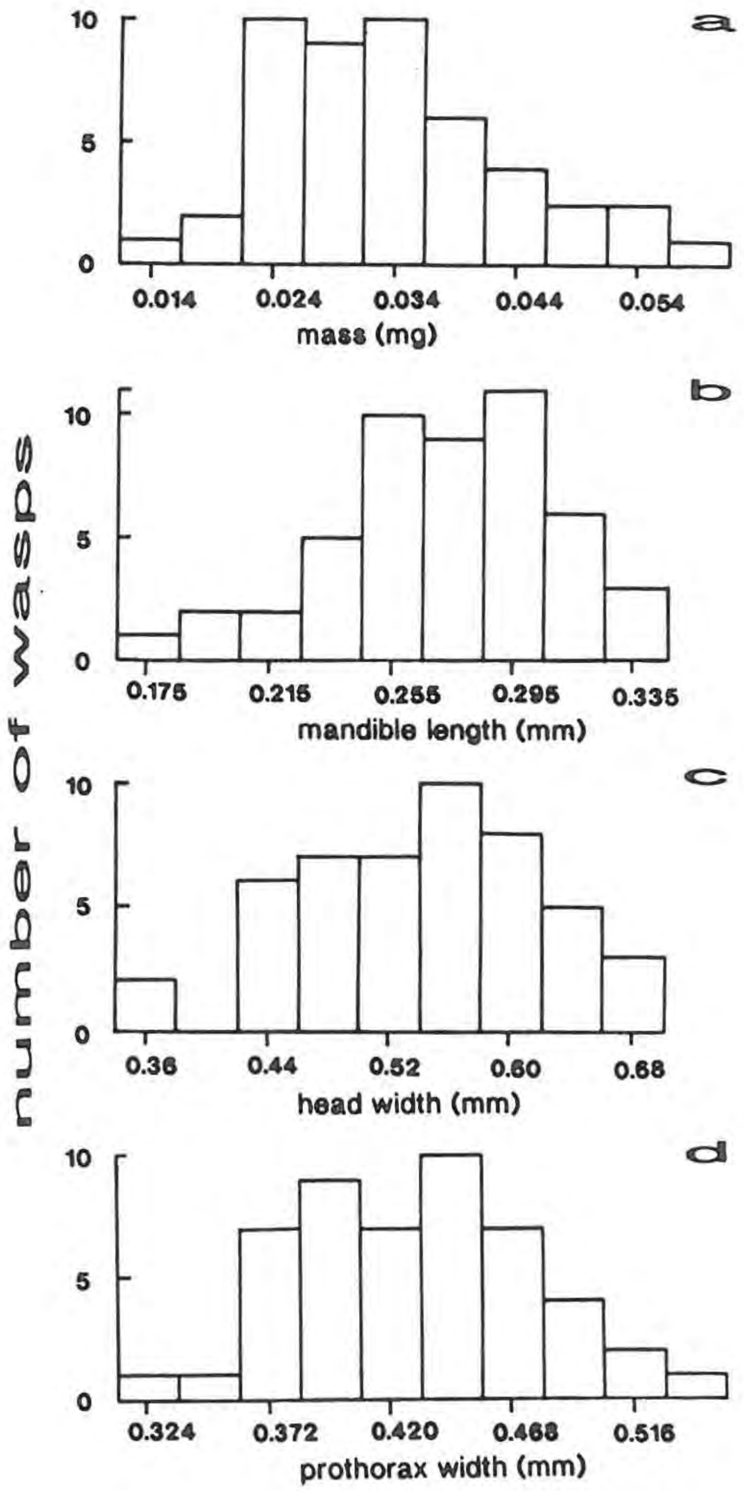


Figure 9.2 Frequency histograms of *Sycoryctes remus* males; a) mass, b) mandible length, c) head width and d) prothorax width.

width were roughly bimodal or irregular in both *P. parca* and *Philotrypesis* sp. N (Figures 9.3 & 9.4).

The males of the two *Philotrypesis* species were divided into large and small forms. In the case of *Philotrypesis* sp. N this separation corresponded to differences in the colour of the insects: large males had black heads while those of small males were light brown. There were no colour intermediates. The colours of the large and small males of *P. parca* were similar, but subtle differences in the general appearance of the large and small males was evident, not just in their size. Large and small males were therefore subjectively distinguished by eye prior to any measurement being taken. Consequently some males were 'incorrectly' grouped as large or small males. Variation in the measurements obtained from the two groups is summarised in Table 9.4.

The slopes of the regressions of prothorax width, head width and mandible length versus mass for the small and large male forms of *P. parca* were not equal (Table 9.5 and Figure 9.5). The slopes of the regressions were steeper among the smaller males, the relatively large size of mandibles in big males is reflected in the difference in the intercepts. The pattern was different in *Philotrypesis* sp. N, where the slopes of the regressions for the light (small) and dark (large) male forms were similar (Table 9.5 and Figure 9.6). For wasps of any given mass there were no differences in mandible length and prothorax width between the two groups, but there were differences in head width (Table 9.6).

Table 9.4 Morphometrics of the large and small wingless males of *Philotrypesis parca* and *Philotrypesis* sp. N

MORPHOLOGICAL CHARACTER	LARGE		SMALL	
	MEAN (mg/mm) ± SD	RANGE	MEAN (mg/mm) ± SD	RANGE
Philotrypesis parca				
mass	0.062 ± 0.019	0.021-0.115	0.021 ± 0.005	0.013-0.033
mandible length	0.313 ± 0.044	0.178-0.393	0.157 ± 0.024	0.106-0.188
head width	0.498 ± 0.053	0.354-0.589	0.329 ± 0.035	0.300-0.386
prothorax width	0.547 ± 0.072	0.357-0.650	0.346 ± 0.045	0.281-0.408
Philotrypesis sp. N				
mass	0.036 ± 0.006	0.023-0.048	0.020 ± 0.008	0.011-0.035
mandible length	0.261 ± 0.097	0.170-0.765	0.146 ± 0.025	0.124-0.219
head width	0.480 ± 0.041	0.415-0.565	0.372 ± 0.044	0.298-0.451
prothorax width	0.437 ± 0.059	0.361-0.667	0.355 ± 0.059	0.294-0.509

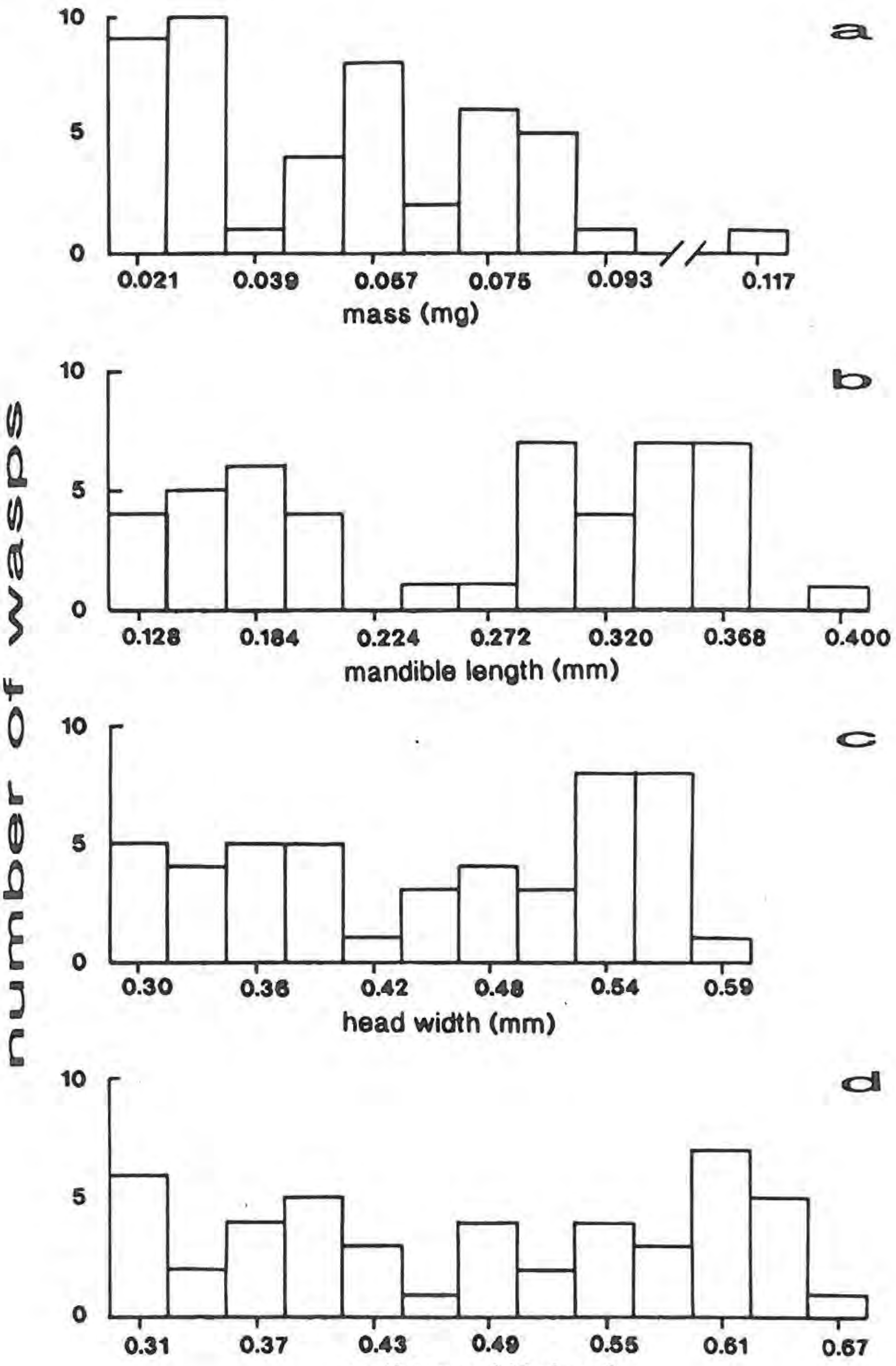


Figure 9.3 Frequency histograms of *Philotrypesis parca* males; a) mass, b) mandible length, c) head width and d) prothorax width.

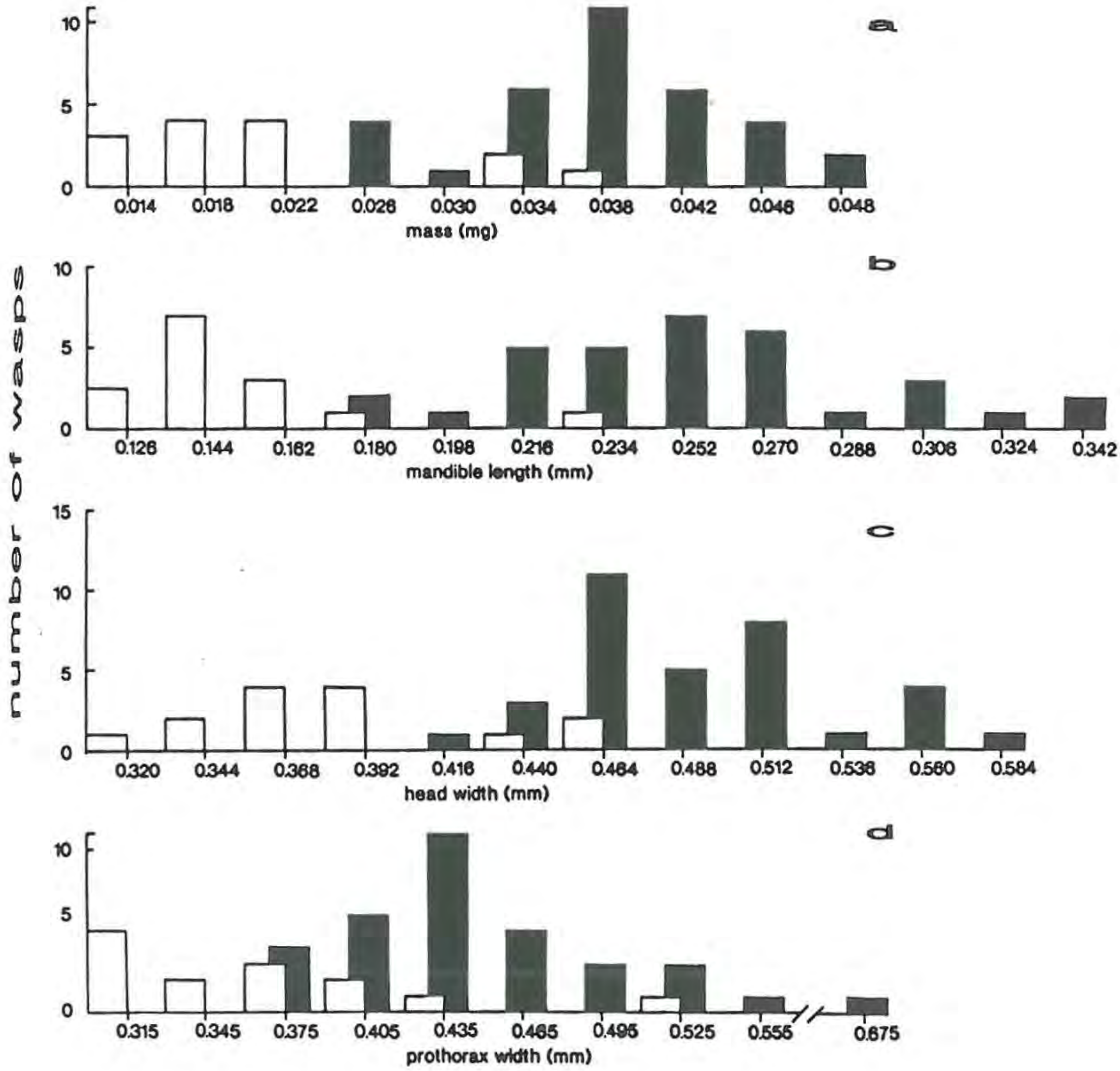


Figure 9.4 Frequency histograms of *Philotrypesis* sp. N males; a) mass, b) mandible length, c) head width and d) prothorax width. Individuals with black heads are distinguished by solid bars.

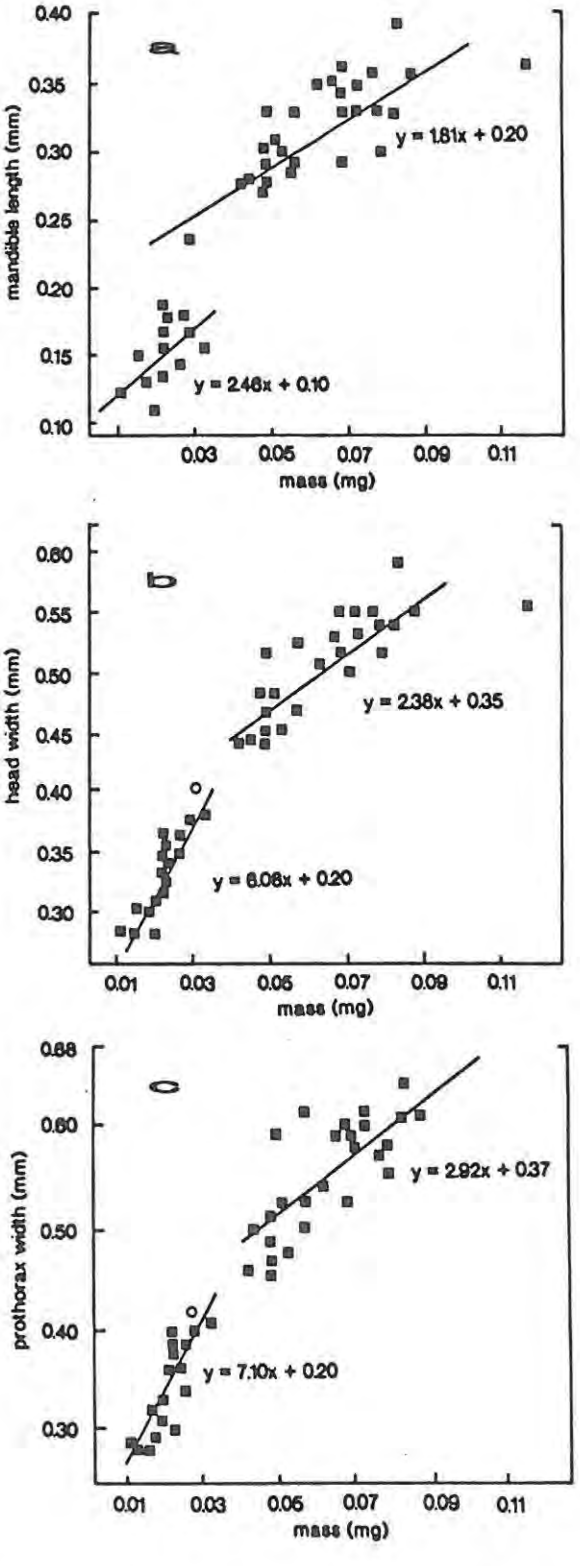


Figure 9.5 Correlations of mass versus morphological characters in male *Philotrypesis parca*; a) mandible length, b) head width and c) prothorax width. Empty circles represent males that were 'incorrectly' coded as small or large on inspection.

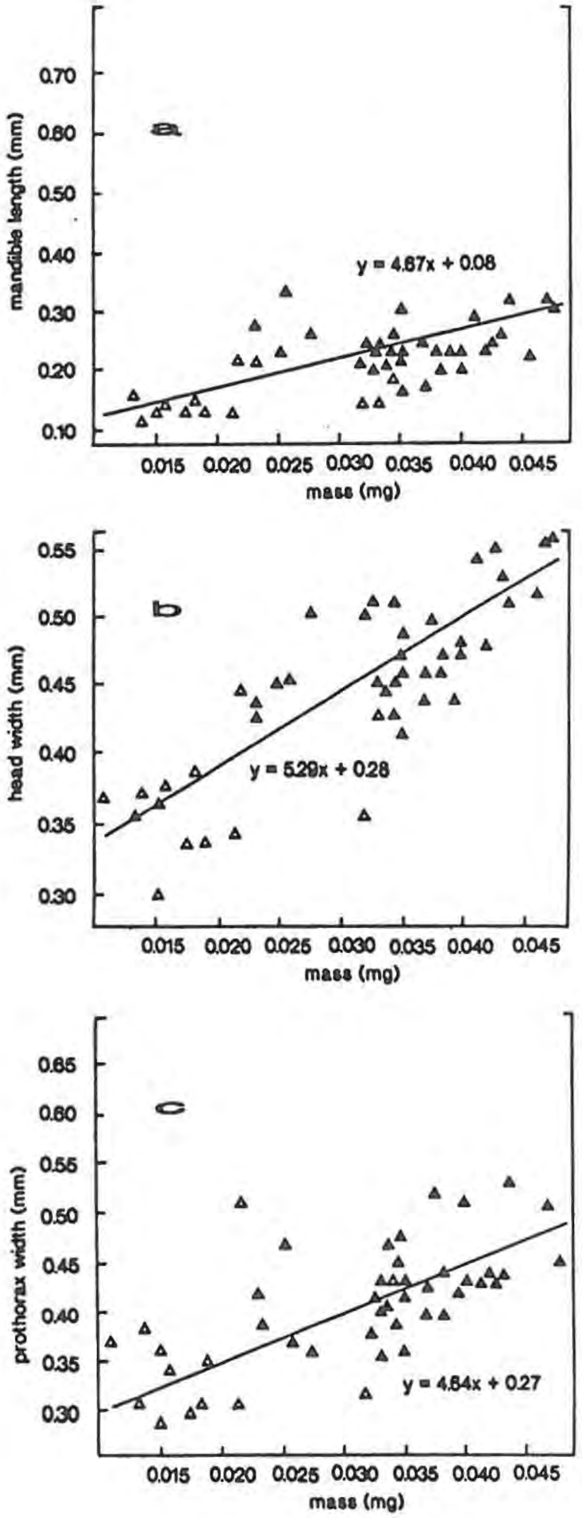


Figure 9.6 Correlations of mass versus morphological characters in male *Philotrypesis* sp. N; a) mandible length, b) head width and c) prothorax width. Solid triangles represent large males and open triangles small males.

Thus the dark males had relatively wider heads than the light males (Figure 9.7).

9.4 DISCUSSION

Philotrypesis displays perhaps the greatest variability in male structure of any fig wasp genus. This variability is reflected both between species, and within them. The males of *Philotrypesis* species range from heavily sclerotised, pugnacious type VI fighters to type II delicate winged pacifists. Less commonly encountered are males such as that of *P. finitimorum* Wiebes (Wiebes, 1971) with half-sized wings similar in appearance to those found in some species of the related genus *Watshamiella* (Wiebes, 1981a). Within species, the most obvious variation is that between alate and flightless males. These have numerous morphological traits separating them. Even among the flightless forms however, there is clearly complex variation between individuals, the details of which differ from species to species. This is in contrast to the continuous variation observed in *S. remus*, which may be more typical of flightless male fig wasps in general.

Grandi (1930) considered that the size variation he observed in Asian *Philotrypesis* species was continuous, but no statistical analyses accompanied his work. Here variation was complex and for some characters effectively discontinuous in both *Philotrypesis* species. Details of the variation in the flightless males of *P. parca* and *Philotrypesis* sp. N were also different. Clearly a wider sample of *Philotrypesis* species will need to be analysed before any general conclusions can be made.

Table 9.5 Tests for the equality of slopes in the linear relationships between body mass and other morphometrics in the large and small males of *Philotrypesis parca* and *Philotrypesis* sp. N.

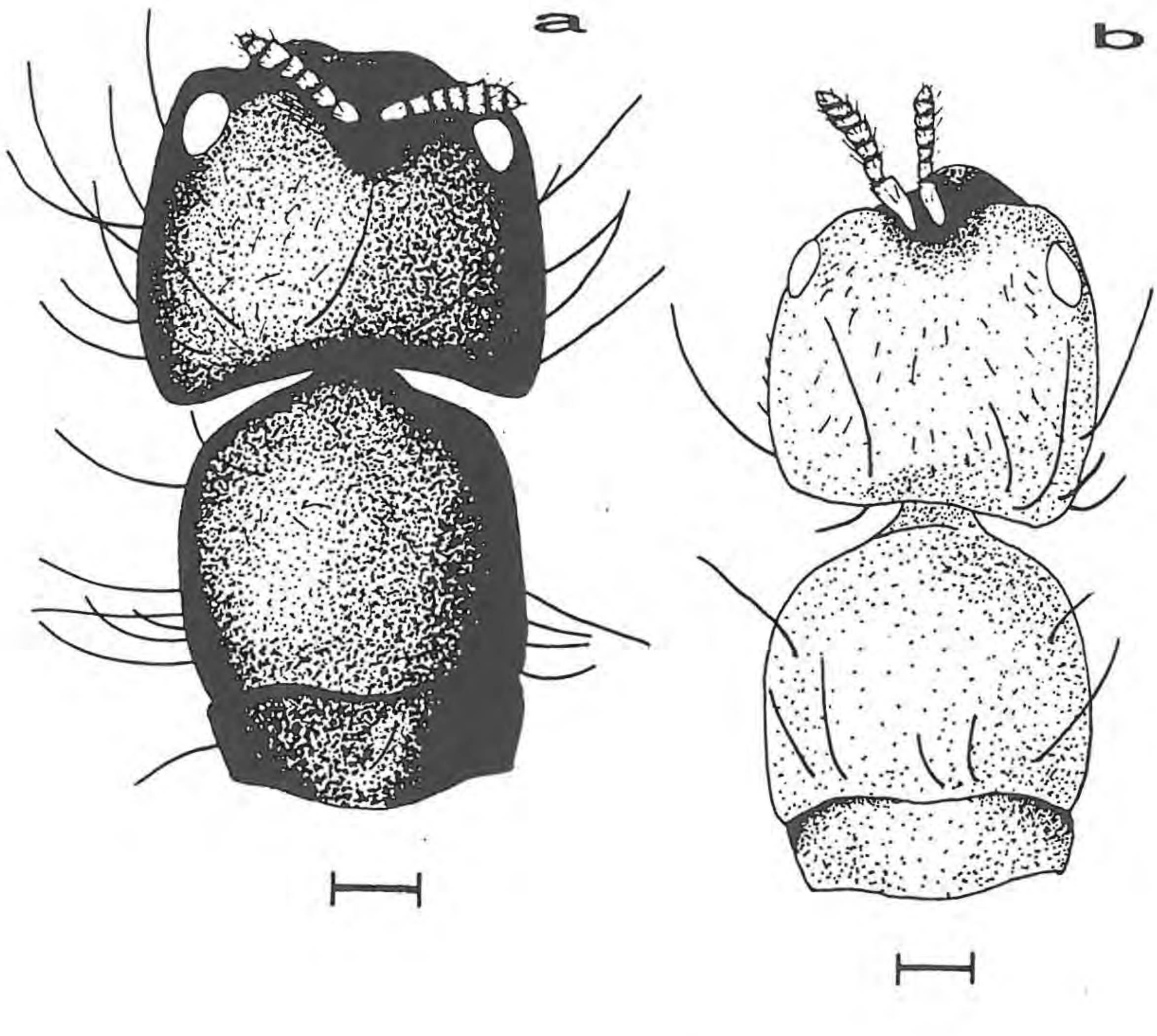
MORPHOLOGICAL CHARACTERS	*Philotrypesis parca*		*Philotrypesis* sp. N	
	$F_{[1, 41]}$	*P*	$F_{[1,42]}$	*P*
MANDIBLE LENGTH	6.86	**	0.008	NS
HEAD WIDTH	10.52	*	0.051	NS
PROTHORAX WIDTH	5.20	*	2.090	NS

NS = not significant, * $P < 0.05$, ** $P < 0.01$

Table 9.6 ANCOVA between large and small males of *Philotrypesis* sp. N for mandible length (mm), head width (mm) and prothorax width (mm) with mass (mg) as the co-variate.

