Azanus mirza (Plötz). Ibaya Hill, Kisiwani River, Ubani Plot.
Azanus moriqua (Wallengren). Mbula, nr. Kisima Hill.
Azanus natalensis (Trimen)
Azanus ubaldus (Stoll). nr. Ubani Plot, Mbula, nr. Kisima Hill.
Eicochrysops hippocrates (Fabricius)
Eicochrysops messapus mahallakoaena (Wallengren)
Euchrysops barkeri (Trimen)
Euchrysops brunneus Bethune-Baker
Euchrysops malathana (Boisduval)
Euchrysops osiris osiris (Hopffer). Ibaya Hill.
Euchrysops subpallida Bethune-Baker. Nyati Plot.
Lepidochrysops lukenia van Someren [Pares]
Lepidochrysops neonegus neonegus (Bethune-Baker)
Freyeria trochylus (Freyer). Ubani Plot.

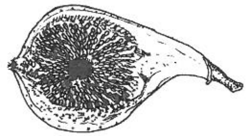

Fig wasps (Hymenoptera: Chalcidoidea: Agaonidae) and fig trees (Moraceae: *Ficus*) of Mkomazi

Simon van Noort & Stephen G. Compton

Introduction

The order Hymenoptera (wasps, bees and ants) is second only to the beetles in terms of species richness and abundance, and includes a diverse range of morphological forms and biologies. The superfamily Chalcidoidea is a large and economically important group of wasps, whose representatives are mostly parasitoids of other insects. 'Fig wasp' is a broad term applied to wasps of the superfamily Chalcidoidea that solely breed in figs (*Ficus*, Moraceae), but excludes wasps from this superfamily that are parasitoids of moth, beetle and fly larvae that sometimes also breed in figs. From a taxonomic perspective the term 'fig wasp' encompasses representatives of three families: Agaonidae, Eurytomidae and Ormyridae. Of the latter two families only a small proportion of their species are associated with figs, whereas all of the species placed in the Agaonidae are fig wasps. Hence the majority of fig wasps belong to the Agaonidae, which currently includes six distinct subfamilies (Boucek 1988).

In this chapter we assesses species richness of both the fig trees and their associated fig wasps in Mkomazi Game Reserve. As with most African countries the fig wasp fauna of Tanzania is poorly known, and this survey has played a valuable role in furthering our knowledge of Tanzanian fig wasps.

Ecology

Fig wasps and their host fig tree species, are important components of tropical and subtropical ecosystems, from both an abundance and diversity perspective and as an integral part of the food chain. The fascinating relationship between pollinating fig wasps (Agaoninae) and their host fig trees is a classic example of an obligate mutualism, where neither partner can reproduce without the other (Galil 1977, Janzen 1979). The interaction between figs and fig wasps is more complicated than first appears, because pollinating wasps are not the only fig wasps that utilise the fig flowers for propagation of their offspring. The fig also provides a suitable breeding site for a diverse array of non-pollinating fig wasps, which are either phytophagous (plant feeding), galling the ovules as do the pollinators, or parasitoids of the gall formers (Compton & van Noort 1992, Kerdelhué & Rasplus 1996a & 1996b).

The mutualism between pollinating fig wasps and fig trees is usually a one-to-one relationship (Ramirez 1970, Wiebes 1979, Wiebes & Compton 1990). Each fig tree species (approximately 750 worldwide) has a single pollinating fig wasp species and each wasp species is only associated with one fig tree species, although there are a few exceptions to this rule. Non-pollinating fig wasps are generally less specific with a number of species associated with more than a single host species, and often each fig tree species has two or three closely related non-pollinating fig wasp species breeding in its figs.

The developmental cycle of the fig comprises five distinct but inter-connecting stages with fig wasp larval development correlating strongly with fig development (Galil 1977). The cycle may encompass anything from 3 to 20 weeks (Bronstein 1992, Ware & Compton 1994). The fig is an urn-shaped receptacle containing hundreds of tiny flowers which line the inside walls of the central cavity and becomes receptive for pollination and oviposition early in the developmental cycle. Female pollinating wasps gain access to the inside of the fig through the ostiole (a tiny, narrow opening at the top end of the fig). The pollinating wasps are uniquely adapted to squeeze their way through the ostiole, having evolved a flattened head and body and many rows of backward pointing mandibular teeth situated on the underside of the head. Once inside the fig cavity, the female proceeds to unload pollen onto the stigmas and inserts her ovipositor down the style of the flower to oviposit within the ovule. The ovary swells up to form a gall and the wasp larvae feed on endosperm tissue in the galled ovary (Verkerke 1989). Although some non-pollinating wasp species also enter the fig for oviposition, and have then evolved similar physical adaptations to squeeze through the ostiole, most of the non-pollinators oviposit through the fig wall from the outside of the fig at various stages of fig development (Kerdelhué & Rasplus 1996a). These wasps often have extremely long ovipositors, the length of which is related to the wall thickness of their host fig. Fig size varies tremendously across species, and ranges from smaller than a marble to as large as a tennis ball. Towards the end of the fig developmental cycle, all the fig wasps breeding in a particular fig emerge from their galls within a short period of each other. Mating