MORPHOLOGICAL CHARACTERS	F- VALUE $_{[1, 42]}$	*P*
MANDIBLE LENGTH	0.696	NS
HEAD WIDTH	10.366	*
PROTHORAX WIDTH	4.24	NS

NS = not significant, * $P < 0.01$



scale bar = 0.10 mm

Figure 9.7 Head and thorax of *Philotrypesis* sp. N a) large, dark male and b) small, light male.

10 MALE DIMORPHISM IN OTITESELLA

10.1 INTRODUCTION

Otitesella larvae develop inside galled ovules, from eggs laid by females from the outside of the figs (Neves, 1987). This genus has been divided into the *Otitesella africana* and *O. digitata* species groups (Wiebes, 1986). These two groups correspond with two different sections of the *Ficus* subgenus *Urostigma*. *Otitesella* of the *africana* group have been described from figs of the African Section *Galoglychia* while members of the *digitata* group have been recorded from Section *Urostigma* in south-east Asia and Africa. Section *Urostigma* is pollinated by agaonids of the genus *Platyscapa* (Wiebes, 1986) while Section *Galoglychia* is pollinated by wasps of several different genera (Wiebes & Compton, 1990). Mainland Africa has over 60 *Ficus* species in Section *Galoglychia* and three species in the Section *Urostigma*, with five included subspecies (Berg, 1990).

A characteristic feature of the *digitata* species group is that the males occur in two discrete wingless forms: the *digitata* and *religiosa* morphs (chapter 2). These are distinguished by the presence or absence respectively of black, swollen terminal tarsal segments on all the legs (Figure 10.1). The morphologies of the males are so distinct that the first recorded member of the group was originally described as two separate species *O. digitata* and *O. religiosa* (Westwood, 1883) (Figure 10.2) and the two were not synonymised for almost one

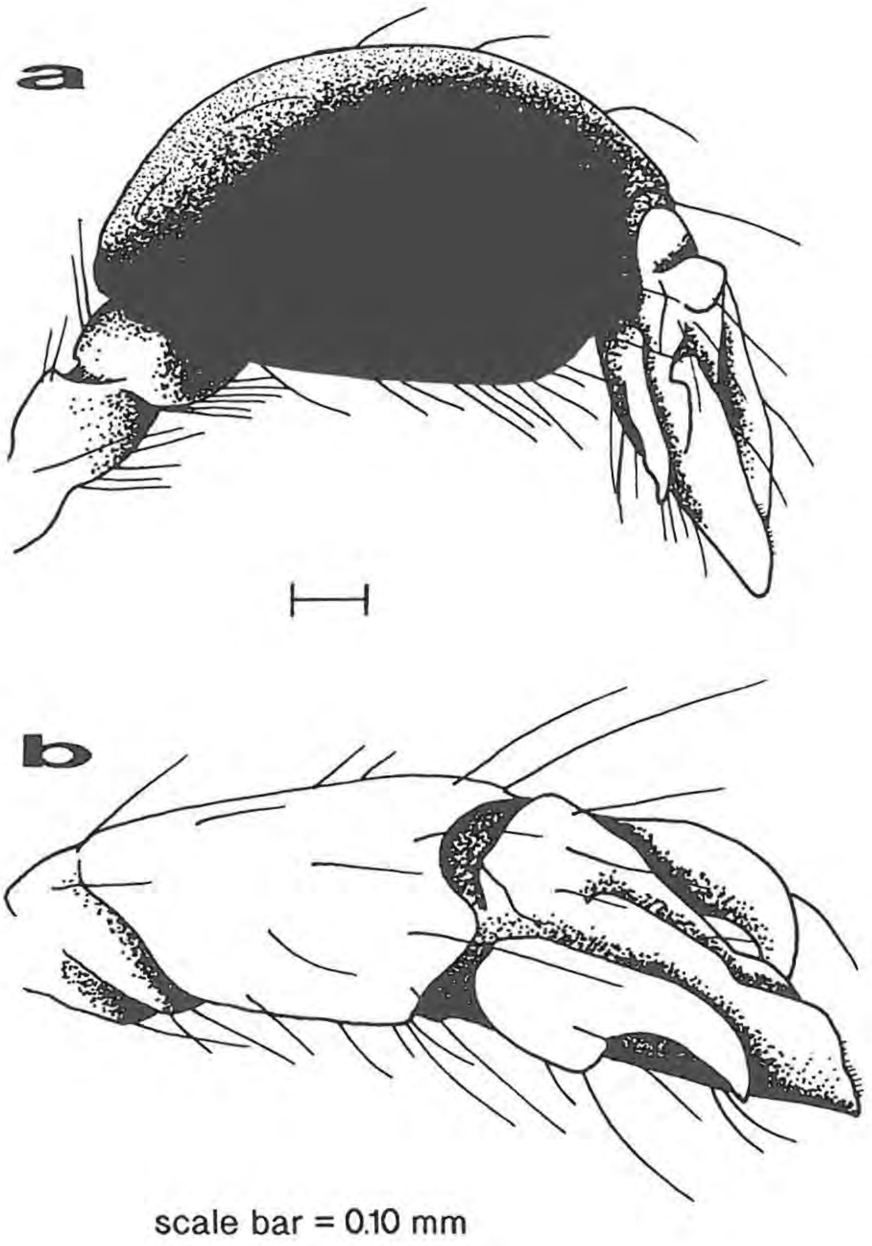


Figure 10.1 The terminal tarsal segments of the middle legs of a) *digitata* and b) *religiosa* morphs of *Otitesella* sp. I.

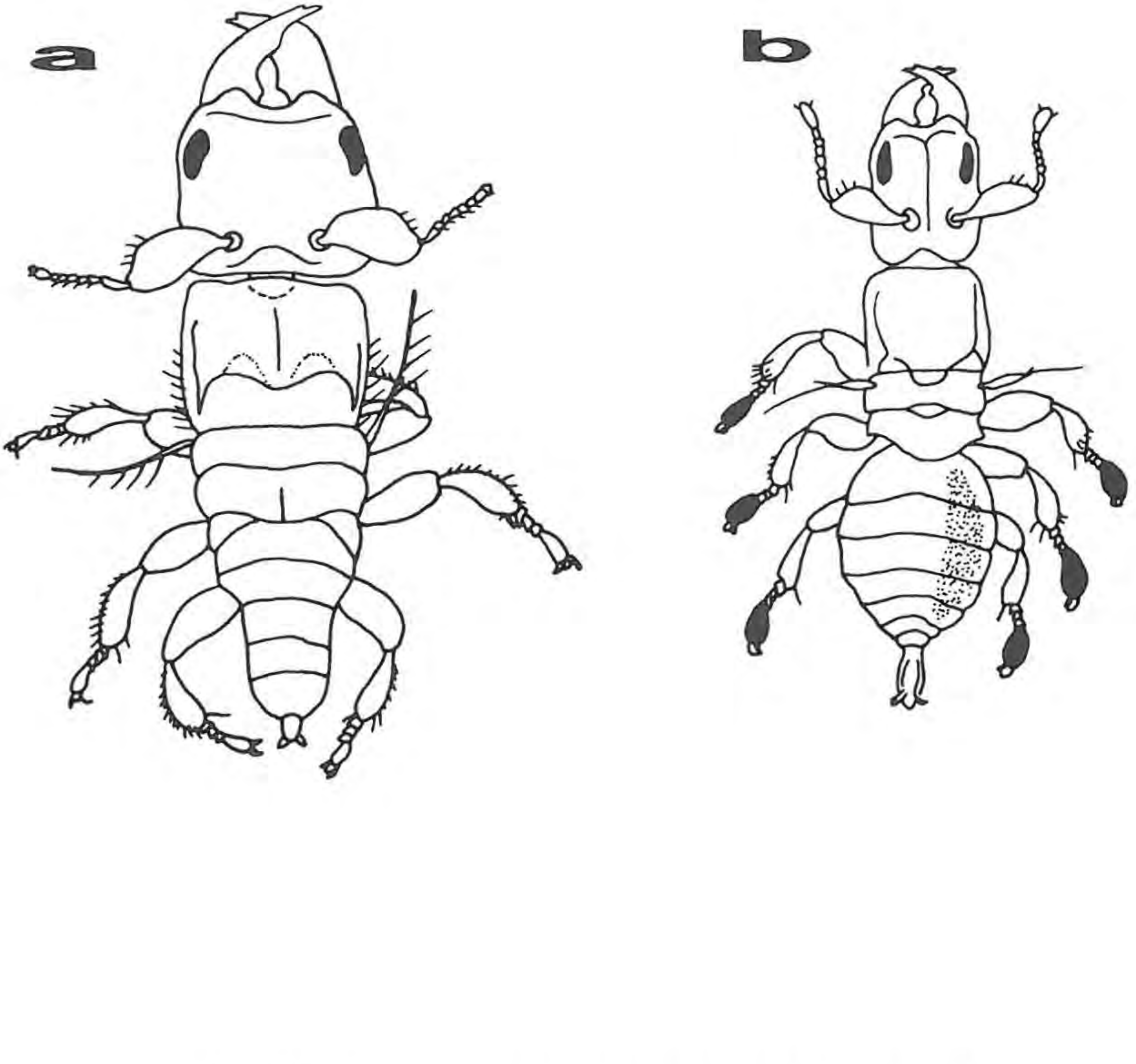


Figure 10.2 The first recorded species of the *Otitesella digitata* group was incorrectly described as two separate species a) *O. digitata* and b) *O. religiosa*. Drawings from Westwood (1883).

hundred years (Wiebes, 1967). The genetic basis, if any, of the dimorphism in *Otitesella* males is unknown.

Here I describe the host relationships of southern African members of the *digitata* and *africana* species groups and provide a detailed morphometric analysis of the differences between the *digitata* and *religiosa* morphs of *Otitesella* sp. I from *F. ingens*.

10.2 MATERIALS AND METHODS

10.2.1 Host relationships and occurrence of *Otitesella* in southern Africa

Fig wasps were obtained from 18 *Ficus* species in southern Africa. Collectors and localities are given in Appendix 3. The presence of *Otitesella* species in the collections was noted, together with whether their males were polymorphic. The species were separated into 'morpho-species' because most are undescribed, but where possible they were compared with species previously described from the same host trees.

10.2.2 Morphometric analyses

Morphometric analyses were carried out on *Otitesella* sp. I reared from *F. ingens* figs collected at Bloukrans, near Grahamstown in the eastern Cape (26° 46' E, 25° 43' S). Measurements of the wasps were taken after they had been killed, dried at 40° C for three days, and weighed on a Cahn C-31 microbalance. For each individual the following features were recorded: coloration, mandible length (in a straight line from the outer base to the tip), head width (across the eyes), pronotum width (across the widest part) and the length and width (across the middle) of the terminal tarsal segment of the middle leg.

10.3 RESULTS

10.3.1 Host relationships of *Otitesella* in southern Africa

Twenty one apparently host-tree specific *Otitesella* species were present in the collections of 15 *Ficus* species from Section *Galoglychia* (Table 10.1). The males of all these species were monomorphic and similar in general appearance to *religiosa* males. Three *Otitesella* species of the *digitata* group were recorded from section *Urostigma*, with both *digitata* and *religiosa* male forms present in most of the larger collections (Table 10.2). The same basic differences between *digitata* and *religiosa* males were present in all three *Otitesella* species (see Figure 10.3 for *Otitesella* sp. I and *O. serrata*). No *Otitesella* species were recorded from *F. cordata* subspecies *cordata*, where the Otitesellinae was represented by a species belonging to an undescribed genus with males that did not display the *digitata* - *religiosa* dimorphism.

10.3.2 Colour differences between male morphs

The *digitata* and *religiosa* males of *Otitesella* sp. I usually had different coloration. *Digitata* males tended to be dark brown and *religiosa* males light brown. This was also the case for *Otitesella* sp. R (Table 10.3). *Digitata* males of *O. serrata* were equally likely to be light brown or dark brown whereas the *religiosa* males were mainly light brown (Table 10.3).

Table 10.1 Host relationships of *Otitesella* species in southern Africa.

FICUS	WASP
Subgenus *Urostigma* section *Urostigma*	
F. cordata cordata	none
F. c. salicifolia	*O. serrata*
F. ingens	*Otitesella* sp. indesc. I
F. verruculosa	*Otitesella* sp. indesc. R
Subgenus *Urostigma* section *Galoglychia*	
Subsection *Galoglychia*	
F. lutea	*Otitesella* sp. indesc. J
	Otitesella sp. indesc. J_2
Subsection *Platyphyllae*	
F. glumosa	*Otitesella* sp. indesc. G
	Otitesella sp. indesc. N
	Otitesella sp. indesc. N_2
F. stuhlmannii	*Otitesella* sp. indesc. S
	Otitesella sp. indesc. S_2
F. tettensis	*Otitesella* sp. indesc. O
F. trichopoda	*Otitesella* sp. indesc. Q
Subsection *Chlamydodorae*	
F. burtt-davyi	*O. sesquianellata*
	O. uluzi
F. craterostoma	*Otitesella* sp. indesc. E
F. fischeri	*Otitesella* sp. indesc. F
F. ilicina	*Otitesella* sp. indesc. H
F. thonningii	*O. tsamvi*
Subsection *Caulocarpae*	
F. bizanae	*Otitesella* sp. indesc. A
F. bubu	*Otitesella* sp. indesc. B
F. polita	*Otitesella* sp. indesc. K
F. sansibarica	*Otitesella* sp. indesc. L
F. tremula	*Otitesella* sp. indesc. P
	Otitesella sp. indesc. P_2

Table 10.2 Collections of *Otitesella* fig wasps of the *digitata* group from southern African fig trees.

FICUS	NUMBER OF COLLECTIONS	NUMBER OF COLLECTIONS WITH *OTITESELLA*	COLLECTIONS WITH		*OTITESELLA*	COUNTRIES
			BOTH MORPHS	ONE MORPH		
F. cordata cordata	18	0	0	0	-	South Africa
F. c. salicifolia	11	11	8	3*	*O. serrata*	South Africa Botswana Zimbabwe
F. ingens	15	15	15	0	*Otitesella* sp. I	South Africa Malawi Zimbabwe
F. verruculosa	4	4	2	2*	*Otitesella* sp. R	South Africa Zambia

* small collections

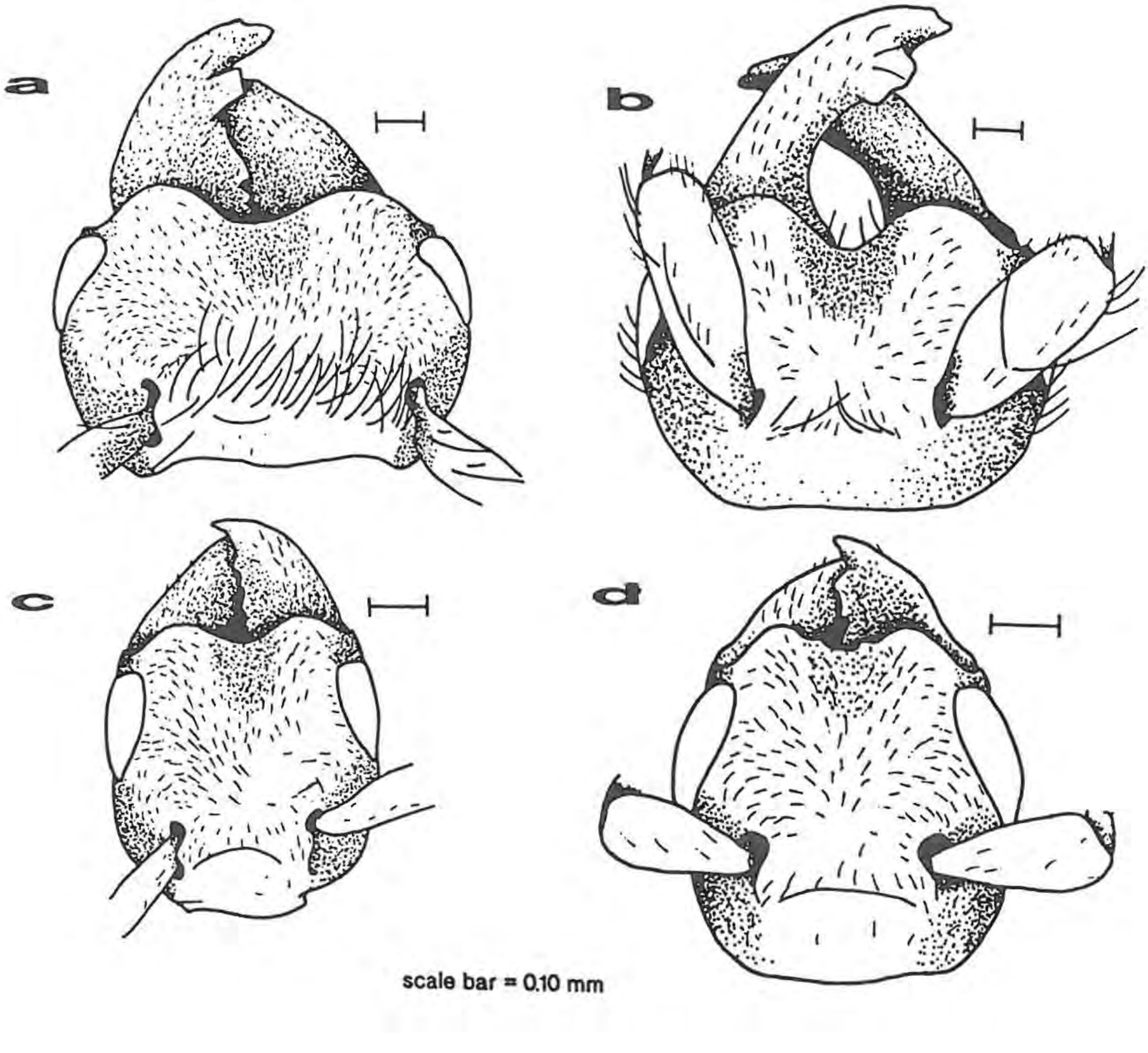


Figure 10.3 Heads of the *religiosa* (a-b) and *digitata* (c-d) males of the *O. serrata* (left) and *Otitesella* sp. I (right).

Some *religiosa* males of *Otitesella* sp. I and most *religiosa* males of *O. serrata* had conspicuous black hind tibiae. In the *religiosa* males of *Otitesella* sp. R the hind tibiae were always concolorous with the rest of the body. Conspicuous dark markings on the hind tibiae were consistently absent in the *digitata* males of all three species.

10.3.3 Morphometric analyses

Measurements of the two morphs of *Otitesella* sp. I are given in Table 10.4 and Figure 10.4. There were significant linear intercorrelations between dry mass, mandible length, head width, prothorax width and the width and length of the hind tarsi in the *digitata* morph (Table 10.5). The same results were obtained for the *religiosa* males except that the tarsal measurements were not significantly correlated with the other morphological characters (Table 10.6).

The *religiosa* males were larger with wider heads, prothoraces and longer mandibles, but had narrower and shorter tarsi than the *digitata* males (Table 10.4). Between-morph comparisons with mass as a covariate are summarised in Table 10.7. The respective bodily proportions of the two morphs was not different. For a given mass, *religiosa* males had larger mandibles and wider heads, but shorter tarsi than *digitata* males (Figure 10.5). The relationships between mass and other morphometric measurements of the two morphs are summarised in Figure 10.5. In *digitata* males the slopes of the

Table 10.3 Numbers of dark and light individuals belonging to the *digitata* and *religiosa* morphs of *Otitesella* sp. I.

OTITESELLA	*DIGITATA*		*RELIGIOSA*		CHI-SQUARE$_{[1]}$	*P*
	LIGHT BROWN	DARK BROWN	LIGHT BROWN	DARK BROWN		
Otitesella sp. I	43	85	92	28	44.61	***
O. serrata	32	30	48	4	22.38	***
Otitesella sp. R	1	27	24	7	32.86	***

*** $P < 0.001$

Table 10.4 Measurements of the morphological characters of the *digitata* (n=18) and the *religiosa* (n=26) morphs.

MORPHOLOGICAL CHARACTER	*DIGITATA*		*RELIGIOSA*	
	MEAN ± SD	RANGE	MEAN ± SD	RANGE
mass (mg)	0.021 ± 0.012	0.007-0.043	0.036 ± 0.018	0.007-0.069
mandible length (mm)	0.186 ± 0.056	0.100-0.267	0.343 ± 0.018	0.151-0.526
head width (mm)	0.385 ± 0.058	0.260-0.482	0.538 ± 0.119	0.343-0.776
prothorax width (mm)	0.403 ± 0.060	0.287-0.479	0.586 ± 0.161	0.377-0.991
mid tarsal length (mm)	0.069 ± 0.010	0.055-0.083	0.045 ± 0.010	0.029-0.072
mid tarsal width (mm)	0.126 ± 0.021	0.086-0.158	0.078 ± 0.023	0.041-0.146

Table 10.5 Correlation coefficients between morphological characters in the *digitata* morph of *Otitesella* sp. I (n = 18).

MORPHOLOGICAL CHARACTERS	MANDIBLE LENGTH		HEAD WIDTH		PROTHORAX WIDTH		TARSAL WIDTH		TARSAL LENGTH	
	r	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*
mass	0.704	***	0.828	***	0.799	***	0.518	*	0.762	***
mandible length	-		0.830	***	0.839	***	0.542	*	0.673	**
head width	-		-		0.886	***	0.714	***	0.830	***
prothorax width	-		-		-		0.606	**	0.764	***
mid tarsal width	-		-		-		-		0.828	***

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Table 10.6 Correlation coefficients between morphological characters in the *religiosa* morph of the *Otitesella* sp. I (n = 26).

MORPHOLOGICAL CHARACTERS	MANDIBLE LENGTH	HEAD WIDTH	PROTHORAX WIDTH	TARSAL WIDTH	TARSAL LENGTH
mass	0.950 ***	0.951 ***	0.807 ***	0.023 NS	-0.078 NS
mandible length	-	0.922 ***	0.763 ***	0.053 NS	-0.005 NS
head width	-	-	0.788 ***	0.139 NS	0.119 NS
prothorax width	-	-	-	-0.060 NS	-0.002 NS
mid tarsal width	-	-	-	-	0.773 ***

NS = not significant, *** $P < 0.001$

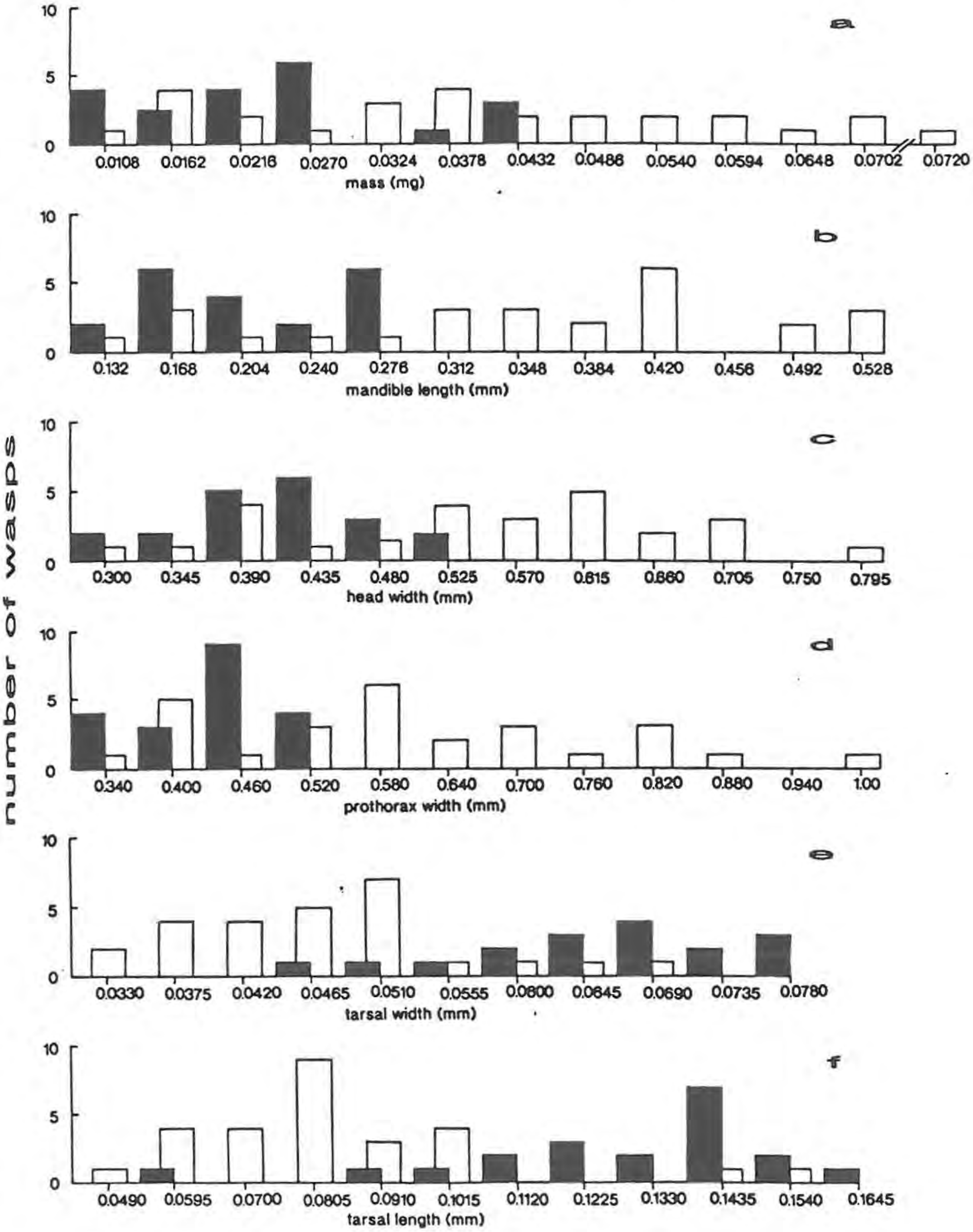


Figure 10.4 Frequency distributions for morphological characters in *digitata* (solid bars) and *religiosa* males (open bars) males of *Otitesella* sp. I; a) mass, b) mandible length, c) head width, d) prothorax width, e) tarsal length and f) tarsal width (middle leg).

tarsal measurements are much steeper than in *religiosa* males. The disproportionate increase in tarsal size of the *digitata* males is also illustrated in Figure 10.6.

10.4 DISCUSSION

This work confirms previous observations that the *digitata* morph is restricted to *Otitesella* species from *Ficus* section *Urostigma* and absent from *Otitesella* species associated with section *Galoglychia*. Three host specific *Otitesella* species with dimorphic males were present in the collections from *F. c. salicifolia*, *F. verruculosa* and *F. ingens*. No *Otitesella* species were collected from *F. c. cordata*, which may merit consideration as a distinct species from *F. c. salicifolia*, because these two trees also have different pollinating fig wasps (Agaoninae) (Wiebes & Compton, 1990).

In addition to tarsal structure the two *Otitesella* morphs could often be distinguished by their coloration: *religiosa* males tended to be light brown and *digitata* males generally dark brown. There was also inter- and intra-specific colour variation between *religiosa* males. Some *religiosa* males of *Otitesella* sp. I and *O. serrata* had prominent black markings on their hind tibiae while others of the same species did not. Superficially similar black markings occur on the legs of males of some Pteromalidae for example *Pegopus inornatus* Walker, *Spaniopus dissimilis* and *Mesopolobus* species (Graham, 1969). The function, if any, of the hind tibial markings in the *religiosa* males is unknown.

Table 10.7 ANCOVA for mandible length, head width, prothorax width, mid tarsal width and tarsal length with mass as a covariate between the *digitata* (n=18) and *religiosa* (n=26) morphs of *Otitesella* sp. I.

SOURCE OF VARIATION	F VALUE	*P*
MANDIBLE LENGTH	$F_{[1, 39]} = 9.39$	**
HEAD WIDTH	$F_{[1, 39]} = 6.55$	*
PROTHORAX WIDTH	$F_{[1, 39]} = 3.38$	NS
TARSAL WIDTH	$F_{[1, 39]} = 1.95$	NS
TARSAL LENGTH	$F_{[1, 39]} = 9.87$	**

NS = not significant, * $P < 0.05$, ** $P < 0.01$

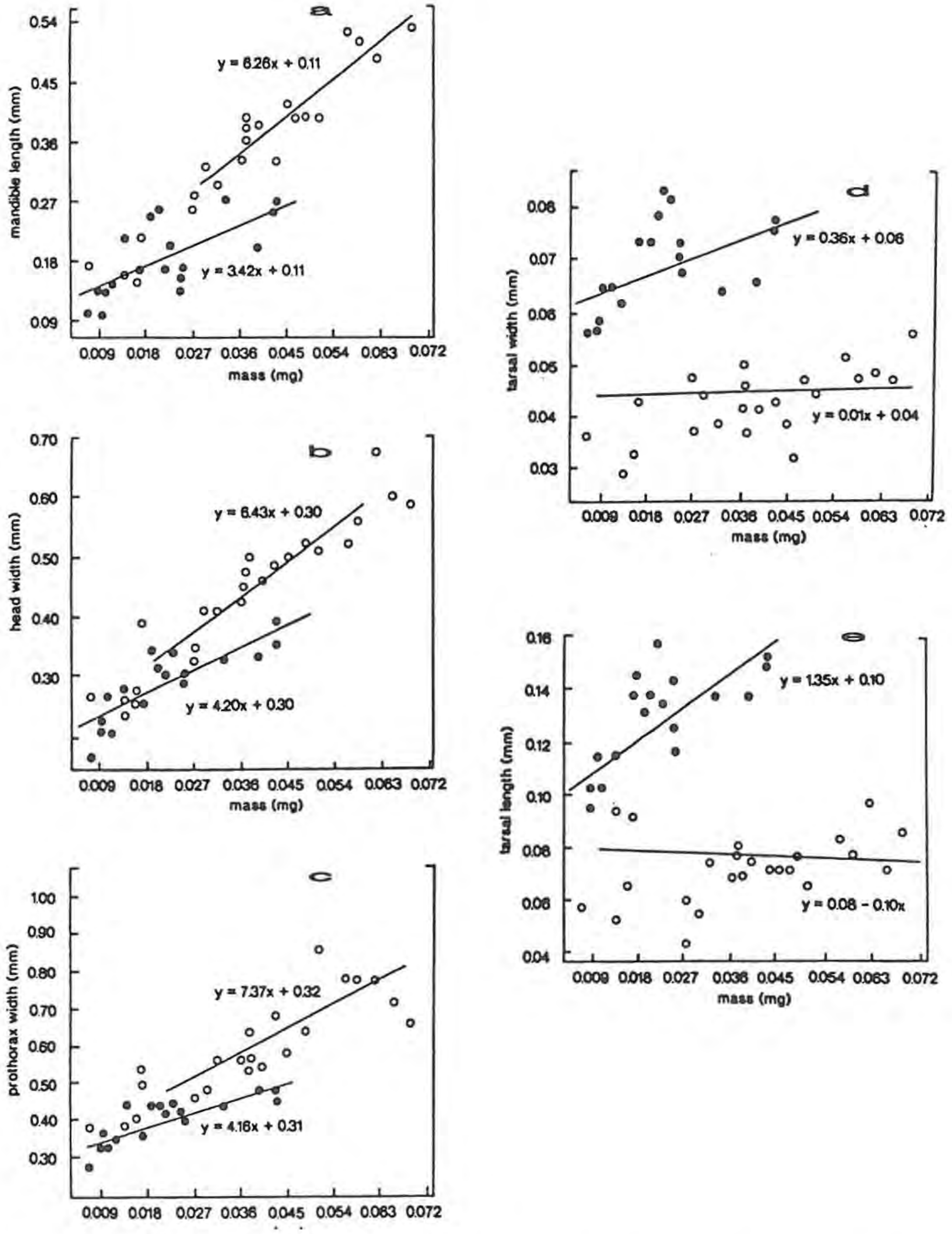


Figure 10.5 Mass versus other morphological characters; a) mandible length, b) head width, c) prothorax width, d) tarsal length and e) tarsal width of middle leg. Solid circles represent *digitata* males and open circles *religiosa* males, insets 1, *digitata* and 2, *religiosa* male for *Otitesella* sp. I of *Otitesella* sp. I.

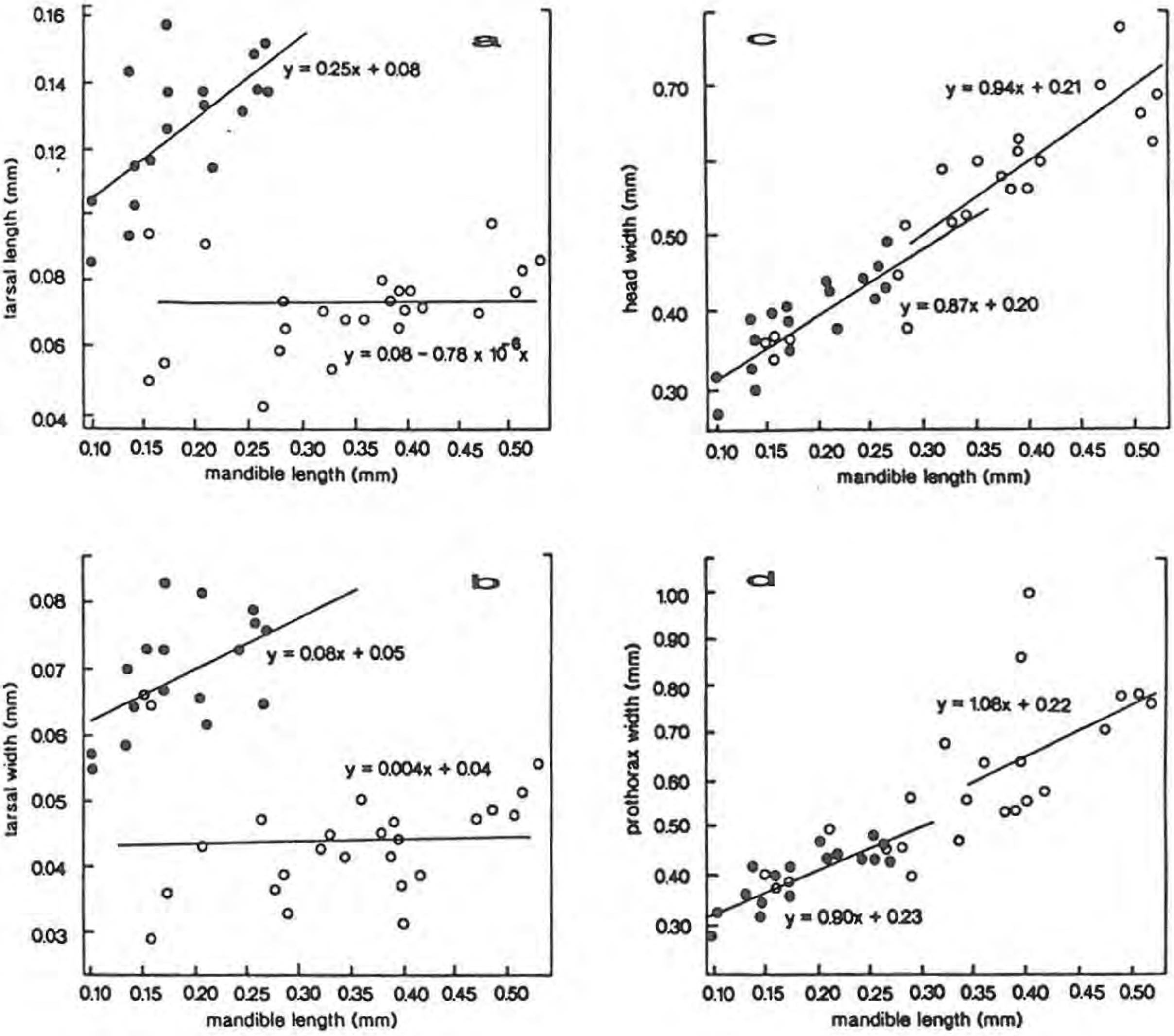


Figure 10.6 Mandible length versus morphological characters; a) mass, b) head width, c) prothorax width, d) tarsal length and e) tarsal width of middle leg; solid circles represent *digitata* males and open circles represent *religiosa* males.

For any given mass *religiosa* males had larger mandibles, wider heads and smaller tarsi than *digitata* males. The relative proportions of mass and tarsal length were also different between the two morphs with *digitata* males, although smaller than *religiosa* males, having relatively larger tarsi. Larger body size and relatively larger mandible size in the *religiosa* male may be linked to its more aggressive behaviour and therefore greater likelihood of being involved in fights, where large size is probably advantageous. This possibility is assessed in the following chapter. The possible functional significance of enlarged *digitata* tarsi during courtship behaviour is examined in chapter 12.

11 BEHAVIOURIAL COMPARISONS BETWEEN THE DIGITATA AND RELIGIOSA MORPHS OF OTITESELLA

11.1 INTRODUCTION

Although each animal species exhibits a characteristic reproductive behaviour, this may be flexible within the constraints imposed by its mating system (Dunbar, 1983). Often this flexibility in behaviour is associated with reducing intraspecific competition for mates (Cade, 1979). These 'alternative reproductive behaviours' (Austad, 1984; Dominey, 1984) are defined as any discontinuous variation in an aspect of reproductive behaviour amongst one sex in a single population. There are typically associated differences in the costs and benefits of the behaviours. Such alternative reproductive behaviours may be practised opportunistically by individuals in appropriate situations or sequentially at different times during the development of an individual, or animals may have fixed strategies, which differ between individuals (Caro & Bateson, 1986; Dominey, 1984).

There is a tremendous diversity of alternative mating behaviours (Waltz & Wolf, 1984). In the bee *Centris pallida* Fox large males search around emergence sites and dig up virgin females, while small males hover by trees waiting for the arrival of airborne females (Alcock, 1979a, 1979b; Alcock *et al*, 1976, 1977, 1978). A similar pattern is exhibited by midges (Chironomidae and Chaoboridae): small males remain in the vegetation and mate with resting females rather than entering the mating swarms formed by the larger males (McLachlan, 1986; McLachlan & Neems, 1989). Another version on the same theme is found in a non-territorial damselfly *Enallagma hageni* (Coenagrionidae) where males either search the river banks for unmated females or wait at oviposition sites for any females that resurface from their underwater oviposition sites (Fincke, 1985).

Some males are 'sneaks' and while the dominant male/owner of a territory is busy defending it from other males they sneak in to mate with any females that are present. This occurs in the ruff, a wading bird, where males with dark ruffs defend leks to which females come to mate, whereas males with pale-coloured ruffs, called 'satellites', opportunistically sneak mating opportunities (van Rhijn, 1973). There are numerous other examples where small males gain access, by sneaking, to females which are fought over by larger males. These include some parasitic wasps (King *et al*, 1969), beetles (Eberhard, 1979, 1980, 1982), salmon (Gross, 1985), and swordtail fish (Ryan & Causey, 1989). A similar phenomenon is where silent 'parasitic' males of various species attempt to intercept and mate with females attracted by the calls of larger, and often older territorial males. Some toads (Howard, 1978, 1981, 1984), frogs (Perrill *et al*, 1978) and field crickets exhibit this kind of behaviour (Cade, 1979, 1980). In bladder grasshoppers (Pneumoridae) nocturnal, winged 'primary' males fight with each other, but exhibit no aggression whatsoever towards flightless, non-calling 'alternative' males that mate during the day (Alexander & Van Staaden, 1989).

Males can also mimic females in order to obtain mates, a phenomenon appropriately termed transvestism. Bluegill sunfish occupy nesting territories in densely packed colonies. Males compete aggressively for position in these colonies and their ability to maintain residency is related to body size. Males that mimic females are smaller than nesting males and succeed in spawning between nesting males and females (Dominey, 1980). Male scorpion flies provide females with prey during copulation, but some males mimic female behaviour in order to obtain prey which they can then offer to genuine females (Thornhill, 1979, Thornhill & Alcock, 1983).

In the previous chapter I have described the morphological differences between the *digitata* and *religiosa* morphs of *Otitesella* sp. I. Here I examine differences in the emergence and fighting behaviour of the two morphs and discuss these differences in terms of alternative reproductive behaviours. The relative abundance of the two morphs is also examined and the possible adaptive significance of morph ratios is tested by relating them to the local abundance of the wasps.

11.2 MATERIALS AND METHODS

Males and females of *Otitesella* sp. I were reared from mature figs of *Ficus ingens* growing at Bloukrans and Hellspoort, in the eastern Cape near Grahamstown. Collection dates and sample sizes are given in Table 11.1.

11.2.1 Morph ratios

To see whether morph ratios were fixed or related to wasp densities I collected mature figs without exit holes from eight trees, placed them individually in netting-covered vials, waited for the fig wasps to emerge, then killed them for subsequent counting.

11.2.2 Emergence from the figs and damage due to fighting

A subsample of ripe figs without exit holes were collected from five different trees. The figs were then placed individually in netting-covered vials and left undisturbed for four days to allow the wasps to emerge. The numbers of *religiosa* and *digitata* males that had emerged from the figs were then compared with those which had remained in the fig lumen. Each male was also examined for evidence of physical damage, which may have been caused by fighting.

When male *Otitesella* emerge from the figs this might be due to an attraction resulting from light permeating through the exit hole created by the male pollinating wasps. The responses of the two morphs to light were therefore tested. Groups of usually three *digitata* or *religiosa* males were placed midway along a horizontal glass tube 19.5 cm long, with a diameter of 1 cm. An irregular light gradient was created by inserting one half of the tube into a black box and shining a 'cold' light from a fibre optic illumination system on the other half. After one hour the position of each male was recorded using 2 cm wide zones delimited along the length of the tube.

11.2.3 Longevity outside the figs

To compare the longevity of the *digitata* and *religiosa* morphs once they had vacated the figs I placed newly wasps that had recently emerged from their galls individually in glass vials. These were kept at a constant humidity (23%) and temperature (24° C). Mortalities were recorded at 12 hourly intervals.

11.3 RESULTS

11.3.1 Morph ratios and sex ratios in relation to population density

Collections of *F. ingens* used in this study are given in Table 11.1. Wasp densities (occupied figs only) and sex ratios are given in Table 11.2. The wasp densities (males and females combined) were significantly variable between crops (ANOVA $F_{[7, 112]} = 3.73$, $P = < 0.001$) with means ranging from 16 to 39 wasps per fig. Sex ratios also differed significantly from tree to tree ($X^2_{[7]} = 94.95$, $P < 0.001$) (Table 11.3), but averaged 45.94% females. Sex ratios were not significantly negatively correlated with population density (although see chapter 6) (Figure 11.1).

Overall, 22.75% of the males belonged to the *digitata* morph (Table 11.4). Although the morph ratios differed significantly from tree to tree ($X^2_{[7]} = 38.05$, $P < 0.001$), the *digitata* males were outnumbered in all 8 collections.

The densities of the *digitata* and *religiosa* males in the figs were

Table 11.1 Collections of *F. ingens* figs and the numbers used in various studies of the *religiosa* and *digitata* dimorphism.

TREE	SAMPLING DATE	LOCALITY	N FIGS	N FIGS UTILISED FOR VARIOUS STUDIES			
				EMERGENCE BEHAVIOUR	DAMAGE LEVELS	MORPH RATIOS	LONGEVITY
1	JANUARY 1990	BLOUKRANS	36	-	-	36	20
2	NOVEMBER 1989	HELLSPOORT	4	4	4	4	-
3	JANUARY 1990	BLOUKRANS	21	-	-	21	-
4	JANUARY 1990	BLOUKRANS	26	-	-	26	-
5	NOVEMBER 1989	BLOUKRANS	5	5	5	5	-
6	NOVEMBER 1989	BLOUKRANS	6	6	6	6	-
7	OCTOBER 1989	BLOUKRANS	10	10	10	10	-
8	NOVEMBER 1989	BLOUKRANS	5	5	5	5	-

Table 11.2 *Otitesella* sp. I in collections from eight *F. ingens* trees.

TREE	N FIGS	FEMALE		*DIGITATA* MALE		*RELIGIOSA* MALE		TOTAL *OTITESELLA*		SEX RATIO (♂/♀)
		MEAN ± SD	RANGE	MEAN ± SD	RANGE	MEAN ± SD	RANGE	MEAN ± SD	RANGE	MEAN
1	36	18.25 ± 9.08	6-41	3.44 ± 2.89	0-11	13.30 ± 8.53	3-36	35.00 ± 17.06	9-79	0.46
2	4	10.50 ± 4.43	6-16	2.75 ± 2.50	0-6	15.75 ± 4.65	11-22	29.00 ± 3.37	25-33	0.63
3	21	8.52 ± 4.84	2-21	3.42 ± 3.75	0-17	7.61 ± 4.63	1-18	19.57 ± 9.52	4-34	0.56
4	26	8.65 ± 6.20	0-20	3.65 ± 3.62	0-14	14.30 ± 9.90	1-33	26.62 ± 17.09	1-62	0.67
5	5	4.80 ± 5.47	0-11	4.60 ± 4.22	2-12	6.20 ± 5.07	0-11	15.60 ± 12.11	2-34	0.75
6	6	8.50 ± 5.47	3-16	2.33 ± 2.50	0-7	11.17 ± 8.75	2-24	22.00 ± 16.49	6-47	0.57
7	10	25.10 ± 12.30	5-42	4.00 ± 3.59	0-10	10.00 ± 8.43	0-25	39.10 ± 17.81	6-66	0.34
8	5	4.00 ± 2.24	1-7	2.20 ± 2.39	0-6	10.40 ± 6.19	4-18	16.60 ± 5.27	11-24	0.74

Table 11.3 Comparisons of the numbers of males and females from the various collections. Chi-squares are testing for equality of sex ratios.

TREE	TOTAL NUMBER OF MALES	TOTAL NUMBER OF FEMALES	CHI-SQUARE$_{[1]}$	*P*
1	594	657	1.58	NS
2	74	42	4.49	*
3	232	179	4.56	*
4	467	225	57.19	***
5	54	24	5.99	*
6	81	51	3.45	NS
7	140	251	16.09	***
8	63	20	12.00	***
TOTAL	1705	1449	10.40	***

NS = not significant, * $P < 0.05$, *** $P < 0.001$

Table 11.4 Comparisons between the total number of *digitata* and *religiosa* males in each of the collections. Chi-squares are testing for equality of morph ratios.

TREE	*DIGITATA*	*RELIGIOSA*	CHI-SQUARE$_{[1]}$	*P*
1	124	479	114.88	***
2	11	63	20.84	***
3	72	160	17.31	***
4	95	372	90.15	***
5	23	31	0.59	NS
6	20	67	31.47	***
7	40	100	13.47	***
8	5	52	24.47	***
TOTAL	390	1324	274.89	***

NS = not significant, *** $P < 0.001$

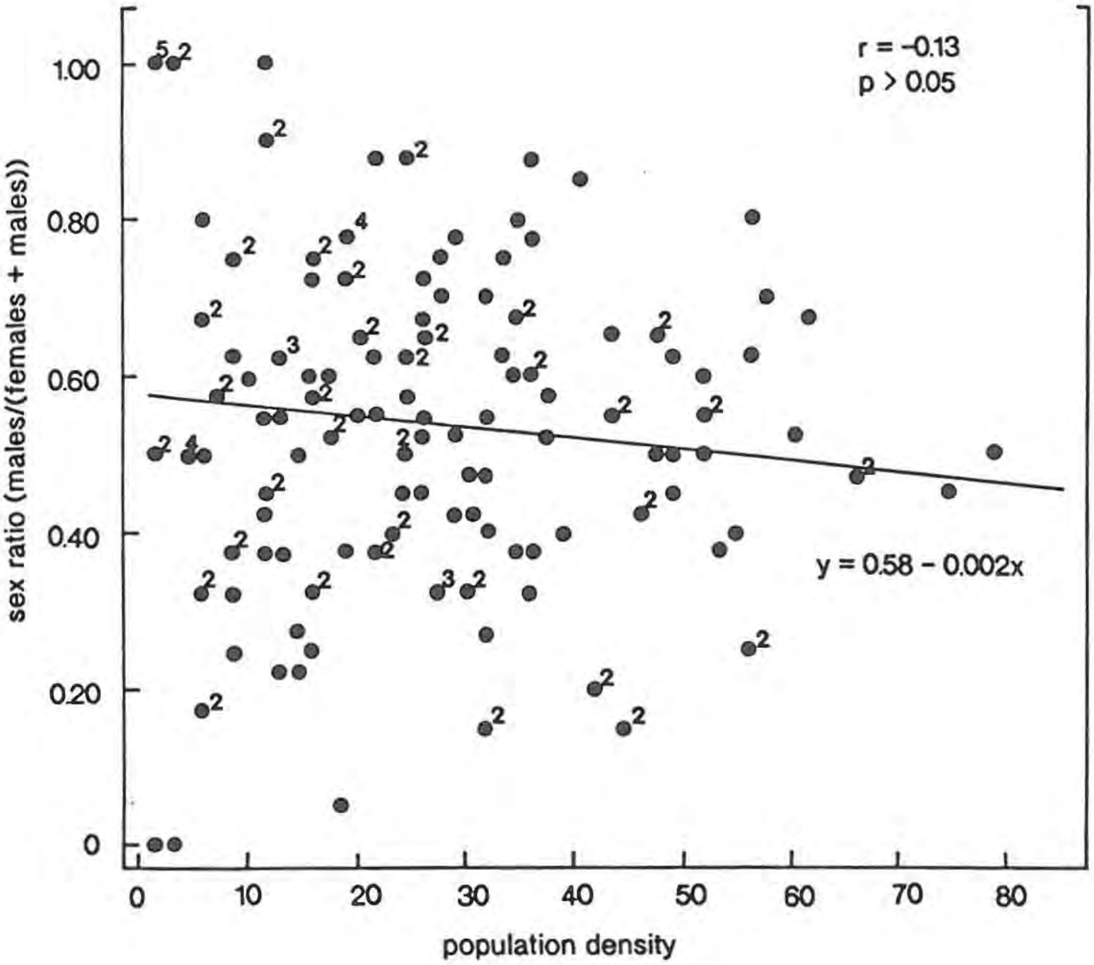


Figure 11.1 The correlation between the sex ratio and wasp density in *Otitesella* sp. I.

positively correlated (Figure 11.2), but the proportion of *digitata* males decreased with increasing wasp density (Figure 11.3).

11.3.2 Emergence behaviour

The numbers of *digitata* and *religiosa* males that either remained inside the figs or emerged from them are summarised in Table 11.5. 84.61% of the 91 *digitata* males emerged from the figs, whereas only 4.40% of the 297 *religiosa* males did so. In all five trees a significantly higher proportion of *digitata* males emerged (Table 11.6). The difference between the emergence behaviour of the two morphs is highlighted by the observation that all the *digitata* males emerged from 16 of the 25 figs where they were present, whereas no *religiosa* males at all emerged from 23 of the 28 figs they occupied. Within morphs, the proportion of males emerging varied significantly between trees in the case of *religiosa* males ($X^2_{[4]} = 155.37$, $P < 0.001$), but not in the *digitata* males ($X^2_{[4]} = 5.33$, $P > 0.05$).

The different emergence patterns of the *digitata* (n = 22) and *religiosa* (n = 43) males may be related to their contrasting responses to light. The frequency distributions along a light gradient of the two morphs were significantly different ($X^2_{[9]} = 70.68$, $P < 0.001$, Figure 11.4). *Digitata* males were strongly attracted to the light half of the tube, whereas the *religiosa* males showed no preference.

11.3.3 Damage in males

13.19% of the 91 *digitata* males showed signs of damage, compared

Table 11.5 *Digitata* and *religiosa* males that emerged or stayed inside the figs.

CROP	N FIGS	*DIGITATA*			*RELIGIOSA*		
		INDIVIDUALS	MEAN ± SD	RANGE	INDIVIDUALS	MEAN ± SD	RANGE
INSIDE FIGS							
1	10	10	1.00 ± 1.24	0-3	95	9.50 ± 8.97	0-25
2	5	1	0.20 ± 0.45	0-1	52	10.40 ± 4.72	4-17
3	4	0	0	0	42	10.50 ± 7.77	5-22
4	5	0	0	0	31	6.20 ± 5.07	0-11
5	6	3	0.50 ± 0.55	0-1	64	10.67 ± 8.17	2-23
TOTAL	30	14	0.47		284	9.47	
OUTSIDE FIGS							
1	10	28	2.80 ± 2.70	0-7	5	0.50 ± 1.58	0-5
2	5	10	2.00 ± 2.55	0-6	5	1.00 ± 1.22	0-3
3	4	4	1.00 ± 1.15	0-2	2	0.50 ± 1.00	0-2
4	5	23	4.60 ± 4.00	2-12	0	0	0
5	6	12	2.00 ± 2.28	0-6	1	0.17 ± 0.41	0-1
TOTAL	30	77	2.57		13	0.43	

Table 11.6 A comparison of the emergence behaviour of *digitata* and *religiosa* males.

CROP	FIG	*DIGITATA*		*RELIGIOSA*		CHI-SQUARE$_{[1]}$	*P*
		INSIDE	OUTSIDE	INSIDE	OUTSIDE		
1	1	0	2	6	0	8.00	**
	2	0	3	10	0	14.00	***
	3	0	1	6	0	7.00	**
	4	3	7	23	0	20.43	***
	5	1	0	0	0	-	-
	6	1	0	25	0	0	NS
	7	0	6	3	0	9.00	**
	8	0	0	0	5	6.00	*
	9	2	3	16	0	9.98	*
	10	3	6	6	0	5.76	*
TOTAL		10	28	95	5	71.40	***
HETEROGENEITY$_{[9]}$						8.77	NS
2	1	1	0	12	1	0.09	NS
	2	0	1	9	0	10.00	**
	3	0	0	10	3	0.29	NS
	4	0	6	4	0	10.00	**
	5	0	3	17	1	14.87	***
TOTAL		1	10	52	5	37.40	***
HETEROGENEITY$_{[4]}$						2.15	NS
3	1	0	0	8	2	0.12	NS
	2	0	2	22	0	24.00	***
	3	0	2	7	0	9.00	**
	4	0	0	5	0	-	-
TOTAL		0	4	42	2	30.55	***
HETEROGENEITY$_{[3]}$						2.57	NS
4	1	0	4	2	0	6.00	*
	2	0	12	11	0	23.00	***
	3	0	3	11	0	14.00	***
	4	0	2	7	0	13.00	***
	5	0	2	0	0	-	-
TOTAL		0	23	31	0	54.00	***
HETEROGENEITY$_{[4]}$						2.00	NS
5	1	1	2	13	0	9.90	**
	2	0	1	3	0	4.00	*
	3	1	6	23	1	18.99	***
	4	0	3	16	0	19.00	***
	5	1	0	7	0	0	NS
	6	0	0	2	0	-	-
TOTAL		3	12	64	1	55.13	***
HETEROGENEITY$_{[5]}$						3.24	NS
TOTAL		14	77	284	13	251.73	***
HETEROGENEITY$_{[4]}$ (BETWEEN TREES)						3.25	*

NS = not significant, $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

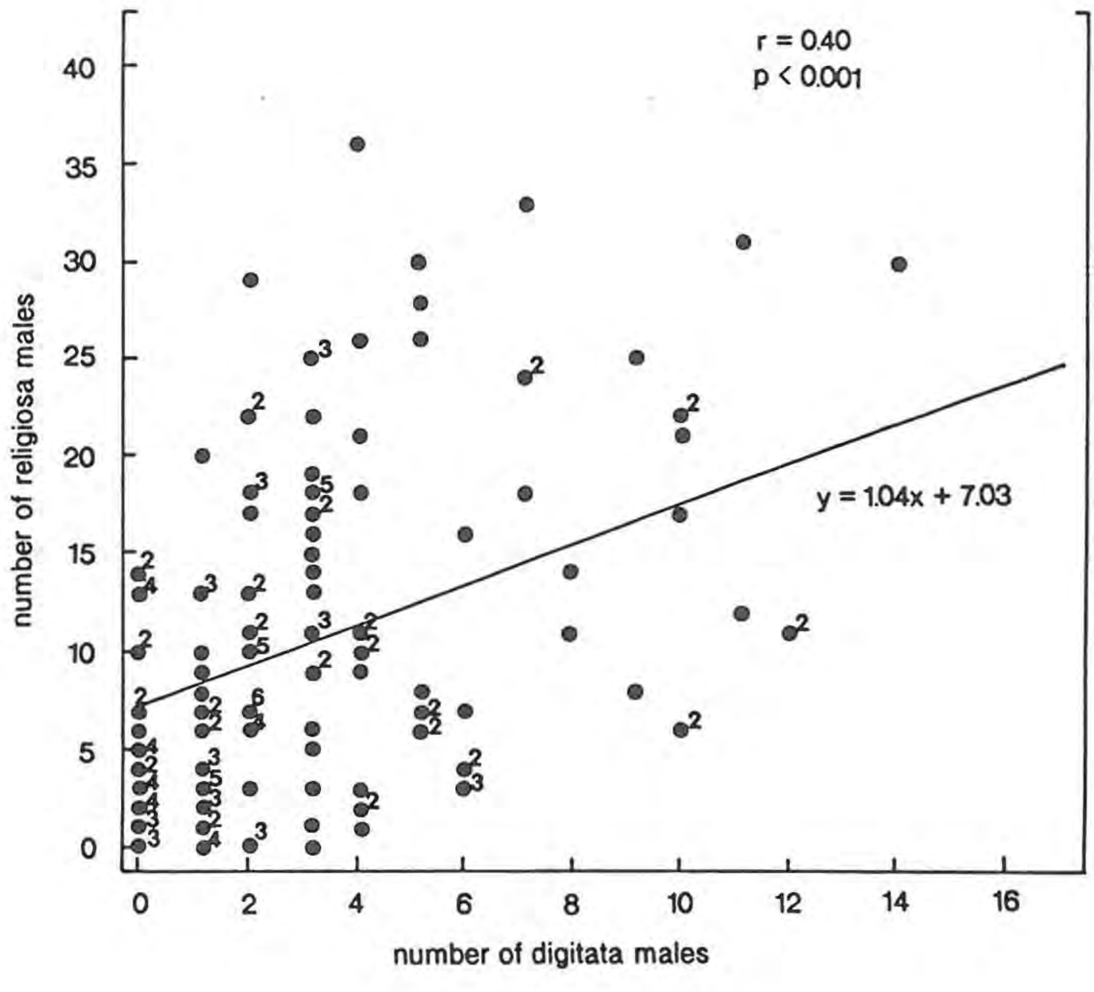


Figure 11.2 The correlation between the numbers of *digitata* males and *religiosa* males of *Otitesella* sp. I.

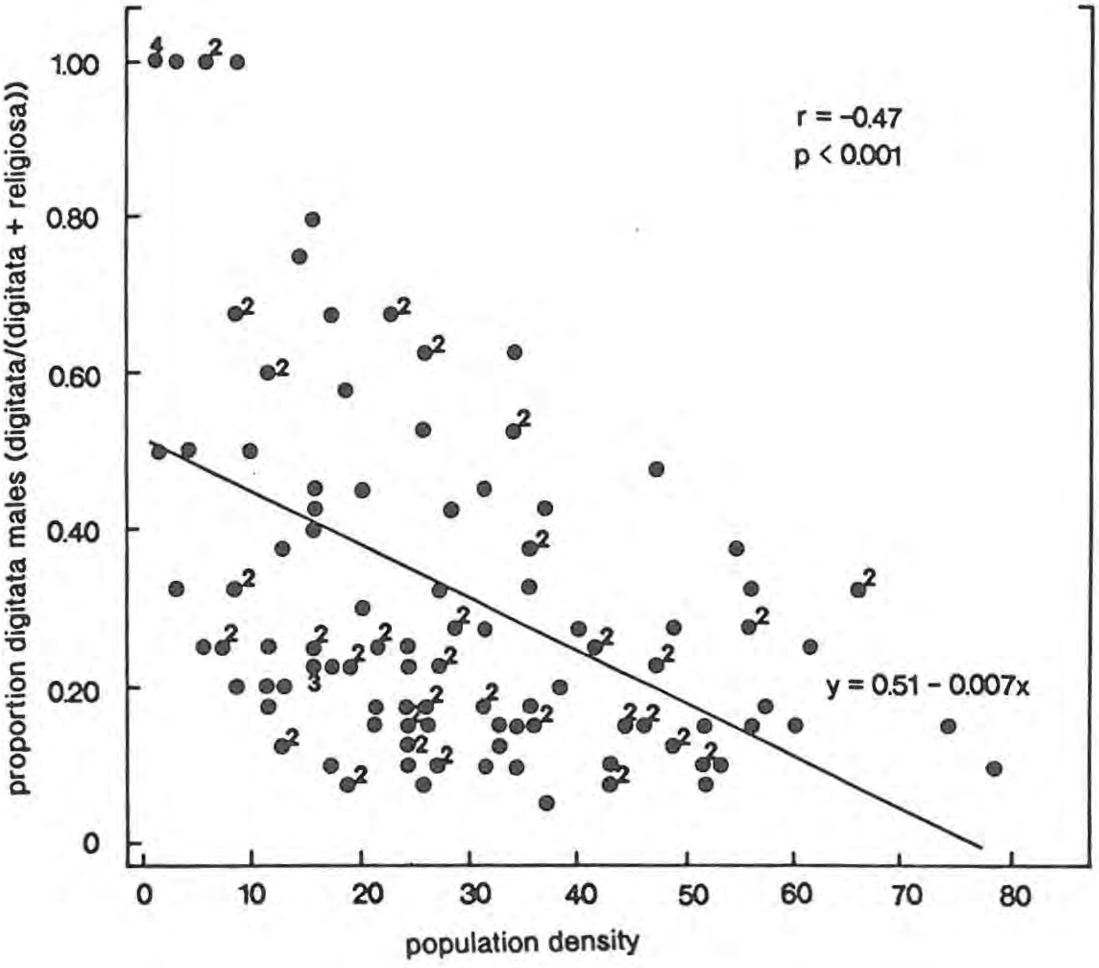


Figure 11.3 The correlation between the proportion of *digitata* males and the population density of *Otitesella* sp. I.

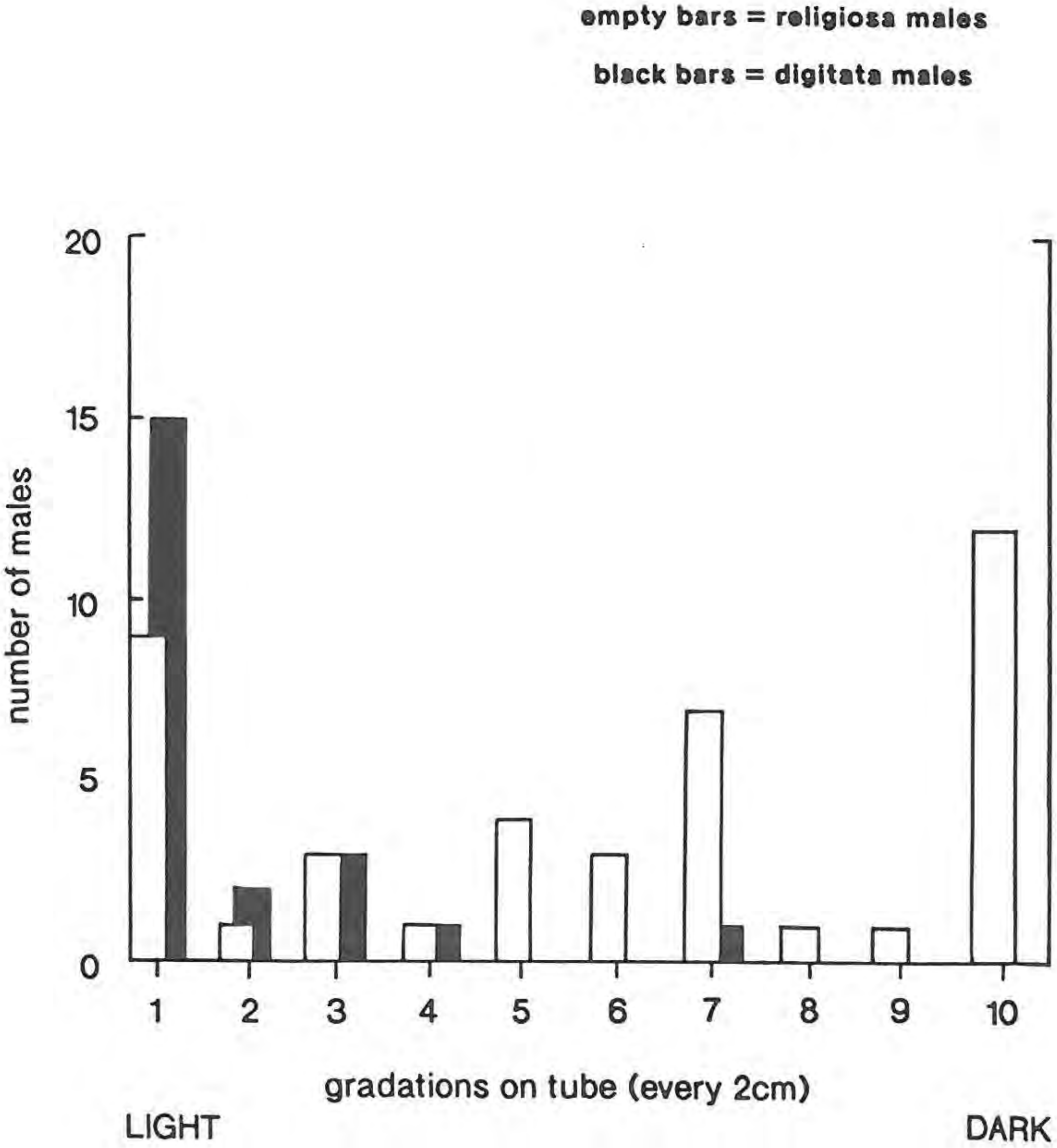


Figure 11.4 The distribution of *digitata* (black bars) and *religiosa* (open bars) males along a light gradient.

with 68.35% of the 297 *religiosa* males. The types of damage sustained by the *digitata* males were typically minor such as the loss of antennal segments, whereas the damage to *religiosa* morphs tended to be more substantial (Table 11.7). The damage included punctured abdomens and severed appendages. Moreover, the *religiosa* males were more likely to have multiple damage - typically excised antennae and legs, whereas the few damaged *digitata* males generally had only one kind of damage (*religiosa* males single: multiple damage, 53:150, *digitata* 9:3, $X^2_{[1]} = 15.69$, $P < 0.001$).

The numbers of damaged and intact *digitata* and *religiosa* males are compared in Table 11.8 and Table 11.9. There were differences in the proportion of males of the two morphs that were damaged, with the proportion of *digitata* males that were injured being significantly less than that for *religiosa* males. Although more of the *religiosa* males had been damaged in all five collections, the relative damaged sustained was not consistent from fig to fig or crop to crop (Table 11.9). The greater damage levels among *religiosa* males could have resulted from more of them staying inside the figs. However, more *religiosa* males were damaged both among those that had emerged from the figs and among those that stayed (Table 11.10). Wasp that remained inside the figs were nonetheless more likely to sustain damage (Table 11.10). This is most likely due to the differences in their fighting behaviour. *Digitata* males will fight with each other, but were not seen to injure or kill opponents in fights. Altercations between these males were of short duration. *Religiosa* males on the otherhand engaged in intense fights

Table 11.7 The types of damage sustained by *digitata* and *religiosa* males of *Otitesella* sp. I. The types of damage are ranked in order of increasing severity. * indicates multiple damage.

TYPE OF DAMAGE	NUMBERS OF DAMAGED MALES	
	DIGITATA	*RELIGIOSA*
Intact	79	94
Segments of one antenna severed	1	41
Antenna removed	6	1
Both antennae with segments severed *	0	2
Segments of a leg severed	0	6
Legs damaged with segments severed *	0	10
Segments of antennae and legs severed *	1	106
Abdomen damaged	1	4
Abdomen and legs damaged *	2	2
Abdomen, legs and antennae damaged *	0	28
Mandible and antennae damaged *	0	1
Head removed	1	1
Head, legs and antennae damaged *	0	1

Table 11.8 Damaged and undamaged *digitata* and *religiosa* males.

CROP	N FIGS	*DIGITATA*			*RELIGIOSA*		
		INDIVIDUALS	MEAN ± SD	RANGE	INDIVIDUALS	MEAN ± SD	RANGE
DAMAGED							
1	10	1	0.1 ± 0.32	0-1	58	5.8 ± 5.18	0-15
2	5	1	0.2 ± 0.45	0-1	50	10.0 ± 5.09	4-17
3	4	0	0	0	31	7.75 ± 6.85	4-18
4	5	8	1.6 ± 3.04	0-7	20	4.0 ± 4.0	0-8
5	6	2	0.33 ± 0.52	0-1	44	7.33 ± 6.74	1-18
	30	12	0.40		203	6.77	
INTACT							
1	10	37	3.7 ± 3.62	0-10	42	4.2 ± 4.41	0-11
2	5	10	2.0 ± 2.55	0-6	7	1.4 ± 1.67	0-4
3	4	4	1.0 ± 1.15	0-2	13	3.25 ± 1.7	1-5
4	5	15	3.0 ± 1.41	2-5	11	2.2 ± 1.3	0-3
5	6	13	2.17 ± 2.14	0-6	21	3.5 ± 1.87	1-6
	30	79	2.63		94	3.13	

Table 11.9 A comparison of the numbers of damaged and intact *digitata* and *religiosa* males.

CROP	FIG	*DIGITATA*		*RELIGIOSA*		CHI-SQUARE$_{[1]}$	*P*
	-	DAMAGED	INTACT	DAMAGED	INTACT		
1	1	1	1	5	1	0.89	NS
	2	0	3	8	2	6.87	*
	3	0	1	5	1	2.92	NS
	4	0	10	15	8	10.57	*
	5	0	1	0	0	-	-
	6	0	1	14	11	1.13	NS
	7	0	6	3	0	9.00	**
	8	0	0	3	2	0.60	NS
	9	0	5	5	11	2.43	NS
	10	0	9	9	6	0	NS
TOTAL		1	37	58	42	4.12	*
HETEROGENEITY$_{[9]}$						21.26	*
2	1	1	0	9	4	0.33	NS
	2	0	1	7	2	2.95	**
	3	0	0	13	0	-	-
	4	0	6	4	0	10.00	**
	5	0	3	17	1	14.87	***
TOTAL		1	10	50	7	30.40	***
HETEROGENEITY$_{[4]}$						2.25	NS
3	1	0	0	5	5	0.47	NS
	2	0	2	18	4	6.55	**
	3	0	2	4	3	1.33	NS
	4	0	0	4	1	0.24	NS
TOTAL		0	4	31	13	7.96	**
HETEROGENEITY$_{[3]}$						0.63	NS
4	1	0	4	0	2	0	NS
	2	7	5	8	3	0.53	NS
	3	1	2	8	3	1.60	NS
	4	0	2	4	3	1.05	NS
	5	0	2	0	0	-	-
TOTAL		8	15	20	11	4.68	*
HETEROGENEITY$_{[4]}$						1.50	NS
5	1	0	3	8	5	3.69	*
	2	0	1	1	2	0.44	NS
	3	1	6	18	6	7.48	**
	4	1	2	12	4	2.03	NS
	5	0	1	4	3	2.40	NS
	6	0	0	1	1	-	-
TOTAL		2	13	44	21	85.79	***
HETEROGENEITY$_{[5]}$						69.75	***
TOTAL		12	79	203	94	85.79	***
HETEROGENEITY$_{[4]}$ (BETWEEN TREES)						23.89	***

NS = not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Table 11.10 Comparisons of damage levels among emerged and not emerged *digitata* and *religiosa* males.

CROP	EMERGED				CHI-SQUARE$_{[1]}$	P	NOT EMERGED				CHI-SQUARE$_{[1]}$	P
	DIGITATA		*RELIGIOSA*				*DIGITATA*		*RELIGIOSA*			
	DAMAGED	NOT DAMAGED	DAMAGED	NOT DAMAGED			DAMAGED	NOT DAMAGED	DAMAGED	NOT DAMAGED		
1	0	28	0	5	-	-	1	9	58	37	9.57	**
2	0	10	2	5	3.24	NS	1	0	48	2	0.04	NS
3	0	4	2	0	6.00	*	0	0	29	13	-	-
4	8	15	0	0	-	-	0	0	20	11	-	-
5	0	12	1	0	13.00	***	2	1	43	21	3.53	NS
TOTAL	8	69	5	10	5.44	*	4	10	198	84	10.67	**

NS = not significant, ** $P < 0.01$

of longer duration with contestants sustaining severe and sometimes fatal injuries. In fights between the *religiosa* males opponents would often grab each other, in a similar fashion to that observed in other *Otitesella* species, with one letting go only when it had killed the other. *Digitata* males were not observed to grab hold of their opponents in this fashion. No altercations were observed between *religiosa* and *digitata* males.

Within individual figs the proportion of males that were damaged was not significantly correlated with male densities for either morph. However, the data for *religiosa* males approached significance (n = 28, $r = 0.11$, $P = 0.056$) whereas there was no hint of a significant relationship with the *digitata* males (n = 25, $r = -0.068$, $P = 0.74$). Unlike the situation with various wasp species in *Ficus burtt-davyi* (chapter 4) the overall proportion of injured males was not significantly correlated with the number of eclosed females (n = 30, $r = 0.22$, $P = 0.25$).

11.3.4 Longevity outside the figs

Digitata males (n = 26) lived longer than *religiosa* males (n = 15) once outside their figs ($X^2_{[4]} = 367.50$, $P < 0.001$, Figure 11.5). The former survived up to 60 hours exposure whereas no *religiosa* males lived longer than 12 hours.

11.4 DISCUSSION

The two male morphs of *Otitesella* sp. I differed in behaviour as well as anatomy. Physiological differences were also indicated. *Digitata* males usually emerged from their figs whereas *religiosa*

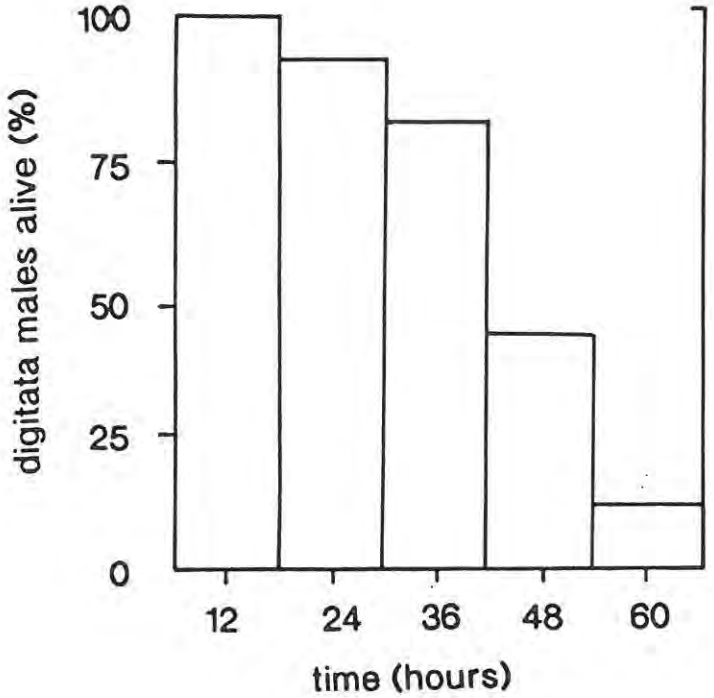


Figure 11.5 Cumulative histogram of the mortalities of *digitata* (white bars) males outside the figs. All the *religiosa* males were already dead after 12 hours and all the wasps had died by 60 hours.

males did not. This may be attributed to their different responses tolight, with only *digitata* males displaying positive phototaxis. Although *digitata* males were smaller (chapter 10) they lived longer than the *religiosa* males once they were outside the figs. This is contrary to the situation in other parasitic wasps where longevity generally increases with size (Van Den Assem *et al*, 1989), and suggests that *digitata* males have developed a greater resistance to desiccation. Perhaps the typically darker coloration of this morph (chapter 10) is related to cuticular modifications to reduce evaporative losses. The two morphs also differed in the extent of the injuries they sustained. This was not only a consequence of the *digitata* males' escape from the figs, and may be a consequence of their reluctance to enter into fights with other males.

The *religiosa* morph is the typical male form found in *Otitesella* species (Wiebes, 1967c) while the *digitata* male appears to represent a morph that is secondarily adapted to mating outside the figs. In other groups of fig wasps, males which mate outside the fig are typically winged, while those which mate within the fig cavity are wingless. In the genus *Philotrypesis*, both winged and wingless males commonly occur in the same species, and these utilize two different mating sites (chapter 3). In *Otitesella*, where all males are wingless, secondary adaptations to mating outside the figs have involved a reduction in both body and mandible size, indicating a decline in fighting ability, and apparent changes in physiology. The large size, enlarged mandibles and heavy sclerotisation of the *religiosa* morph is typical of other male fig wasps adapted for fighting (chapter 2), and may reflect the selective advantage of larger individuals in fights (chapter 4). Fighting males also typically mate in the cavity of the fig, like the *religiosa* morph. In contrast, smaller aggressive fig wasps, like the *digitata* morph, typically mate either outside the fig or in galls where female wasps have developed (chapter 3).

It is difficult to determine the lifetime reproductive success of males exhibiting alternative reproductive behaviours (Dominey, 1984). Gadgil (1972) postulated that two different types of behaviour could be maintained in a population if 'costs' and behaviour were interlinked. *Religiosa* males may incur high damage levels, but they are able to mate with females as soon as they emerge into the fig lumen. *Digitata* males emerge more readily from the figs and have lower damage levels, but sacrifice local mating opportunities by doing so. This is because females may escape from their figs and disperse without any contact with *digitata* males. Moreover, after being mated within a fig the females may be less receptive to subsequent male advances. Morph ratios were found to vary with wasp density. At higher densities more *religiosa* males were present. This is similar to the morph ratio changes exhibited by *Philotrypesis* sp. C (chapter 8). Irrespective of the mechanisms that achieve morph ratio adjustment, it suggests that the relative reproductive success of *digitata* males may be greater at low densities.

12 MATING BEHAVIOUR OF AN OTITESELLA FIG WASP WITH DIMORPHIC MALES

11.1 INTRODUCTION

Otitesella sp. I from *F. ingens* belongs to the *O. digitata* species group hich is characterised by having dimorphic males (Wiebes, 1969). The two forms, referred to as the *digitata* and *religiosa* morphs, are both wingless, but can be distinguished from one another by the presence or absence respectively of a swollen, black terminal tarsal segment on all the legs (chapter 2). In addition to physical differences, the two forms display contrasting mating site preferences and fighting behaviour. The *religiosa* form is a fighter which generally remains inside the figs and is therefore restricted to mating in the lumen of figs, whereas the *digitata* males are also less aggressive and exit from their natal figs to mate on the outside of the figs (chapter 11).

Here, elements of the mating behaviour of the *religiosa* and *digitata* males of *Otitesella* sp. I are compared. The aim was to determine whether the contrasting mating site preferences of the two morphs were linked to any differences in their mating behaviour and to determine the functional significance of the enlarged black tarsi of the *digitata* males.

11.2 MATERIALS AND METHODS

Otitesella sp. I were collected from figs of several *F. ingens* trees growing at Coombs near Grahamstown, South Africa. To observe their mating behaviour, five groups of six females were placed with either three *digitata* or three *religiosa* males in standard glass vials (7.5 cm x 2.5 cm) vials. Conditions in the vials were presumed to be more representative of those outside the fig than inside. The wasps were newly emerged from their galls and were used once only. The behaviour of each group was recorded for 45 minutes using a VHS video recorder. Particular mating sequences were viewed frame by frame during subsequent analyses and for measurement of their duration.

12.3 RESULTS

12.3.1 General mating behaviour of both male morphs

Males of both morphs were observed to interfere with other mating males and females. Fights would ensue, which would break up when either one of the males or the female left.

Males, whether of the *digitata* or *religiosa* forms, were always the initiator of sexual advances, while the female would determine whether they were successful and copulation would take place. The sequence of behaviour common to the two morphs was as follows:

1. **Following**. Males would follow females they encountered; females either increased their rate of walking and were pursued by the males or were apparently unaware of his presence.

2. **Touching**. Upon contact with female, the males placed their front tarsi on her wings. They could maintain this position behind a female whether she was walking or stationary. Once a male had

achieved this position an attempt at copulation usually followed.

3. **Female choice**. Mounted females were never passive, but would kick or spring off the substrate. If a female did not succeed in dislodging a persistent male, copulation would occur. At this point females would become still, even if they had struggled earlier. After a while the females struggling was resumed and copulation was terminated. No post copulatory displays were observed.

4. **Mating position**. During copulation, males held the last pair of the female's legs off the substrate with his middle pair. At the same time his front tarsi were placed on the thorax of the female.

12.3.2 Mating behaviour of *religiosa* males

The general sequence of events, once contact with a female was made is depicted in using diagrams of action sequences (Figure 12.1).

The number of observations of mating behaviour by *religiosa* males was relatively small (n = 9) because these slow moving males proved to be inefficient at contacting females under the experimental conditions. The *religiosa* males largely ignored the females and rarely followed and touched them. Females were only mounted when they happened to come sufficiently close to a male. If the female was

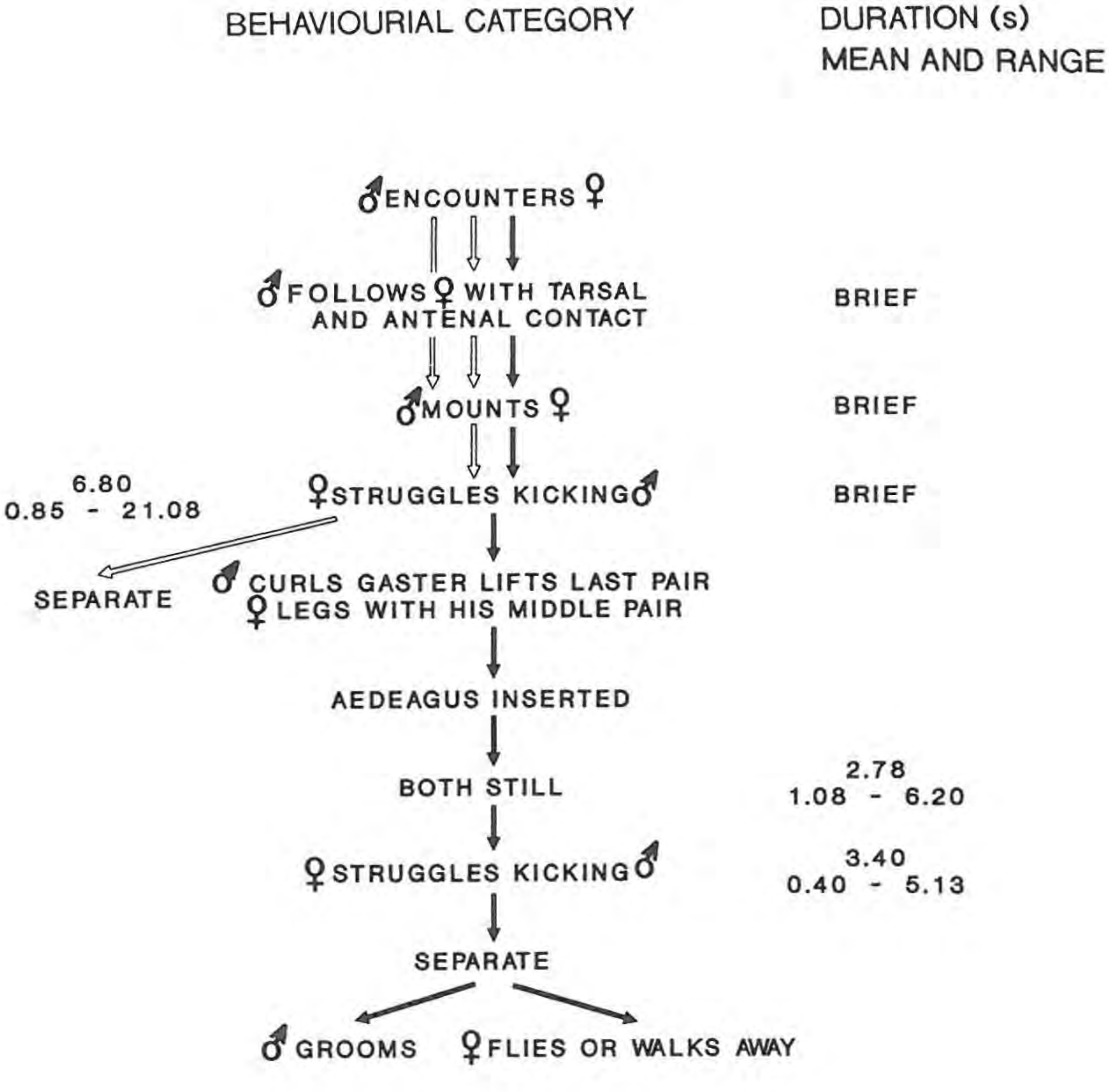


Figure 12.1 *Religiosa* male mating behaviour: action sequences leading to copulation (dark arrows) and attempts at copulation (empty arrows). Numbers represent the mean duration and range (seconds) of certain actions.

receptive then mating would follow, but if not she would dislodge any persistent male off her back. Successful copulations were observed on five occasions and failed attempts at copulation on four occasions.

12.3.3 Mating behaviour of *digitata* males

The series of actions by *digitata* males leading to copulation (n=18 observations) and failed attempts at copulation (n=15 observations) are depicted as action sequences in Figure 12.2. *Digitata* males would often approach the female from behind (that is, from the 180° away from the direction the female was facing) and follow her until she stopped (n = 18 observations). They would then touch her with their front tarsi. This led to an attempt at copulation (n=9 observations) and if the female was receptive, copulation would occur (n=9 observations). This continued until terminated by the females' struggling.

Digitata males would also sometimes approach the female from the front (n = 15 observations). In most cases (12 from 15) the female would stop briefly for between 0.24 to 0.68 seconds. The female would then turn and walk away to be followed by the male. Nine of the instances of frontal approaches terminated in copulation and the other three in attempts at copulation. However, a *digitata* male was not more likely to succeed, in copulation from the front than from the back (front, fail:succeed, 6:9, behind, fail:succeed, 9:9; Chi-square$_{[1]}$ = 0.33, $P > 0.05$).

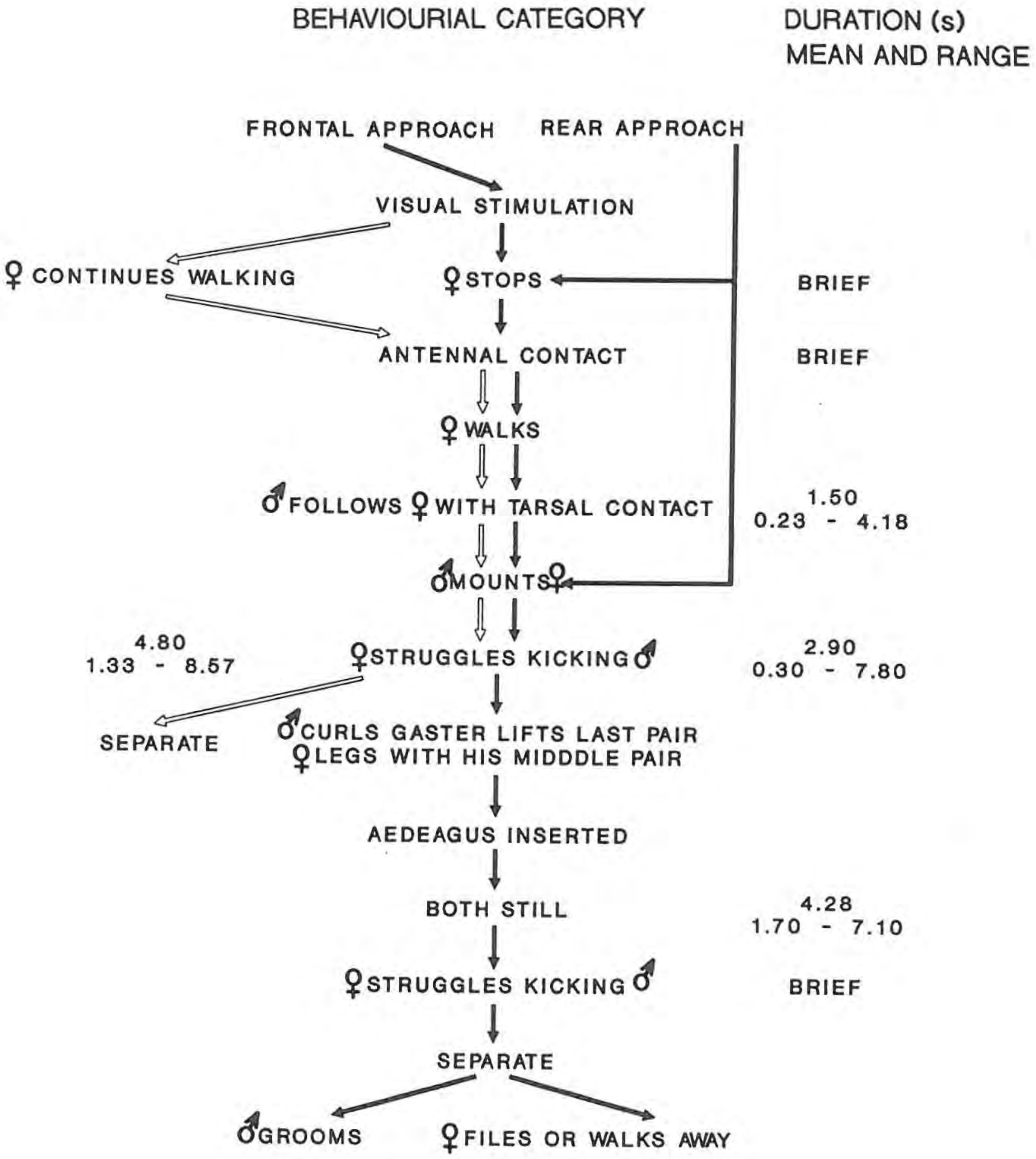


Figure 12.3 *Digitata* male mating behaviour: action sequences leading to copulation (dark arrows) and attempts at copulation (empty arrows). Numbers represent the mean duration and range (seconds) of certain actions.

12.3.4 Responses of females to males

The courtship and mating behaviour of both the *digitata* and *religiosa* males was simple and of short duration. Males approached the females from any angle. Females often stopped walking if they were approached from the front by a *digitata* male, but not if approached from behind (front, stop: not stop 12:3, behind 0:18, Chi-square$_{[1]}$ = 20.12, $P < 0.001$). In contrast, females did not stop if approached from the front by *religiosa* males (*digitata*, stop: not stop 12:3, *religiosa* 0:9, Chi-square$_{[1]}$ = 14.40, $P < 0.001$). This arrestance response by the females had been elicited in all nine of the successful *digitata* copulations that were recorded, and three of the six unsuccessful. Although the females did not stop for them, *religiosa* males nonetheless attempted copulation on nine occasions, five of which were successfully mated. Females were therefore likely to stop for *digitata*, but not *religiosa* males, but the morphs were equally likely to copulate once contact with a female had been achieved (*digitata*, succeed:fail, 9:6, *religiosa*, suceed:fail, 5:4, Chi-square$_{[1]}$ = 0.045, $P > 0.05$).

12.4 DISCUSSION

Mating behaviour has been described in chalcid wasps belonging to the families Eulophidae (Bryan, 1980; Dahms, 1973; Evans & Matthew, 1976; Gonzalez *et al*, 1985; Hamerski & Hall, 1989; Matthews, 1975; Van Den Assem & Putters, 1980), Pteromalidae (Miller & Tsao, 1974; Van Den Assem, 1975, 1976; Van Den Assem & Putters, 1980; Van Den Assem *et al*, 1980, 1981), Torymidae (Goodpasture, 1975) and Chalcididae (Leonard & Ringo, 1978). A major contrast between the mating behaviour of *Otitesella* and that of these other chalcids is with respect to the duration of courtship. In *Otitesella* the entire pre-mating process is of a short duration, rarely lasting longer than 20 seconds. This is in contrast to the more sophisticated courtships of for example eulophids (Bryan, 1980; Hamerski & Hall, 1989) and torymids (Goodpasture, 1975) which may last for several minutes.

Another major difference between the mating behaviour of *Otitesella* and that other chalcids is with respect to the complexity of courtship. The male *Otitesella* attempted copulation as soon as he had mounted the female and did not perform any of the more complex repertoires such as antennal slashing, body bobbing, head swivelling and wing pressing observed in other male Chalcidoidea while in this position (Evans & Matthews, 1976; Goodpasture, 1975; Hamerski & Hall, 1989; Miller & Tsao, 1974). In chalcids such as *Melittobia* species (Dahms, 1973; Evans & Matthews, 1976) and *Nasonia vitripennis* (Miller & Tsao, 1974), the male also continues to court the female once he has completely mounted her. While courtship in some species of Pteromalidae, for example entails frontal displays where the male, once he has mounted the female, places his tarsi on her head (Van den Assem, 1976). Frontal displays are considered to be more advanced than courtship at the back of the female (Van Den Assem, 1976; Van Den Assem,1986; Van Den Assem & Jachmann, 1982). The placement of the males' tarsi on the females thorax as observed in some Miscogasterinae and Asaphinae (Van den Assem, 1986), and in *Otitesella* sp. I, is regarded as intermediate. The lifting of the female's back pair of legs by the male *Otitesella* seems to be an unusual feature which prevents the female from walking away and serves as a form of physical restraint.

Complex courtship sequences often entail a combination of visual, tactile, chemical and auditory cues. We do not know if auditory signals are a feature of the mating behaviour of *Otitesella* sp. I. However, the males are wingless and auditory signals often entail wing movement (Burk & Webb, 1983; Kyriacou & Webb, 1989; Leonard & Ringo, 1978). Since *Otitesella* males are wingless they have limited dispersal ability. For this reason pheromone production by females to attract males over long distances is unlikely and mating by the *digitata* morph is likely to be restricted to the vicinity of the figs where individual males developed. However, short-range attractant chemicals may be produced by the females and males were sometimes observed to be attracted to intact galls containing females.

Whereas pheromonal cues might be important for mating inside the dark confines of a fig, visual cues would be expected to be more useful during mating on the surface of a fig. The most familiar type of visual cues in insects entails wing movements, as for example in *Drosophila* (Ringo, 1976), which are often facilitated by maculate wings. Among fig wasps this may be the case with males of *Aepocerus* and *Sycophila* which have prominent dark markings on the wings and mate outside the figs (Bronstein, 1991; personal observations).

In addition to their differing propensity for fighting (chapter 11), two differences were noted between the mating behaviour of the *digitata* and *religiosa* morphs of *Otitesella* sp. I. The first was the persistence of the *digitata* males: they relentlessly pursued the females, whereas the *religiosa* morphs rarely showed interest before making physical contact. Secondly, and of particular interest, were the different female responses they elicited. *Digitata*, but not *religiosa* morphs were able to elicit an arrestant response (albeit of short duration) from the females. While no particular movements of the *digitata* males' tarsi were observed, the females' response can be tentatively ascribed to the swollen black tarsi of the *digitata* males. These are highly conspicuous, at least to the human eye, and are highlighted by the normal leg movements of the males. The modified tarsi may therefore represent an additional component to the courtship repertoire of *Otitesella* sp. I (and other males of the *digitata* species group), evolved in connection with the change in mating sites from the fig lumen to the exterior. Such visual cues as black tarsi would seem to be unimportant for mating within the dark, enclosed cavities of the figs, where in any case females have little chance of avoiding courting *religiosa* males. In contrast, the *digitata* males, which are more adept at following females, mate out in the open on the surface of the fig. Any signals which result in female arrestance under these circumstances would clearly facilitate contact between the sexes. The different morphology and behaviour of the two *Otitesella* morphs may therefore be due to the alternative suites of adaptations which favour successful mating in two rather different environments.

13 DISCUSSION

"*... quantification has no intrinsic virtues, is associated with the vice of hubris, and can set back the cause of science by giving a false air of great certainity of conclusion.*" (Grafen, 1987).

The approach adopted in this thesis has been essentially empirical - examining correlates of variation in male fig wasps' morphology and behaviour. These findings have then been related to sexual selection theory.

The answer to why fig wasps exhibit such a variety of different mating systems may be found in the relationships between ecological variables and mating success. Assuming that similar selection pressures should select for convergence in analogous traits among different taxa, comparisons of ecological variables between groups of fig wasps should provide insights into the selective forces acting on the traits (Wilkinson *et al*, 1987) and the mechanisms of advantage they confer (Grafen, 1987).

Male fig wasp morphology can be divided simplistically into winged and flightless males. Winged males are rather homogeneous, but considerable variation is present among wingless males, suggesting differences in their biology. The classification scheme introduced in chapter 2, based on simple morphological characters, provides a framework for describing the anatomy of male fig wasps in general. The usefulness of the classification scheme must be judged by its relevance to the biology of the wasps. In the sub-sample of the fig wasp species where behaviour was noted, it was found to correspond closely with male anatomy. The behaviourial classification into pacifists, aggressors and fighters, while consisting of somewhat arbitrary terms that may cause semantic problems, was therefore generally adequate for summarising each species' behaviour. In the polymorphic species that have more than one type of male, the differences in their anatomy corresponding reassuringly to the differences in their behaviour.

Hamilton (1979) suggested that differences in the oviposition behaviour of female fig wasps were important in determining whether the males of these species would fight or not. Hamilton based his argument on predictions that relatives are not expected to fight because of their genetical closeness (Hamilton, 1967) and that within a single fig the offspring of 'internally' ovipositing fig wasp species are likely to be more closely related than those of 'externally' ovipositing species. In agreement with these preditions, fighting among 'internally' ovipositing species may be uncommon. Nonetheless, 'internally' ovipositing aggressors such as *Alfonsiella* species do occur. Furthermore, there are several 'externally' ovipositing fig wasp species, for example *Apocrypta* and *Apocryptophagus* species, whose males do not fight. Method of oviposition is therefore not a good predictor of male fighting ability.

Based on the results of chapter 3, I suggest that mating site, rather than oviposition method, is more important in determining the behaviour (and anatomy) of male fig wasps along the fighter-pacifist continuum. Where females are clustered in space the likelihood of a male being able to monopolize mating opportunites increases and sexual selection may favour the evolution of increased male size and fighting behaviour (Emlen & Oring, 1977). Where females are not monopolizable, conditions favour the evolution of non-aggressive attempts to locate mates (Emlen & Oring, 1977). Gall maters are typically pacifists and mating occurs while the females are scattered over the interior of fig. In contrast, lumen-maters are often fighters. These species mate after the females have emerged into the fig cavity. Consequently, the females are readily available and hence monopolizable. The differences in mating sites between male morphs belonging to the same wasp species provides perhaps the strongest evidence linking mating sites and male behaviour.

While mating sites may be the major determinant of the likelihood of fighting, it is not the only factor. The microenvironment found in the wasp's host figs may also be important (Compton & McLaren, 1989, chapter 3), and there are exceptions to the general pattern, such as the males of *Philotrypesis pilosa* which are wingless fighters, yet mate inside the galls (Murray, 1987).

Mating sites may be important determinants of male behaviour because of their influence on the ratio of fertilizable females to sexually active males (the operational sex ratio (OSR) - Emlen & Oring, 1977). The greater the degree of imbalance in the OSR, the greater the expected variation in reproductive opportunity, inferring greater selective differentials. The sex ratios of fig wasps are heavily female biased in 'internally' ovipositing species and approach 50:50 in 'externally' ovipositing species (chapter 6), in agreement with Hamilton's (1967) LMC predictions. Males of some fighting species may nonetheless locally outnumber females inside the cavities of figs where their mating takes place. OSR and 'true' sex ratios may therefore be quite different (chapter 7).

LMC and inbreeding are not the only selective forces that influence OSR. Sex ratios are also adjusted by ecological factors. In fighting fig wasps, such as *Otitesella*, *Philotrypesis* and *Sycoryctes* species the OSR is expected to be more female biased than the sex ratio at adult emergence due to the fatalities and debilitating injuries incurred during fighting. In contrast, where fig wasps are pacifist gall maters there is little difference between the emergence sex ratio and OSR.

A factor which interrelates with the OSR in fig wasps is the degree to which multiple matings may occur. Although multiple matings have been reported in some species of gall mating fig wasps, females are apparently reluctant to mate repeatedly (Murray, 1987, 1990, personal observations). The number of times a female is mated might be expected to be lower in lumen mating species than in gall maters and even lower still in those fig wasps that mate outside the figs. This is because females inside the galls may be essentially passive, and are available to mate for extended periods. Inside the fig lumen there may be a relatively short period when each female is available, while she is in transit to the exterior, while in species which mate outside the figs there are clearly many oppurtunites for females to escape from males once they have mated.

Sexual size dimorphism (SSD) in fig wasps is related to mating sites, apparently because of associated differences in male behaviour. Males that are gall maters and those that mate outside figs tend to be smaller than conspecific females, while lumen maters tend to be larger than their conspecific females. Large male size in fighters is probably the consequence of selection operating through large males being more successful in fights. While I have shown that larger males tend to win fights, I did not confirm that the winners of fights mate more often than losers and hence have greater reproductive success (chapter 4). Male biased SSD is often attributed to sexual selection for large males (Carothers, 1984; Ralls, 1977; Selander, 1972) although this may not always be the case (Thornhill & Alcock, 1983). Because the adult males in fighting species of fig wasp are so short-lived it is unlikely that other selective forces such as predation are important. Moreover, evidence from the general lack of relationship between individual gall and wasp sizes, and because fighters are larger than conspecific females, suggests that there is a genetic component to body size and therefore that responses to sexual selection have taken place.

The genetic and selective contraints acting on enlarged body size and the weaponry of fighting fig wasp males is not known.

Selective contraints acting on these characters will consist of the intensities and directions of natural and sexual selection. These include inherant costs (Mousseau & Dingle, 1991), such as nonadaptive genetic correlations between males and females (Lande, 1980). Females of 'internally' ovipositing fig wasps for example must be able to enter the fig through the ostiole and increased body size in this sex may be highly disadvantageous (Frank, 1987). How these constraints might affect those species with polymorphic males provides intriguing problems.

Models for the evolution of polymorphism (Gadgil, 1972; Gadgil & Taylor, 1975) apply to male mating strategies that are genetically distinct and predict that different forms will be maintained in a population if the mating success between forms is equivalent. One form may nonetheless be at an advantage relative to the other under certain local conditions. Where two distinct behaviours are observed, but only one is practised by any one individual, as for example in the bluegill sunfish *Lepomis macrochirus*, the possibility of such a genetic polymorphism being present can be considered (Dominey, 1980). Polymorphism in fig wasps is of this form, but although the *digitata* and winged male morphs were consistently rarer than the alternatives in *Otitesella* and *Philotrypesis*, morph ratios were not fixed and changed with local population density. Given that density-related differential survivorship of morphs during the larval stages is unlikely, this suggests that morph determination is not genetic (Ford, 1975). This is in contrast to certain aphids, where morph frequencies are fixed, but differ among clones of *Myzus persicae* (Blackman, 1972), while in

Acyrthosiphon pisum (Smith & MacKay, 1989) there are three clonal types, one which produces only alate males, another only apterous males and a third produces both apterous and alate males in a fixed frequency. Similarly, the different forms of the isopod *Paracerceis sculpta* are genetically determined, and occur at fixed frequencies (Shuster & Wade, 1991). The alternative to genetic morph determination in fig wasps is environmental control, acting on the ovipositing female, or directly on the developing eggs or larvae.

Morph ratios in some hymenopteran polymorphisms are determined by the host species the larvae feed on, as in a *Trichogramma* species (Trichogrammatidae) where the apterous and alate forms emerge from different hosts (Salt, 1937). In a colonial *Melittobia* species (Eulophidae) it is the density of larvae developing in a host that determines which morphs develop. At higher densities a greater percentage of alates are produced (Freeman & Ittyeipe, 1982). In ants and other social hymenopterans numerous factors including larval nutrition and temperature play a role in caste determination (Wilson, 1971).

Otitesella fig wasps are gall formers (Neves, 1987; personal observations) ovipositing at about the same time as the pollinating wasps and feeding on enlarged ovules in the figs. Because fig wasp larvae typically develop one to a gall, competition for food between larvae is unlikely to be important, and given that both morphs develop in the same figs, it is not likely that environmental factors such as larval crowding or temperature can play a role in determining *digitata/religiosa* ratios.

The larvae of several *Philotrypesis* species are initially phytophagous, devouring endosperm tissue, but eventually killing the pollinator larvae (Abdurahiman & Joseph, 1978; Joseph, 1959b). Whether inquilinism is typical of all *Philotrypesis* is not known. The presence of large and small males in several *Philotrypesis* species (Grandi, 1930; Joseph, 1959b) was attributed by Abdurahiman and Joseph (1978) to the quantity of food left by the host larvae. This is likely to vary from ovule to ovule depending on the duration of the period when the host larvae are alive, and hence the timing of *Philotrypesis* oviposition. However, parasitoids such as *Sycoryctes* and *Apocrypta* attack hosts of different sizes yet do not display the variation exhibited by *Philotrypesis* (chapter 9), which again suggests that variation in larval nutrition might not be involved.

Possibly factors involving ovipositing females are important determinants of morph ratios. Females might in some way be able to 'measure' the densities of other females on a fig surface. Alternatively, interference by other females could result in an increase in the time intervals between ovipositions, or result in interference with oviposition *per se*.

The proportions of the different *Otitesella* and *Philotrypesis* morphs show similar patterns of variation in relation to population density, suggesting that these changes in morph ratios are adaptive (chapters 8 & 11). This is because winged males and *digitata* males predominate at low population densities, when chances of encountering mates within figs are reduced. As both forms emerge from their figs to find mates this may put them at an advantage over their alternative morphs, which mate inside the figs. Damage due to fighting also varies with density, which could influence the relative success of the different morphs. Whether other fig wasps with polymorphic males, for example some *Camarothorax* species, show similar patterns in morph ratios is not known.

Looking ahead, the work described in this thesis could be extended by looking at morph ratio changes in other polymorphic species, the mating success of different male morphs within species and particularly mechanisms of morph determination. Although large males were shown to win fights, whether or not winners get to mate and more often than the surviving losers was not confirmed. Thus the costs, and benefits, of fighting need to be more accurately determined. Given the hundreds of *Ficus* species, and the thousands of wasp species they support, there is clearly scope for many more studies. Nonetheless, hopefully the empirical data presented here will help *"provide the material which theoreticians will find interesting in five years' time and beyond"* (Grafen, 1987).

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15 APPENDICES

APPENDIX 1 Classification of fig wasps referred to in the thesis, with male morpholgical types, larval feeding behaviour and female ovipositional behaviour. Fig wasps are listed in taxonomic order. With the exception of the Agaoninae and Sycoecinae, wasp species from the same host *Ficus* were routinely distinguished from each other, but not from wasps with different host *Ficus*. Consequently, where wasp species are not host specific, duplication will have occurred. This was necessary in the absence of systematic revisions of most groups of African fig wasps. Male morphological types were determined as described in chapter 2. Oviposition behaviour is deduced from adult female anatomy or observations. Larval feeding biology was largely determined by extrapolation from that recorded from congenerics. If generic consistency in larval biology is not as developed as appears at present, then some extrapolations may be incorrect. Host *Ficus* of described species may be obtained from the corresponding reference source, while the hosts of undescribed species are given in Appendix 2.

MORPHOLOGICAL TYPES = I,II,III,IV,V,VI
OVIPOSITION BEHAVIOUR = EXTERNAL OR INTERNAL
LARVAL BIOLOGY = GALLER OR PARASITOID, (INCLUDING INQUILINES)
SOURCES : from literature (given in full in the reference list) or the collection housed at Rhodes University Zoology Department.

FAMILY/SUBFAMILY	FIG WASP	SOURCE	MALE MORPHOLOGICAL TYPE	OVIPOSITION BEHAVIOUR	LARVAL BIOLOGY	NOTES ON TAXONOMY
EURYTOMIDAE						
EURYTOMINAE						
	Sycophila butcheri Burks	Burks (1969)	I	EXTERNAL	PARASITOID	
	S. flaviclava Boucek	Boucek *et al* (1981)	I	EXTERNAL	PARASITOID	
	S. kestraneura Masi.	Boucek *et al* (1981)	I	EXTERNAL	PARASITOID	
	S. naso Boucek	Boucek *et al* (1981)	I	EXTERNAL	PARASITOID	
	S. punctum Boucek	Boucek *et al* (1981)	I	EXTERNAL	PARASITOID	
	Sycophila sp. indet. A	collection	I	EXTERNAL	PARASITOID	
	Sycophila sp. indet. A_2	collection	I	EXTERNAL	PARASITOID	

FAMILY/SUBFAMILY	FIG WASP	SOURCE	MALE MORPHOLOGICAL TYPE	OVIPOSITION BEHAVIOUR	LARVAL BIOLOGY	NOTES ON TAXONOMY
	Sycophila sp. indet. A_3	collection	I	EXTERNAL	PARASITOID	
	Sycophila sp. indet. B	collection	I	EXTERNAL	PARASITOID	
	Sycophila sp. indet. B_2	collection	I	EXTERNAL	PARASITOID	
	Sycophila sp. indet. B_3	collection	I	EXTERNAL	PARASITOID	
	Sycophila sp. indet. C	collection	I	EXTERNAL	PARASITOID	
	Sycophila sp. indet. C_2	collection	I	EXTERNAL	PARASITOID	
	Sycophila sp. indet. C_3	collection	I	EXTERNAL	PARASITOID	
	Sycophila sp. indet. D	collection	I	EXTERNAL	PARASITOID	
	Sycophila sp. indet. D_2	collection	I	EXTERNAL	PARASITOID	
	Sycophila sp. indet. D_3	collection	I	EXTERNAL	PARASITOID	
	Sycophila sp. indet. D_4	collection	I	EXTERNAL	PARASITOID	
	Sycophila sp. indet. E	collection	I	EXTERNAL	PARASITOID	
	Sycophila sp. indet. E_2	collection	I	EXTERNAL	PARASITOID	
	Sycophila sp. indet. E_3	collection	I	EXTERNAL	PARASITOID	
	Sycophila sp. indet. E_4	collection	I	EXTERNAL	PARASITOID	
	Sycophila sp. indet. E_5	collection	I	EXTERNAL	PARASITOID	
	Sycophila sp. indet. F	collection	I	EXTERNAL	PARASITOID	
	Sycophila sp. indet. F_2	collection	I	EXTERNAL	PARASITOID	
	Sycophila sp. indet. G	collection	I	EXTERNAL	PARASITOID	
	Sycophila sp. indet. G_2	collection	I	EXTERNAL	PARASITOID	
	Sycophila sp. indet. H	collection	I	EXTERNAL	PARASITOID	
	Sycophila sp. indet. H_2	collection	I	EXTERNAL	PARASITOID	
	Sycophila sp. indet. H_3	collection	I	EXTERNAL	PARASITOID	
	Sycophila sp. indet. I	collection	I	EXTERNAL	PARASITOID	
	Sycophila sp. indet. I_2	collection	I	EXTERNAL	PARASITOID	
	Sycophila sp. indet. I_3	collection	I	EXTERNAL	PARASITOID	
	Sycophila sp. indet. I_4	collection	I	EXTERNAL	PARASTOID	
	Sycophila sp. indet. J	collection	I	EXTERNAL	PARASITOID	
	Sycophila sp. indet. V	collection	I	EXTERNAL	PARASITOID	
	Sycophila sp. indet. V_2	collection	I	EXTERNAL	PARASITOID	
	Sycophila sp. indet. V_3	collection	I	EXTERNAL	PARASITOID	
	Sycophila sp. indet. V_4	collection	I	EXTERNAL	PARASITOID	
	Sycophila sp. indet. V_5	collection	I	EXTERNAL	PARASITOID	
	Pseudisa smicroides Walker	Burks (1969)	I	EXTERNAL	PARASITOID	= *Sycophila* ?
	Decatoma fici Joseph	Joseph (1959)	I	EXTERNAL	PARASITOID	= *Eurytoma* ? Boucek (1988)

FAMILY/SUBFAMILY	FIG WASP	SOURCE	MALE MORPHOLOGICAL TYPE	OVIPOSITION BEHAVIOUR	LARVAL BIOLOGY	NOTES ON TAXONOMY
	Eurytoma ficus-gallae Boucek	Boucek *et al* (1981)	I	EXTERNAL	PARASITOID	
	Syceurytoma ficus Boucek	Boucek *et al* (1981)	I	EXTERNAL	PARASITOID	
	Ficomila curtivena Boucek	Boucek *et al* (1981)	I	EXTERNAL	PARASITOID	
	F. gambiensis Risbec.	Boucek *et al* (1981)	I	EXTERNAL	PARASITOID	
	Ficomila sp. indet. A	collection	I	EXTERNAL	PARASITOID	
	Ficomila sp. indet. B	collection	I	EXTERNAL	PARASITOID	
	Ficomila sp. indet. C	collection	I	EXTERNAL	PARASITOID	
	Ficomila sp. indet. C_2	collection	I	EXTERNAL	PARASITOID	
	Ficomila sp. indet. C_3	collection	I	EXTERNAL	PARASITOID	
	Ficomila sp. indet. C_4	collection	I	EXTERNAL	PARASITOID	
	genus indet. B	collection	I	EXTERNAL	PARASITOID	
TORYMIDAE						
	Physothorax bidentulus Burks	Burks (1969)	I	EXTERNAL	PARASITOID	
	P. deseiger Mayr	Burks (1969)	I, VI	EXTERNAL	PARASITOID	
ORMYRIDAE						
	Ormyrus watshami Boucek	Boucek *et al* (1981)	I	EXTERNAL	PARASITOID	
	O. flavipes Boucek	Boucek *et al* (1981)	I	EXTERNAL	PARASITOID	
	O. subconicus Boucek	Boucek *et al* (1981)	I	EXTERNAL	PARASITOID	
	Ormyrus sp. indet. A	collection	I	EXTERNAL	PARASITOID	
	Ormyrus sp. indet. B	collection	I	EXTERNAL	PARASITOID	
AGAONIDAE EPICHRYSOMALLINAE						
	Neosycophila sp. indet. A	collection	I	EXTERNAL	PARASITOID	
	Acophila sp. indet. A	collection	I	EXTERNAL	PARASITOID	
	Acophila sp. indet. A_2	collection	I	EXTERNAL	PARASITOID	
	Camarothorax brevimucro Boucek	Boucek *et al* (1981)	I	EXTERNAL	GALLER	
	C. equicollis Boucek	Boucek *et al* (1981)	I	EXTERNAL	GALLER	
	C. hemimucro Wiebes	Wiebes (1981a)	I	EXTERNAL	GALLER	

FAMILY/SUBFAMILY	FIG WASP	SOURCE	MALE MORPHOLOGICAL TYPE	OVIPOSITION BEHAVIOUR	LARVAL BIOLOGY	NOTES ON TAXONOMY
	C. longimucro Boucek	Boucek *et al* (1981)	I	EXTERNAL	GALLER	
	'Camarothorax' sp. indet. A	collection	I	EXTERNAL	GALLER	= *'Camarothorax'* in the broad sense of Boucek *et al* (1981)
	'Camarothorax' sp. indet. B	collection	I	EXTERNAL	GALLER	
	'Camarothorax' sp. indet. C	collection	I	EXTERNAL	GALLER	
	'Camarothorax' sp. indet. C_2	collection	I	EXTERNAL	GALLER	
	'Camarothorax' sp. indet. C_3	collection	I	EXTERNAL	GALLER	
	'Camarothorax' sp. indet. D	collection	I	EXTERNAL	GALLER	
	'Camarothorax' sp. indet. E	collection	I	EXTERNAL	GALLER	
	'Camarothorax' sp. indet. F	collection	I	EXTERNAL	GALLER	
	'Camarothorax' sp. indet. F_2	collection	I	EXTERNAL	GALLER	
	'Camarothorax' sp. indet. G	collection	I	EXTERNAL	GALLER	
	'Camarothorax' sp. indet. H	collection	I	EXTERNAL	GALLER	
	'Camarothorax' sp. indet. I	collection	I	EXTERNAL	GALLER	
	'Camarothorax' sp. indet. J	collection	I	EXTERNAL	GALLER	
	'Camarothorax' sp. indet. K	collection	I	EXTERNAL	GALLER	
	'Camarothorax' sp. indet. K_2	collection	I	EXTERNAL	GALLER	
	'Camarothorax' sp. indet. K_3	collection	I	EXTERNAL	GALLER	
	'Camarothorax' sp. indet. S	collection	I	EXTERNAL	GALLER	
	'Camarothorax' sp. indet. T	collection	I, III	EXTERNAL	GALLER	
	Camarothorax sp. indet. A	collection	I, V	EXTERNAL	GALLER	= *Camarothorax* in the restricted sense of Boucek (1988)
	Camarothorax bimasculinus (Joseph)	Joseph (1959)	I, V	EXTERNAL	GALLER	
	Parapilkhanivora testacea Farooqi & Ramdas Menon	Farooqi & Ramdas Menon (1973)	I	EXTERNAL	GALLER	= *Camarothorax* in the restricted Boucek (1988)
	Odontofroggatia corneri Wiebes	Wiebes (1980b)	II	EXTERNAL	GALLER	
	O. galili Wiebes	Wiebes (1980b)	II	EXTERNAL	GALLER	
	O. ishii Wiebes	Wiebes (1980b)	II	EXTERNAL	GALLER	

FAMILY/SUBFAMILY	FIG WASP	SOURCE	MALE MORPHOLOGICAL TYPE	OVIPOSITION BEHAVIOUR	LARVAL BIOLOGY	NOTES ON TAXONOMY
	Sycobia africana Wiebes	Wiebes (1971)	I	EXTERNAL	GALLER	
	Sycophiloides moniliformis Joseph	(only ♂) Joseph (1959)	I	EXTERNAL	GALLER	
	Sycotetra serricornis Boucek	Boucek *et al* (1981)	I	EXTERNAL	GALLER	
	Sycotetra sp. indet. A	collection	I	EXTERNAL	GALLER	
OTITESELLINAE						
	Otitesella digitata Westwood	Wiebes (1967c)	IV, V	EXTERNAL	GALLER	
	O. clarae Wiebes	Wiebes (1974b)	IV, V	EXTERNAL	GALLER	
	O. corneri Wiebes	Wiebes (1967c)	V	EXTERNAL	GALLER	
	O. epicarioides Grandi	Grandi (1922)	V	EXTERNAL	GALLER	
	O. luzonensis Wiebes	Wiebes (1967c)	V	EXTERNAL	GALLER	
	O. royi Wiebes	Wiebes (1971)	V	EXTERNAL	GALLER	
	O. tsamvi Wiebes	collection	V	EXTERNAL	GALLER	
	O. serrata Mayr	collection	IV, V	EXTERNAL	GALLER	
	O. sesquianellata van Noort	collection	V	EXTERNAL	GALLER	
	O. uluzi Compton	collection	V	EXTERNAL	GALLER	
	Otitesella sp. indet. A	collection	V	EXTERNAL	GALLER	
	Otitesella sp. indet. B	collection	V	EXTERNAL	GALLER	
	Otitesella sp. indet. C	collection	V	EXTERNAL	GALLER	
	Otitesella sp. indet. D	collection	V	EXTERNAL	GALLER	
	Otitesella sp. indet. E	collection	V	EXTERNAL	GALLER	
	Otitesella sp. indet. F	collection	V	EXTERNAL	GALLER	
	Otitesella sp. indet. G	collection	V	EXTERNAL	GALLER	
	Otitesella sp. indet. H	collection	V	EXTERNAL	GALLER	
	Otitesella sp. indet. I	collection	IV, V	EXTERNAL	GALLER	
	Otitesella sp. indet. J	collection	V	EXTERNAL	GALLER	
	Otitesella sp. indet. J_2	collection	V	EXTERNAL	GALLER	
	Otitesella sp. indet. K	collection	V	EXTERNAL	GALLER	
	Otitesella sp. indet. L	collection	V	EXTERNAL	GALLER	
	Otitesella sp. indet. M	collection	V	EXTERNAL	GALLER	
	Otitesella sp. indet. N	collection	V	EXTERNAL	GALLER	
	Otitesella sp. indet. N_2	collection	V	EXTERNAL	GALLER	
	Otitesella sp. indet. O	collection	V	EXTERNAL	GALLER	

FAMILY/SUBFAMILY	FIG WASP	SOURCE	MALE MORPHOLOGICAL TYPE	OVIPOSITION BEHAVIOUR	LARVAL BIOLOGY	NOTES ON TAXONOMY
	Otitesella sp. indet. P	collection	V	EXTERNAL	GALLER	
	Otitesella sp. indet. P_2	collection	V	EXTERNAL	GALLER	
	Otitesella sp. indet. Q	collection	V	EXTERNAL	GALLER	
	Otitesella sp. indet. R	collection	IV, V	EXTERNAL	GALLER	
	Otitesella sp. indet. S	collection	V	EXTERNAL	GALLER	
	Otitesella sp. indet. S_2	collection	V	EXTERNAL	GALLER	
	Walkerella tremeraria Westwood	Wiebes (1967c)	V	EXTERNAL	GALLER	
	Sycobiella boschmai Wiebes	Wiebes (1964a)	V	EXTERNAL	GALLER	= *Micranisa* see Boucek (1988)
	S. monstruosa Grandi	(only ♂) Grandi (1922)	V	EXTERNAL	GALLER	
	Tetrastiozoon jacobsoni Grandi	Grandi (1922)	V	EXTERNAL	GALLER	
	Grandiana armadillo Boucek	Boucek (1988)	IV	EXTERNAL	GALLER	
	G. corneliae Wiebes	Wiebes (1966)	IV	EXTERNAL	GALLER	
	G. wassae Wiebes	Wiebes (1961)	IV	EXTERNAL	GALLER	
	Lipothymus panchoi Wiebes	Wiebes (1974b)	IV	EXTERNAL	GALLER	
	Micrognathophora leptoptera Grandi	Grandi (1922)	IV	EXTERNAL	GALLER	
	Gaudalia vissali Wiebes	Wiebes (1967a)	IV	EXTERNAL	GALLER	
	Eujacobsonia genalis Wiebes	(only ♂) Wiebes (1967b)	IV	INTERNAL	GALLER	
	Grasseiana callosa Abdurahiman & Joseph	Wiebes (1974b)	IV	INTERNAL	GALLER	
	genus indet. A	collection	IV	EXTERNAL	GALLER	

FAMILY/SUBFAMILY	FIG WASP	SOURCE	MALE MORPHOLOGICAL TYPE	OVIPOSITION BEHAVIOUR	LARVAL BIOLOGY	NOTES ON TAXONOMY
	Philosycus collaris Wiebes	Wiebes (1969)	V	EXTERNAL	GALLER	
	Philosycus sp. indet. A	collection	V	EXTERNAL	GALLER	
SYCOECINAE						
	Diaziella falcata Wiebes	Wiebes (1974d)	II	INTERNAL	GALLER	
	Robertsia mandibularis Boucek	Boucek (1988)	IV	INTERNAL	GALLER	
	R. xylosyciae Boucek	Boucek (1988)	IV	INTERNAL	GALLER	
	Crossogaster odorans Wiebes	Boucek *et al* (1981)	II	INTERNAL	GALLER	
	Crossogaster sp. indet. A	collection	II	INTERNAL	GALLER	
	Crossogaster sp. indet. A_2	collection	II	INTERNAL	GALLER	
	Crossogaster sp. indet. B	collection	II	INTERNAL	GALLER	
	Crossogaster sp. indet. C	collection	II	INTERNAL	GALLER	
	Crossogaster sp. indet. D	collection	II	INTERNAL	GALLER	
	Phagoblastus liodontus Wiebes	Wiebes (1979b)	II	INTERNAL	GALLER	
	P. barbarus Grandi	Boucek *et al* (1981)	II	INTERNAL	GALLER	
	Phagoblastus sp. indet. A	collection	II	INTERNAL	GALLER	
	Phagoblastus sp. indet. B	collection	II	INTERNAL	GALLER	
	Phagoblastus sp. indet. C	collection	II	INTERNAL	GALLER	
	Phagoblastus sp. indet. D	collection	II	INTERNAL	GALLER	
	Phagoblastus sp. indet. E	collection	II	INTERNAL	GALLER	
	Phagoblastus sp. indet. E_2	collection	II	INTERNAL	GALLER	
	Philocaenus sp. indet. A	collection	II	INTERNAL	GALLER	
	Seres sp. indet. A	collection	II	INTERNAL	GALLER	
	Seres sp. indet. A_2	collection	II	INTERNAL	GALLER	
	Seres sp. indet. B	collection	II	INTERNAL	GALLER	
SYCORYCTINAE Sycoryctini						
	Philotrypesis affinis Westwood	Wiebes (1967c)	V	EXTERNAL	PARASITOID	
	P. africana Grandi	Grandi (1930)	IV, V	EXTERNAL	PARASITOID	

FAMILY/SUBFAMILY	FIG WASP	SOURCE	MALE MORPHOLOGICAL TYPE	OVIPOSITION BEHAVIOUR	LARVAL BIOLOGY	NOTES ON TAXONOMY
	P. aterrima Saunders	Grandi (1930)	V	EXTERNAL	PARASITOID	
	P. anguliceps Westwood	Wiebes (1967c)	I, V	EXTERNAL	PARASITOID	
	P. caricae L.	Grandi (1930)	IV, V	EXTERNAL	PARASITOID	
	P. cnephaea Wiebes	Wiebes (1981c)	V	EXTERNAL	PARASITOID	
	P. distallatoria Grandi	Grandi (1930)	IV, V	EXTERNAL	PARASITOID	
	P. dunia Joseph	Joseph (1954)	IV, V	EXTERNAL	PARASITOID	
	P. emeryi Grandi	Grandi (1930)	IV, V	EXTERNAL	PARASITOID	
	P. erythraea Grandi	Grandi (1930)	IV, V	EXTERNAL	PARASITOID	
	P. finitimorum Wiebes	Wiebes (1971)	V, VI	EXTERNAL	PARASITOID	
	P. longicornis Grandi	Grandi (1930)	V	EXTERNAL	PARASITOID	
	P. longispinosa Joseph	Joseph (1954)	V	EXTERNAL	PARASITOID	
	P. minuta Mayr	Grandi (1930)	IV, V	EXTERNAL	PARASITOID	
	P. ornata Grandi	Grandi (1930)	IV, V	EXTERNAL	PARASITOID	
	P. palmata Joseph	Joseph (1954)	IV, V	EXTERNAL	PARASITOID	
	P. parca Wiebes	Boucek *et al* (1981)	I, IV, V	EXTERNAL	PARASITOID	
	P. pilosa Mayr	Joseph (1954)	IV, V	EXTERNAL	PARASITOID	
	P. quadrisetosa Westwood	Joseph (1954)	IV, V	EXTERNAL	PARASITOID	
	P. spinipes Mayr	Grandi (1930)	V	EXTERNAL	PARASITOID	
	P. similis Baker	Grandi (1930)	IV, V	EXTERNAL	PARASITOID	
	P. transiens Walker	Wiebes (1967c)	IV, V	EXTERNAL	PARASITOID	
	P. travancoricus Joseph only ♂	Joseph (1954)	IV, V	EXTERNAL	PARASITOID	
	P. tristis Grandi	Grandi (1930)	IV, V	EXTERNAL	PARASITOID	
	P. thompsoni Grandi	Grandi (1930)	IV, V	EXTERNAL	PARASITOID	
	P. unispinosa Mayr	Grandi (1930)	IV, V	EXTERNAL	PARASITOID	
	Philotrypesis sp. indet. A	collection	IV, V	EXTERNAL	PARASITOID	
	Philotrypesis sp. indet. B	collection	V	EXTERNAL	PARASITOID	
	Philotrypesis sp. indet. C	collection	I, IV	EXTERNAL	PARASITOID	
	Philotrypesis sp. indet. D	collection	V	EXTERNAL	PARASITOID	
	Philotrypesis sp. indet. E	collection	IV, V	EXTERNAL	PARASITOID	
	Philotrypesis sp. indet. F	collection	I, V	EXTERNAL	PARASITOID	
	Philotrypesis sp. indet. G	collection	I, V	EXTERNAL	PARASITOID	
	Philotrypesis sp. indet. H	collection	V	EXTERNAL	PARASITOID	
	Philotrypesis sp. indet. I	collection	IV, V	EXTERNAL	PARASITOID	
	Philotrypesis sp. indet. I_2	collection	IV, V	EXTERNAL	PARASITOID	
	Philotrypesis sp. indet. J	collection	IV, V	EXTERNAL	PARASITOID	
	Philotrypesis sp. indet. K	collection	IV, V	EXTERNAL	PARASITOID	

FAMILY/SUBFAMILY	FIG WASP	SOURCE	MALE MORPHOLOGICAL TYPE	OVIPOSITION BEHAVIOUR	LARVAL BIOLOGY	NOTES ON TAXONOMY
	Philotrypesis sp. indet. L	collection	I, V	EXTERNAL	PARASITOID	
	Philotrypesis sp. indet. M	collection	I, IV	EXTERNAL	PARASITOID	
	Philotrypesis sp. indet. M_2	collection	V	EXTERNAL	PARASITOID	
	Philotrypesis sp. indet. N	collection	IV, V	EXTERNAL	PARASITOID	
	Dobunabaa flava Boucek	Boucek (1988)	IV	EXTERNAL	PARASITOID	
	Watshamiella alata Wiebes	Boucek *et al* (1981)	I	EXTERNAL	PARASITOID	
	W. fictitia Wiebes	Wiebes (1981a)	I, VI	EXTERNAL	PARASITOID	
	W. lucens Wiebes	Wiebes (1981a)	I	EXTERNAL	PARASITOID	
	Watshamiella sp. indet. A	collection	I	EXTERNAL	PARASITOID	
	Watshamiella sp. indet. B	collection	I	EXTERNAL	PARASITOID	
	Watshamiella sp. indet. C	collection	I	EXTERNAL	PARASITOID	
	Watshamiella sp. indet. D	collection	I	EXTERNAL	PARASITOID	
	Watshamiella sp. indet. E	collection	I	EXTERNAL	PARASTOID	
	Watshamiella sp. indet. F	collection	I	EXTERNAL	PARASITOID	
	Watshamiella sp. indet. G	collection	I	EXTERNAL	PARASITOID	
	Sycoscapter anceps Wiebes	Wiebes (1981a)	V	EXTERNAL	PARASITOID	
	S. concephalus Wiebes	Wiebes (1964b)	V	EXTERNAL	PARASITOID	
	S. cornutus Wiebes	Boucek *et al* (1981)	V	EXTERNAL	PARASITOID	
	S. gibbus Saunders	Wiebes (1978a)	V	EXTERNAL	PARASITOID	
	S. infectorius Joseph	Joseph (1959)	V	EXTERNAL	PARASITOID	
	S. montis Wiebes	Wiebes (1971)	V	EXTERNAL	PARASITOID	
	S. reticulatus Wiebes	Wiebes (1966)	IV, V	EXTERNAL	PARASITOID	
	S. tibialis Wiebes	Wiebes (1981a)	V	EXTERNAL	PARASITOID	
	S. stabilis Walker	Wiebes (1967c)	V	EXTERNAL	PARASITOID	
	Sycoscapter sp. indet. A	collection	V	EXTERNAL	PARASITOID	
	Sycoscapter sp. indet. B	collection	V	EXTERNAL	PARASITOID	
	Sycoscapter sp. indet. C	collection	V	EXTERNAL	PARASITOID	
	Sycoscapter sp. indet. D	collection	V	EXTERNAL	PARASITOID	
	Sycoscapter sp. indet. E	collection	V	EXTERNAL	PARASITOID	
	Sycoscapter sp. indet. F	collection	V	EXTERNAL	PARASITOID	
	Sycoscapter sp. indet. G	collection	V	EXTERNAL	PARASITOID	
	Sycoscapter sp. indet. H	collection	V	EXTERNAL	PARASITOID	
	Sycoscapter sp. indet. H_2	collection	V	EXTERNAL	PARASITOID	
	Sycoscapter sp. indet. I	collection	V	EXTERNAL	PARASITOID	
	Sycoscapter sp. indet. I_2	collection	V	EXTERNAL	PARASITOID	

FAMILY/SUBFAMILY	FIG WASP	SOURCE	MALE MORPHOLOGICAL TYPE	OVIPOSITION BEHAVIOUR	LARVAL BIOLOGY	NOTES ON TAXONOMY
	Sycoscapter sp. indet. K	collection	V	EXTERNAL	PARASITOID	
	Sycoscapter sp. indet. L	collection	V	EXTERNAL	PARASITOID	
	Sycoscapter sp. indet. M	collection	V	EXTERNAL	PARASITOID	
	Sycoscapter sp. indet. N	collection	V	EXTERNAL	PARASITOID	
	Sycoscapter sp. indet. N_2	collection	V	EXTERNAL	PARASITOID	
	Sycoryctes hilli Wiebes	Wiebes (1966)	V	EXTERNAL	PARASITOID	Boucek (1988) places *Sycoryctes* and *Sycoscapteridea* in *Sycoscapter*. Here they are placed separately because in Africa the genera are easily distinguished from each other in both sexes.
	S. hirtus Wiebes	Boucek *et al* (1981)	V	EXTERNAL	PARASITOID	
	S. lomaensis Wiebes	(only ♂) Wiebes (1971)	V	EXTERNAL	PARASITOID	
	S. remus Wiebes	Boucek *et al* (1981)	V	EXTERNAL	PARASITOID	
	S. religiosae Wiebes	Wiebes (1967c)	V	EXTERNAL	PARASITOID	
	Sycoryctes sp. indet. A	collection	V	EXTERNAL	PARASITOID	
	Sycoryctes sp. indet. A_2	collection	V	EXTERNAL	PARASITOID	
	Sycoryctes sp. indet. A_3	collection	V	EXTERNAL	PARASITOID	
	Sycoryctes sp. indet. B	collection	V	EXTERNAL	PARASITOID	
	Sycoryctes sp. indet. B_2	collection	V	EXTERNAL	PARASITOID	
	Sycoryctes sp. indet. C	collection	V	EXTERNAL	PARASITOID	
	Sycoryctes sp. indet. D	collection	V	EXTERNAL	PARASITOID	
	Sycoryctes sp. indet. E	collection	V	EXTERNAL	PARASITOID	
	Sycoryctes sp. indet. F	collection	V	EXTERNAL	PARASITOID	
	Sycoryctes sp. indet. G	collection	V	EXTERNAL	PARASITOID	
	Sycoryctes sp. indet. G_2	collection	V	EXTERNAL	PARASITOID	
	Sycoryctes sp. indet. H	collection	V	EXTERNAL	PARASITOID	
	Sycoryctes sp. indet. I	collection	V	EXTERNAL	PARASITOID	
	Sycoryctes sp. indet. J	collection	V	EXTERNAL	PARASITOID	
	Sycoryctes sp. indet. K	collection	V	EXTERNAL	PARASITOID	
	Sycoryctes sp. indet. K_2	collection	V	EXTERNAL	PARASITOID	
	Sycoryctes sp. indet. L	collection	V	EXTERNAL	PARASITOID	

FAMILY/SUBFAMILY	FIG WASP	SOURCE	MALE MORPHOLOGICAL TYPE	OVIPOSITION BEHAVIOUR	LARVAL BIOLOGY	NOTES ON TAXONOMY
	Sycoryctes sp. indet. L_2	collection	V	EXTERNAL	PARASITOID	
	Sycoryctes sp. indet. M	collection	V	EXTERNAL	PARASITOID	
	Sycoryctes sp. indet. M_2	collection	V	EXTERNAL	PARASITOID	
	Sycoryctes sp. indet. M_3	collection	V	EXTERNAL	PARASITOID	
	Sycoryctes sp. indet. N	collection	V	EXTERNAL	PARASITOID	
	Sycoryctes sp. indet. N_2	collection	V	EXTERNAL	PARASITOID	
	Sycoryctes sp. indet. O	collection	V	EXTERNAL	PARASITOID	
	Sycoryctes sp. indet. P	collection	V	EXTERNAL	PARASITOID	
	Sycoryctes sp. indet. Q	collection	V	EXTERNAL	PARASITOID	
	Sycoryctes sp. indet. R	collection	V	EXTERNAL	PARASITOID	
	Sycoryctes sp. indet. S	collection	V	EXTERNAL	PARASITOID	
	Sycoryctes sp. indet. S_2	collection	V	EXTERNAL	PARASITOID	
	Sycoryctes sp. indet. T	collection	V	EXTERNAL	PARASITOID	
	Sycoryctes sp. indet. U	collection	V	EXTERNAL	PARASITOID	
	Sycoryctes sp. indet. V	collection	V	EXTERNAL	PARASITOID	
	Sycoryctes sp. indet. V_2	collection	V	EXTERNAL	PARASITOID	
	Sycoryctes sp. indet. W	collection	V	EXTERNAL	PARASITOID	
	Sycoryctes sp. indet. W_2	collection	V	EXTERNAL	PARASITOID	
	Sycoryctes sp. indet. X	collection	V	EXTERNAL	PARASITOID	
	Sycoscapteridea monilifera Westwood	Wiebes (1967c)	V	EXTERNAL	PARASITOID	
	Sycoscapteridea sp. indet. A	collection	V	EXTERNAL	PARASITOID	
	Sycoscapteridea sp. indet. B	collection	V	EXTERNAL	PARASITOID	
	Sycoscapteridea sp. indet. C	collection	V	EXTERNAL	PARASITOID	
	Sycoscapteridea sp. indet. C_2	collection	V	EXTERNAL	PARASITOID	
	Sycoscapteridea sp. indet. D	collection	V	EXTERNAL	PARASITOID	
	Sycoscapteridea sp. indet. E	collection	V	EXTERNAL	PARASITOID	
	Sycoscapteridea sp. indet. E_2	collection	V	EXTERNAL	PARASITOID	
	Sycoscapteridea sp. indet. F	collection	V	EXTERNAL	PARASITOID	
	Sycoscapteridea sp. indet. G	collection	V	EXTERNAL	PARASITOID	
	Sycoscapteridea sp. indet. G_2	collection	V	EXTERNAL	PARASITOID	
	Sycoscapteridea sp. indet. H	collection	V	EXTERNAL	PARASITOID	
SYCORYCTINAE Apcryptini						
	Apocrypta guineensis Grandi	collection	V	EXTERNAL	PARASITOID	
	A. longitarsus Grandi	collection	V	EXTERNAL	PARASITOID	

FAMILY/SUBFAMILY	FIG WASP	SOURCE	MALE MORPHOLOGICAL TYPE	OVIPOSITION BEHAVIOUR	LARVAL BIOLOGY	NOTES ON TAXONOMY
	Apocrypta sp. A	collection	V	EXTERNAL	PARASITOID	
SYCOPHAGINAE						
	'*Eukoebelea*' *sycomori* Wiebes	collection	V	EXTERNAL	GALLER	for true *Eukoebelea* see Boucek (1988)
	'*Eukoebelea*' sp. indet. A	collection	V	EXTERNAL	GALLER	
	'*Eukoebelea*' sp. indet. B	collection	V	EXTERNAL	GALLER	
	'*Eukoebelea*' sp. indet. B	collection	V	EXTERNAL	GALLER	
	'*Idarnes*' *gracile* Wiebes	(only ♂) Wiebes (1968b)	V	EXTERNAL	GALLER	for true *Idarnes* see Wiebes (1968)
	'*Idarnes*' sp. indet. A	collection	V	EXTERNAL	GALLER	
	'*Idarnes*' sp. indet. B	collection	V	EXTERNAL	GALLER	
	'*Idarnes*' sp. indet. B_2	collection	V	EXTERNAL	GALLER	
	'*Idarnes*' sp. indet. C	collection	V	EXTERNAL	GALLER	
	Parakoebelea gigas Mayr	Wiebes (1968b)	V	EXTERNAL	GALLER	
	'*Parakoebelea*' sp. indet. A	collection	V	EXTERNAL	GALLER	
	'*Parakoebelea*' sp. indet. B	collection	V	EXTERNAL	GALLER	
	Sycophaga cyclostigma Waterston	collection	V	INTERNAL	GALLER	
	S. sycomori L.	collection	V	INTERNAL	GALLER	
	Sycophaga sp. indet. A	collection	V	INTERNAL	GALLER	
AGAONINAE						
	Pleistodontes blandus Wiebes	Wiebes (1963)	V	INTERNAL	GALLER	
	P. b. rennellensis Wiebes	Wiebes (1968)	V	INTERNAL	GALLER	
	P. plebejus Wiebes	Wiebes (1963)	V	INTERNAL	GALLER	
	P. rieki Wiebes	Wiebes (1963)	V	INTERNAL	GALLER	
	Deilagaon annulatae Wiebes	Wiebes (1977c)	V	INTERNAL	GALLER	
	D. chrysolepidis Wiebes	Wiebes (1977c)	V	INTERNAL	GALLER	
	D. megarhopalum Grandi	Wiebes (1977c)	V	INTERNAL	GALLER	

FAMILY/SUBFAMILY	FIG WASP	SOURCE	MALE MORPHOLOGICAL TYPE	OVIPOSITION BEHAVIOUR	LARVAL BIOLOGY	NOTES ON TAXONOMY
	Waterstoniella borneana Wiebes	Wiebes (1982b)	V	INTERNAL	GALLER	
	W. javana Wiebes	Wiebes (1982b)	V	INTERNAL	GALLER	
	W. malayana Wiebes	Wiebes (1982b)	V	INTERNAL	GALLER	
	W. sumatrana Wiebes	Wiebes (1982b)	V	INTERNAL	GALLER	
	W. williamsi Wiebes	Wiebes (1982b)	V	INTERNAL	GALLER	
	Ceratosolen adenospermae Wiebes	Wiebes (1965b)	V	INTERNAL	GALLER	
	C. abnormis Wiebes	Wiebes (1963)	V	INTERNAL	GALLER	
	C. albulus Wiebes	Wiebes (1963)	V	INTERNAL	GALLER	
	C. arabicus Mayr &.	collection	V	INTERNAL	GALLER	
	C. armipes Wiebes	Wiebes (1963)	V	INTERNAL	GALLER	
	C. bianchii Wiebes	Wiebes (1963)	V	INTERNAL	GALLER	
	C. bimerus Wiebes	Wiebes (1963)	V	INTERNAL	GALLER	
	C. bisulcatus Wiebes	Wiebes (1963)	V	INTERNAL	GALLER	
	C. boschmai Wiebes	Wiebes (1963)	V	INTERNAL	GALLER	
	C. brongersmai Wiebes	Wiebes (1963)	V	INTERNAL	GALLER	
	C. calopilinae Wiebes	Wiebes (1963)	V	INTERNAL	GALLER	
	C. constrictus Mayr	Wiebes (1963)	V	INTERNAL	GALLER	
	C. capensis Grandi &	collection	V	INTERNAL	GALLER	
	C. corneri Wiebes	Wiebes (1963)	V	INTERNAL	GALLER	
	C. crassitarsus Mayr	Wiebes (1963)	V	INTERNAL	GALLER	
	C. dentifer Wiebes	Wiebes (1963)	V	INTERNAL	GALLER	
	C. emarginatus Mayr	Wiebes (1963)	V	INTERNAL	GALLER	
	C. flabellatus Grandi	collection	V	INTERNAL	GALLER	
	C. fusciceps Mayr	Wiebes (1963)	V	INTERNAL	GALLER	
	C. galili Wiebes	collection	V	INTERNAL	GALLER	
	C. gracilis Wiebes	Wiebes (1963)	V	INTERNAL	GALLER	
	C. grandii Wiebes	Wiebes (1963)	V	INTERNAL	GALLER	
	C. gressitti Wiebes	Wiebes (1963)	V	INTERNAL	GALLER	
	C. gravelyi Grandi	Wiebes (1963)	V	INTERNAL	GALLER	
	C. hooglandi Wiebes	Wiebes (1963)	V	INTERNAL	GALLER	
	C. humatus Wiebes	Wiebes (1963)	V	INTERNAL	GALLER	
	C. immanis Wiebes	Wiebes (1963)	V	INTERNAL	GALLER	
	C. indigenus Wiebes	Wiebes (1963)	V	INTERNAL	GALLER	
	C. internatus Wiebes	Wiebes (1963)	V	INTERNAL	GALLER	
	C. iodotrichae Wiebes	Wiebes (1963)	V	INTERNAL	GALLER	

FAMILY/SUBFAMILY	FIG WASP	SOURCE	MALE MORPHOLOGICAL TYPE	OVIPOSITION BEHAVIOUR	LARVAL BIOLOGY	NOTES ON TAXONOMY
	C. josephi Wiebes	Wiebes (1963)	V	INTERNAL	GALLER	
	C. manus Wiebes	Wiebes (1963)	V	INTERNAL	GALLER	
	C. marshalli Grandi	Wiebes (1963)	V	INTERNAL	GALLER	
	C. medlerianus Wiebes	Wiebes (1980a)	V	INTERNAL	GALLER	
	C. megacephalus Grandi	collection	V	INTERNAL	GALLLER	
	C. migatorius Grandi	Wiebes (1963)	V	INTERNAL	GALLER	
	C. moderatus Wiebes	Wiebes (1963)	V	INTERNAL	GALLER	
	C. nexilis Wiebes	Wiebes (1980a)	V	INTERNAL	GALLER	
	C. notus Baker	Wiebes (1963)	V	INTERNAL	GALLER	
	C. nugatorius Grandi	Wiebes (1963)	V	INTERNAL	GALLER	
	C. orientalis Wiebes	Wiebes (1963)	V	INTERNAL	GALLER	
	C. pilipes Wiebes	Wiebes (1963)	V	INTERNAL	GALLER	
	C. praestans Wiebes	Wiebes (1963)	V	INTERNAL	GALLER	
	C. pygmaeus Grandi	Wiebes (1963)	V	INTERNAL	GALLER	
	C. solmsi Mayr	Wiebes (1963)	V	INTERNAL	GALLER	
	C. sordidus Wiebes	Wiebes (1963)	V	INTERNAL	GALLER	
	C. striatus Mayr	Wiebes (1963)	V	INTERNAL	GALLER	
	C. vechti Wiebes	Wiebes (1963)	V	INTERNAL	GALLER	
	C. vissali Wiebes	Wiebes (1981b)	V	INTERNAL	GALLER	
	Blastophaga boschmai Wiebes	Wiebes (1964a)	V	INTERNAL	GALLER	
	B. copiosae Wiebes	Wiebes (1980a)	V	INTERNAL	GALLER	
	B. jacobsi Wiebes	Wiebes (1964b)	V	INTERNAL	GALLER	
	B. massii Grandi	Wiebes (1966)	V	INTERNAL	GALLER	
	B. wassae Wiebes	Wiebes (1980a)	V	INTERNAL	GALLER	
	Kradibia brownii Ashmead	Wiebes (1978b)	V	INTERNAL	GALLER	
	K. cowani Saunders	Wiebes (1978b)	V	INTERNAL	GALLER	
	K. gestroi afrum Wiebes	collection	V	INTERNAL	GALLER	
	K. hilli Wiebes	Wiebes (1978b)	V	INTERNAL	GALLER	
	K. setigera Wiebes	Wiebes (1978b)	V	INTERNAL	GALLER	
	Dolichoris flabellata Wiebes	Wiebes (1979b)	V	INTERNAL	GALLER	
	D. inornata Wiebes	Wiebes (1979b)	V	INTERNAL	GALLER	
	Wiebesia partita Boucek	Wiebes (1969	V	INTERNAL	GALLER	
	Agaon armatum Wiebes	Wiebes (1974c)	V	INTERNAL	GALLER	
	A. baliolum Wiebes	Wiebes (1974c)	V	INTERNAL	GALLER	

FAMILY/SUBFAMILY	FIG WASP	SOURCE	MALE MORPHOLOGICAL TYPE	OVIPOSITION BEHAVIOUR	LARVAL BIOLOGY	NOTES ON TAXONOMY
	A. bekiliensis Risbec	Wiebes (1970)	V	INTERNAL	GALLER	
	A. camerunensis Wiebes	Wiebes (1974c)	V	INTERNAL	GALLER	
	A. hladikae Wiebes	Wiebes (1979b)	V	INTERNAL	GALLER	
	A. kielandi Wiebes	Wiebes (1974c)	V	INTERNAL	GALLER	
	A. medleri Wiebes	Wiebes (1972a)	V	INTERNAL	GALLER	
	A. megalopon Wiebes	Wiebes (1976)	V	INTERNAL	GALLER	
	A. michaloudi Wiebes	Wiebes (1979b)	V	INTERNAL	GALLER	
	A. paradoxum Dalman	Wiebes (1968c)	V	INTERNAL	GALLER	
	A. peniculum Wiebes	Wiebes (1974c)	V	INTERNAL	GALLER	
	Alfonsiella bergi Wiebes	collection	IV	INTERNAL	GALLER	
	A. binghami Wiebes	Wiebes (1988)	IV	INTERNAL	GALLER	
	A. brongersmai Wiebes	collection	IV	INTERNAL	GALLER	
	A. fimbriata Waterston	Wiebes (1988)	IV	INTERNAL	GALLER	
	A. longiscapa Wiebes	collection	IV	INTERNAL	GALLER	
	A. michaloudi Wiebes	Wiebes (1988)	IV	INTERNAL	GALLER	
	A. natalensis Wiebes	Wiebes (1972a)	IV	INTERNAL	GALLER	
	Allotriozoon heterandromorphum Grandi	collection	V	INTERNAL	GALLER	
	A. nigeriense Wiebes	Wiebes (1974c)	V	INTERNAL	GALLER	
	A. prodigiosum Grandi	collection	V	INTERNAL	GALLER	
	Nigeriella excavata Compton	collection	IV	INTERNAL	GALLER	
	N. fusciceps Wiebes	Wiebes (1974a)	IV	INTERNAL	GALLER	
	N. letouzeyi Wiebes	Wiebes (1974a)	IV	INTERNAL	GALLER	
	Courtella armata (Wiebes)	collection	V	INTERNAL	GALLER	
	C. bekiliensis (Risbec)	collection	V	INTERNAL	GALLER	
	C. gabonensis Wiebes	Michaloud *et al* (1985)	V	INTERNAL	GALLER	
	C. michaloudi (Wiebes)	collection	V	INTERNAL	GALLER	
	C. wardi Compton	collection	V	INTERNAL	GALLER	
	Elisabethiella baijnathi Wiebes	collection	V	INTERNAL	GALLER	
	E. bergi Wiebes	collection	V	INTERNAL	GALLER	
	E. comptoni Wiebes	collection	V	INTERNAL	GALLER	
	E. enriquesi (Grandi)	collection	V	INTERNAL	GALLER	
	E. glumosae Wiebes	collection	V	INTERNAL	GALLER	

FAMILY/SUBFAMILY	FIG WASP	SOURCE	MALE MORPHOLOGICAL TYPE	OVIPOSITION BEHAVIOUR	LARVAL BIOLOGY	NOTES ON TAXONOMY
	E. platyscapa Wiebes	collection	V	INTERNAL	GALLER	
	E. socotrensis Mayr	collection	V	INTERNAL	GALLER	
	E. stuckenbergi (Grandi)	Boucek *et al* (1981)	V	INTERNAL	GALLER	
	Platyscapa arnottiana Wiebes	Wiebes & Abdurahiman (1980)	V	INTERNAL	GALLER	
	P. awekei Wiebes	Wiebes & Abdurahiman (1980)	V	INTERNAL	GALLER	
	P. binghami Wiebes	Wiebes & Abdurahiman (1980)	V	INTERNAL	GALLER	
	P. corneri Wiebes	Wiebes & Abdurahiman (1980)	V	INTERNAL	GALLER	
	P. desertorum Compton	collection	V	INTERNAL	GALLER	
	P. etiennei Wiebes	Wiebes (1977b)	V	INTERNAL	GALLER	
	P. fischeri Wiebes	Wiebes (1977b)	V	INTERNAL	GALLER	
	P. soraria Wiebes	Wiebes & Abdurahiman (1980)	V	INTERNAL	GALLER	
	Pegoscapus tomentellae Wiebes	Wiebes (1983)	V	INTERNAL	GALLER	
	P. flagellatus Wiebes	Wiebes (1983)	V	INTERNAL	GALLER	

APPENDIX 2 Fig wasps and their host *Ficus* species that were used to determine male morphological types in chapter 2. *Ficus* are listed in taxonomic order and classified according to Berg (1990). Fig wasps are listed in alphabetical order for each *Ficus* species.

FICUS SPECIES	FIG WASP	LOCALITY	COLLECTOR/S
subgenus **Ficus** section **Sycidium** Miq.			
F. asperiifolia Miq.	*Eukoebelea* sp. indet. A	Katalemwa, Uganda	D. Hill
	Kradibia hilli Wiebes	"	"
	Sycoryctes sp. indet. B	"	"
	Sycoryctes sp.indet. B_2	"	"
F. capreifolia Delile	*Kradibia gestroi afrum* Wiebes	Gona-Re-Zhou, near Chipinda Pools, Lundi River, Zimbabwe 32° 00' E, 22° 00' S	A. Gardiner
	Philotrypesis sp. indet. D	Botanical Gardens, Pretoria, Transvaal, South Africa 28° 09' E, 24° 43' S	S.G. Compton
	Sycoryctes sp. indet. E	Gona-Re-Zhou, near Chipinda Pools, Lundi River, Zimbabwe 32° 00' E, 22° 00' S	A. Gardiner
subgenus **Sycomorus** (Gasp.) Mildbr. & Burret			
F. sycomorus L.	*Apocrypta longitarsus* Grandi	Windhoek Gardens, Windhoek, Namibia 17° 05' E, 22° 35' S	S.G. Compton
	Ceratasolen arabicus Mayr	Mapalane, Swamp Forest,Natal, South Africa 32° 22' E, 28° 22' S	S.G. Compton

FICUS SPECIES	FIG WASP	LOCALITY	COLLECTOR/S
	Ceratosolen galili Wiebes	Abel Erasmus Pass, Transvaal, South Africa 30° 40' E, 24° 30' S	S.G. Compton
	'Eukoebelea' sycomori Wiebes	Mkuzi Game Park, Natal, South Africa 32° 18' E, 27° 10' S	S. Vincent
	'Idarnes' sp. indet. B	Louis Trichardt, eastern Transvaal, South Africa 29° 54' E, 23° 02' S	S.G. Compton
	'Idarnes' sp. indet. B_2	Mazoe Citrus Estates, Mazoe, Zimbabwe 31° 00' E, 17° 05' S	A. Gardiner
	Parakoebelea gigas Mayr	"	"
	Sycophaga sycomori L.	Mapalane, Swamp Forest,Natal, South Africa32° 22' E, 28° 22' S	S.G. Compton
	Sycoscapter sp. indet. K	Abel Erasmus Pass, Transvaal, South Africa 30° 40' E, 24° 30' S	S.G. Compton
	Sycoscapteridea sp. indet. G	"	"
	Sycoscapteridea sp. indet. G_2	"	"
	Watshamiella sp. indet. D	Louis Trichardt, eastern Transvaal, South Africa 29° 54' E, 23° 02' S	S.G. Compton
F. mucoso Ficalho	*Ceratosolen arabicus* Mayr &. (only ♀)	Budongo Forest Reserve, Uganda 31° 00' E, 00° 45' S	D. Hill
	'Eukeobelea' sp. indet. B (only ♀)	"	"
	'Idarnes' sp. indet. A (only ♀)	"	"
	'Parakoebelea' sp. indet. A (only ♀)	"	"

FICUS SPECIES	FIG WASP	LOCALITY	COLLECTOR/S
	Sycophaga sp. indet. A (only ♀)	"	"
	Sycophila sp. indet. C (only ♂)	"	"
	Sycoryctes sp. indet. O	"	"
	Sycoscapteridea sp. indet. C (only ♀)	"	"
	Sycoscapteridea sp. indet. C_2 (only ♀)	"	"
	Watshamiella sp. indet. A	"	"
F. sur Forssk.	*Apocrypta guineensis* Grandi	Hluhluwe Rest Camp, Natal, South Africa 32°15' E, 28° 02' S	S.G. Compton
	Ceratosolen capensis Grandi &	Mapalane, Natal, South Africa 32° 22' E, 28° 22' S	S.G. Compton
	Ceratosolen flabellatus Grandi	Bomana, Cameroon	S.G. Compton
	Ficomila sp. indet. C	Mapalane, Natal, South Africa 32° 22' E, 28° 22' S	S.G. Compton
	Ficomila sp. indet. C_2	Budongo Forest Reserve, Uganda 31° 00' E, 00° 45' S	D. Hill
	Ficomila sp. indet. C_3	Katalemwa, Uganda	D. Hill
	Ficomila sp. indet. C_4	"	"
	'Idarnes' sp. indet. B	Abel Erasmus Pass, Eastern Transvaal, South Africa 30° 40' E, 24° 30' S	S.G. Compton
	'Parakoebelea' sp. indet. B	Blyde Rivier Poort, Eastern Transvaal, South Africa 30° 52' E, 24° 38' S	S.G. Compton
	Sycophaga cyclostigma Waterston	Mapalane, Natal, South Africa 32° 22' E, 28° 22' S	S.G. Compton

FICUS SPECIES	FIG WASP	LOCALITY	COLLECTOR/S
	Sycoscapteridea sp. indet. F	Hluhluwe Rest Camp, Natal, South Africa 32° 15' E, 28° 02' S	S.G. Compton
	Watshamiella sp. indet. C	Tzaneen, eastern Transvaal, South Africa 30° 10' E, 23° 50' S	S.G. Compton
F. vallis-choudae Delile	*Apocrypta* sp. indet. A	Kampala, Uganda 32° 10' E, 00° 40' S	D. Hill
	Ceratosolen megacephalus Grandi	"	"
	Camarothorax sp. indet. J	"	"
	Eukoebelea sp. indet. C	"	"
	Sycophila sp. indet. J	"	"
	Sycoscapteridea sp. indet. H	"	"
subgenus **Urostigma** (Gasp.) Miq. section **Urostigma**			
F. ingens (Miq.) Miq.	*Acophila* sp. indet. A	road to Martindale, Eastern Cape, South Africa	S.G. Compton
	Acophila sp. indet. A_2	island off Monkey Bay, Lake Malawi, Malawi	M. Farqhuar
	'*Camarothorax*' sp. indet. D	Coombs, eastern Cape, South Africa 26° 50' E, 33° 19' S	S.G. Compton
	'*Camarothorax*' sp. indet. A	"	"
	Camarothorax sp. indet. A	"	"
	genus indet. B	"	"
	Otitesella sp. indet. I	"	"
	Philotrypesis sp. indet. H	south-west of Nzhelele, Transvaal, South Africa	S.G. Compton
	Platyscapa soraria Wiebes	Coombs, eastern Cape, South Africa 26° 50' E, 33° 19' S	S. Vincent

FICUS SPECIES	FIG WASP	LOCALITY	COLLECTOR/S
	Sycophila sp. indet. D	Coombs, eastern Cape,South Africa 26° 50' E, 33° 19' S	R.J. Nefdt
	Sycophila sp. indet. D_2	"	"
	Sycophila sp. indet. D_3	"	"
	Sycophila sp. indet. D_4	road to Martindale, Eastern Cape, South Africa	S.G. Compton
	Sycoryctes sp. indet. M	north-east of Ubombo, Natal, South Africa	S.G. Compton
	Sycoryctes sp. indet. M_2	"	"
	Sycoryctes sp. indet. M_3	Coombs, eastern Cape, South Africa 26° 50' E, 33° 19' S	S. Vincent
F. cordata cordata Thunb.	genus indet. A	Augrabies Falls, northern Cape, South Africa 20° 25' E, 28° 40' S	S.G. Compton
	Platyscapa desertorum Compton	"	"
	Sycoryctes sp. indet. G	"	"
	Sycoryctes sp. indet. G_2	"	"
subsp. *salicifolia* (Vahl). C.C. Berg	*Otitesella serrata* Mayr	Kruger Park, Olifants Camp,Transvaal, South Africa 31° 45' E, 24° 00' S	S.G. Compton
	Philotrypesis sp. indet. E	"	S.G. Compton
	Platyscapa awekei Wiebes	Tuli Block, Mashatu Game Reserve, Botswana 28° 00' E, 22° 00' S	P. Lloyd
	Sycoryctes sp. indet. H	Pretoria Botanical Gardens, Pretoria, Transvaal,South Africa 28° 09' E, 24° 43' S	S.G. Compton

FICUS SPECIES	FIG WASP	LOCALITY	COLLECTOR/S
F. verruculosa Warb.	*Otitesella* sp. indet. R	Kosi Bay, at camp site,Natal, South Africa 26° 58' E, 32° 45' S	S. Vincent
	Philotrypesis sp. indet. N	"	"
	Platyscapa binghami Wiebes	Sultrutex, Lusaka, Zambia 28° 20' E, 15° 30' S	R. Nefdt
	Sycoryctes sp. indet. X	"	"
subgenus **Urostigma** section **Galoglychia** subsection **Galoglychia**			
F. saussureana DC	*Allotriozoon prodigiosum* Grandi	Mpenga Forest, on the Masaka road, Uganda	D. Hill
	'Camarothorax' sp. indet. F	"	"
	'Camarothorax' sp. indet. F_2	"	"
	Otitesella sp. indet. M	"	"
	Philotrypesis sp. indet. J	"	"
	Sycoryctes sp. indet. R	"	"
	Sycoscapter sp. indet. H	"	"
	Sycoscapter sp. indet. H_2	"	"
F. chlamydocarpa Mildbr. & Burret	*Allotriozoon nigeriense* Wiebes	Bambili, Cameroon	S.G. Compton
	'Camarothorax' sp. indet. E	"	"
	Otitesella sp. indet. C	"	"
	Sycophila sp. indet. B	"	"
	Sycophila sp. indet. B_2	"	"

FICUS SPECIES	FIG WASP	LOCALITY	COLLECTOR/S
	Sycophila sp. indet. B_3	"	"
	Sycoryctes sp. indet. F	"	"
	Sycoscapter sp. indet. D	"	"
F. lutea Vahl	*Allotriozoon heterandromorphum* Grandi	Umhlanga Rocks, Durban, Natal, South Africa 31° 06' E, 29° 45' S	S.G. Compton
	'Camarothorax' sp. indet. K	Hibberdene, South Coast, Natal, South Africa 30° 35' E, 30° 35' S	S.G. Compton
	'Camarothorax' sp. indet. K_2	north of Embu, Kenya	C. van Someren
	'Camarothorax' sp. indet. K_3	"	"
	Crossogaster sp. indet. B	Hibberdene, South Coast, Natal, South Africa 30° 35' E, 30° 35' S	S.G. Compton
	Otitesella sp. indet. J	Mtunzini, Natal, South Africa 31° 45' E, 28° 52' S	S.G. Compton
	Otitesella sp. indet. J_2	north of Embu, Kenya	C. van Someren
	Philotrypesis sp. indet. I	Farthill, Kenya	C. van Someren
	Philotrypesis sp. indet. I_2	"	"
	Sycophila sp. indet. E	"	"
	Sycophila sp. indet. E_2	Hibberdene, South Coast, Natal, South Africa 30° 35' E, 30° 35' S	S.G. Compton
	Sycophila sp. indet. E_3	"	"
	Sycophila sp. indet. E_4	north of Embu, Kenya	C. van Someren

FICUS SPECIES	FIG WASP	LOCALITY	COLLECTOR/S
	Sycophila sp. indet. E_5	Hibberdene, South Coast, Natal, South Africa 30° 35' E, 30° 35' S	S.G. Compton
	Sycoryctes sp. indet. N	Umhlanga Rocks, Durban, Natal, South Africa 31° 06' E, 29° 45' S	S.G. Compton
	Sycoryctes sp. indet. N_2	Mtunzini, Natal, South Africa 31° 45' E, 28° 52' S	S.G. Compton
	Sycoscapter sp. indet. F	"	"
subgenus **Urostigma** section **Galoglchia** subsection **Platyphyllae**			
F. bussei Mildbr. & Burret	*'Camarothorax'* sp. indet. T	north of Mangocni, Malawi	S.G. Compton
F. glumosa Delile	*'Camarothorax'* sp. indet. C	Mtamvuna, Natal, South Africa 29° 50' E, 30° 45' S	S.G. Compton
	'Camarothorax' sp. indet. C_2	north of Jozini, Natal, South Africa	S.G. Compton
	'Camarothorax' sp. indet. C_3	south of Jozini, Natal, South Africa	S.G. Compton
	Crossogaster sp. indet. A	Pongola, Natal, South Africa 31° 40' E, 27° 20' S	S. van Noort & A. Ware
	Crossogaster sp. indet. A_2	"	"
	Elisabethiella glumosae Wiebes	south of Jozini, Natal, South Africa	S.G. Compton
	Otitesella sp. indet. G	Mazoe Citrus Estates, Zimbabwe 31° 00' E, 17° 05' S	A. Gardiner

FICUS SPECIES	FIG WASP	LOCALITY	COLLECTOR/S
	Otitesella sp. indet. N	north of Jozini, Natal, South Africa	"
	Otitesella sp. indet. N_2	Oribi Gorge, Natal, South Africa 30° 18' E, 30° 40' S	S.G. Compton
	Phagoblastus sp. indet. D	Mazoe Citrus Estates, Zimbabwe 31° 00' E, 17° 05' S	A. Gardiner
	Philotrypesis sp. indet. F	north of Jozini, Natal, South Africa	S.G. Compton
	Sycophila sp. indet. C	south-west of Nzhelele, Transvaal, South Africa	S.G. Compton
	Sycophila sp. indet. C_2	"	"
	Sycophila sp. indet. C_3	Mtamvuna, Natal, South Africa 29° 50' E, 30° 45' S	S.G. Compton
	Sycoryctes sp. indet. K	north of Jozini, Natal, South Africa	S.G. Compton
	Sycoryctes sp. indet. K_2	"	"
	Sycoscapter sp. indet. E	"	"
F. stuhlmannii Warb.	*Alfonsiella binghami* Wiebes	Lusaka Cathedral, Zambia 28° 20' E, 15° 30' S	R. Nefdt
	'Camarothorax' sp. indet. G	Hluhluwe Game Park, Natal, South Africa 32° 15' E, 28° 02' S	S.G. Compton
	Crossogaster sp. indet. C	Lusaka Cathedral, Zambia 28° 20' E, 15° 30' S	R.J. Nefdt
	Otitesella sp. indet. S	"	"

FICUS SPECIES	FIG WASP	LOCALITY	COLLECTOR/S
	Otitesella sp. indet. S_2	north of Nelspruit, Transvaal, South Africa	P. Hulley
	Phagoblastus sp. indet. E	Hluhluwe Game Park, Natal, South Africa 32° 15' E, 28° 02' S	S.G. Compton
	Phagoblastus sp. indet. E_2	Lusaka Cathedral, Zambia 28° 20' E, 15° 30' S	R. Nefdt
	Philotrypesis sp. indet. L	Tshongwe, Natal, South Africa	S.G. Compton
	Sycophila sp. indet. H	Pongola, Natal, South Africa 31° 40' E, 27° 20' S	S. van Noort & A. Ware
	Sycophila sp. indet. H_2	Hluhluwe Game Park, Natal, South Africa 32° 15' E, 28° 02' S	S.G. Compton
	Sycophila sp. indet. H_3	"	"
	Sycoryctes sp. indet. S	Mbaswana, Natal, South Africa	S.G. Compton
	Sycoryctes sp. indet. S_2	Ingwavuma, Natal, South Africa 32° 05' E, 27° 10' S	S.G. Compton
	Sycoscapter sp. indet. I	Hluhluwe Game Park, Natal, South Africa 32° 15' E, 28° 02' S	S.G. Compton
	Sycoscapter sp. indet. I_2	Lusaka Cathedral, Zambia 28° 20' E, 15° 30' S	R. Nefdt
	Watshamiella sp. indet. B	Tshongwe, Natal, South Africa	S.G. Compton
F. tettensis Hutch.	*Nigeriella excavata* Compton	north-eastern part of Tuli Block, Botswana	P. Lloyd

FICUS SPECIES	FIG WASP	LOCALITY	COLLECTOR/S
	Otitesella sp. indet. O	north of Sibasa, Transvaal, South Africa	S.G. Compton
	Sycoryctes sp. indet. T (only ♀)	"	"
F. abutilifolia (Miq.) Miq.	*Camarothorax equicollus* Boucek	Kariba boarder post, Zimbabwe	P. Lloyd
	Elisabethiella comptoni Wiebes	Abel Erasmus Pass, Transvaal, South Africa 30° 40' E, 24° 30' S	S.G. Compton
	Ficomila sp. indet. A	Kariba boarder post, Zimbabwe	P. Lloyd
	Phagoblastus sp. indet. A	Abel Erasmus Pass, Transvaal, South Africa 30° 40' E, 24° 30' S	S.G. Compton
	Philotrypesis sp. indet. A	"	"
	Sycophila sp. indet. A	Biyani area, Transvaal, South Africa	S.G. Compton
	Sycophila sp. indet. A_2	"	"
	Sycophila sp. indet. A_3	Jozini, Natal, South Africa 32° 05' E, 27° 25' S	S.G. Compton
	Sycoryctes sp. indet. A	Abel Erasmus Pass, Transvaal, South Africa 30° 40' E, 24° 30' S	S.G. Compton
	Sycoryctes sp. indet. A_2	"	"
	Sycoryctes sp. indet. A_3	♀ Mkuzi Game Park, Natal, South Africa 32° 18' E, 27° 10' S	S.G. Compton
		♂ Botanical Gardens, Pretoria, Transvaal, South Africa 28° 09' E, 24° 43' S	"

FICUS SPECIES	FIG WASP	LOCALITY	COLLECTOR/S
	Sycoscapter sp. indet. A	Abel Erasmus Pass, Transvaal, South Africa 30° 40' E, 24° 30' S	S.G. Compton
F. trichopoda Baker	*'Camarothorax'* sp. indet. I	Sodwana, Natal, South Africa 32° 40' E, 27° 35' S	S.G. Compton
	Crossogaster sp. indet. D	Kosi Bay, campsite, Natal, South Africa 26° 58' E, 32° 45' S	S. Vincent
	Elisabethiella bergi Wiebes	north of Sibaya, Natal, South Africa	S.G. Compton
	Ormyrus sp. indet. B	Mselini, near Sibaya, Natal, South Africa	S.G. Compton
	Otitesella sp. indet. Q	"	"
	Philocaenus sp. indet. A	Kosi Bay, campsite, Natal, South Africa 26° 58' E, 32° 45' S	S. Vincent
	Philotrypesis sp. indet. M	north of Sibaya, Natal, South Africa	S.G. Compton
	Philotrypesis sp. indet. M_2	"	"
	Sycophila sp. indet. I	"	"
	Sycophila sp. indet. I_2	Sodwana, Natal, South Africa 32° 40' E, 27° 35' S	S.G. Compton
	Sycophila sp. indet. I_3	"	"
	Sycophila sp. indet. I_4	"	"
	Sycoryctes sp. indet. W	north of Sibaya, Natal, South Africa	S.G. Compton
	Sycoryctes sp. indet. W_2	Mselini, near Sibaya, Natal, South Africa	S.G. Compton
	Sycoscapter sp. indet. N	"	"

FICUS SPECIES	FIG WASP	LOCALITY	COLLECTOR/S
	Sycoscapter sp. indet. N_2	"	"
	Watshamiella sp. indet. F	"	"
subgenus **Urostigma** section **Galoglychia** subsection **Chlamydodorae** (Mildbr. & Burret) C.C. Berg			
F. fischeri Mildbr. & B	*'Camarothorax'* sp. indet. B	Barclay Farm, Chisamba, Zambia 28° 20' E, 14° 54' S	R. Nefdt
	Elisabethiella platyscapa Wiebes	Zambezi Farm, Livingstone, Zambia 25° 50' E, 17° 40' S	S.Vincent
	Ficomila sp. indet. B	"	"
	Otitesella sp. indet. F	"	"
	Sycoryctes sp. indet. J	"	"
F. craterostoma Mildbr. & Burret	*Alfonsiella michaloudi* Wiebes	Pipithi Waterfalls, Venda, South Africa	S.G.Compton
	'Camarothorax' sp. indet. S	"	"
	Otitesella sp. indet. E	"	"
	Phagoblastus sp. indet. C	"	"
	Sycoryctes sp. indet. I	"	
F. burtt-davyi Hutch.	*Elisabethiella baijnathi* Wiebes	Grahamstown, eastern Cape, South Africa 26° 03' E, 33° 05' S	S.G. Compton
	Otitesella uluzi Compton	"	"
	Otitesella sesquianellata van Noort	"	"
	Phagoblastus sp. indet. B	"	"
	Philotrypesis sp. indet. C	"	"

FICUS SPECIES	FIG WASP	LOCALITY	COLLECTOR/S
	Sycoryctes sp. indet. D	"	"
F. ilicina (Sonder) Miq.	*Elisabethiella eriquesi* (Grandi)	Springbok-Garies road, northern Cape, South Africa	A. Ware
	Otitesella sp. indet. H	Aneneus Pass, northern Cape, South Africa	A. Ware
	Philotrypesis sp. indet. G	Springbok-Garies road, northern Cape, South Africa	A. Ware
	Sycoryctes sp. indet. L	Spektafelberg Pass, northern Cape, South Africa 17° 40' E, 29° 42' S	S.G. Compton
	Sycoryctes sp. indet. L_2	Springbok-Garies road, northern Cape, South Africa	A. Ware
F. thonningii Bl.	*Camarothorax brevimucro* Boucek	Port St. Johns, Transkei, South Africa 29° 35' E, 31° 38' S	A. Pretorius
	'*Camarothorax*' sp. indet. H	Hluhluwe Game Park, Natal, South Africa 32° 15' E, 28° 02' S	S.G. Compton
	Camarothorax equicollus Boucek	Port St. Johns, Transkei, South Africa 29° 35' E, 31° 38' S	A. Pretorius
	Elisabethiella stuckenbergi Grandi &	Grahamstown, eastern Cape, South Africa 26° 03' E, 33° 05' S	S.G. Compton
	Eurytoma ficusgallae Boucek	"	"

FICUS SPECIES	FIG WASP	LOCALITY	COLLECTOR/S
	Otitesella tsamvi Wiebes	"	"
	Phagoblastus barbarus Grandi	"	"
	Philotrypesis parca Wiebes	"	"
	Syceurytoma ficus Boucek	"	"
	Sycophila punctum Boucek	Port St. Johns, Transkei, South Africa 29° 35' E, 31° 38' S	A. Pretorius
	Sycophila sp. indet. V	"	"
	Sycophila sp. indet. V_2	False Bay, Natal, South Africa 32° 20' E, 28° 00' S	S.G. Compton
	Sycophila sp. indet. V_3	Grahamstown, Eastern Cape, South Africa 26° 03' E, 33° 05' S	S.G. Compton
	Sycophila sp. indet. V_4	"	"
	Sycophila sp. indet. V_5	west of Ubombo, Natal, South Africa	S.G. Compton
	Sycoryctes hirtus Wiebes	Abel Erasmus Pass, Transvaal, South Africa 30° 40' E, 24° 30' S	S.G. Compton
	Sycoryctes remus Wiebes	Mazoe Citrus Estates, Zimbabwe 31° 00' E, 17° 05' S	A. Gardiner
	Sycoryctes sp. indet. U	Abel Erasmus Pass, Transvaal, South Africa 30° 40' E, 24° 30' S	S.G. Compton
	Sycoscapter sp. indet. L	Louis Trichardt, Eastern Transvaal, South Africa 29° 54' E, 23° 02' S	S.G. Compton
	Sycotetra sp. indet. A	"	"

FICUS SPECIES	FIG WASP	LOCALITY	COLLECTOR/S
	Watshamiella sp. indet. E	Umhlanga Rocks, Durban, Natal, South Africa 31° 06' E, 29° 45' S	S.G. Compton
subgenus **Urostigma** section **Galoglychia** subsection **Caulocarpae** (Mildbr. & Burret) C.C. Berg			
F. tremula Warb.	*Courtella wardi* Compton	Sihangwane, Natal, South Africa 32° 05' E, 27° 10' S	M. Ward
	Otitesella sp. indet. P	"	"
	Otitesella sp. indet. P_2	"	"
	Seres sp. indet. B (only ♀)	"	"
	Sycoryctes sp. indet. V	♀ Sihangwane, Natal, South Africa 32° 05' E, 27° 10' S	M. Ward
		♂ Kosi Bay, Natal, South Africa	"
	Sycoryctes sp. indet. V_2	Sihangwane, Natal, South Africa 32° 05' E, 27° 10' S	M. Ward
	Sycoscapter sp. indet. M	"	"
F. polita Vahl	'*Camarothorax*' sp. indet. D	Umhlanga Rocks, Durban, Natal, South Africa 31° 06' E, 29° 45' S	S.G. Compton
	Courtella bekiliensis (Risbec)	♂ east Lake Sibaya, Natal, South Africa	M. Ward
		♀ Umhlanga Rocks, Durban, Natal, South Africa 31° 06' E, 29° 45' S	S.G. Compton

FICUS SPECIES	FIG WASP	LOCALITY	COLLECTOR/S
	Otitesella sp. indet. K	Umhlanga Rocks, Durban, Natal, South Africa 31° 06' E, 29° 45' S	S.G. Compton
	Sycophila sp. indet. F	"	"
	Sycophila sp. indet. F_2	"	"
	Sycoryctes sp. indet. P	"	"
	Sycoscapteridea sp. indet. D	"	"
F. bizanae Hutch. & Burtt Davy	*Otitesella* sp. indet. A	Mtamvuna, Natal, South Africa 29° 50' E, 30° 45' S	S.G. Compton
	Philotrypesis sp. indet. B	"	"
	Sycoscapter sp. indet. B	"	"
	Sycoscapteridea sp. indet. A	"	"
F. sansibarica Warb. subsp. *macrosperma* (Mildbr. & Burret) C.C. Berg	*Courtella armata* Wiebes	Olifants Camp, Kruger Park, Transvaal, South Africa 31° 45' E, 24° 00' S	S.G. Compton
	Ormyrus sp. indet. A	"	"
	Otitesella sp. indet. L	Kabompo, Zambia 24° 30' E, 13° 40' S	R. Nefdt
	Philotrypesis sp. indet. K	"	"
	Seres sp. indet. A	"	"
	Seres sp. indet. A_2	"	"
	Sycophila sp. indet. G	Victoria, Natal, South Africa 30° 22' E, 29° 35' S	S.G. Compton
	Sycophila sp. indet. G_2	"	"
	Sycoryctes sp. indet. Q	"	"

FICUS SPECIES	FIG WASP	LOCALITY	COLLECTOR/S
F. s. macrosperma	*Sycoscapter* sp. indet. G	Kabompo, Zambia 24° 30' E, 13° 40' S	R. Nefdt
	Sycoscapteridea sp. indet. E	"	"
	Sycoscapteridea sp. indet. E_2	"	"
	Watshamiella sp. indet. G	Olifants Camp, Kruger Park, Transvaal, South Africa 31° 45' E, 24° 00' S	S.G. Compton
F. bubu Warb.	*Courtella michaloudi* (Wiebes)	east Lake Sibaya, Natal, South Africa	M. Ward
	Neosycophila sp. indet. A	"	"
	Otitesella sp. indet. B	"	"
	Philosycus sp. indet. A	"	"
	Sycoryctes sp. indet. C	"	"
	Sycoscapter sp. indet. C	"	"
	Sycoscapteridea sp. indet. B	"	"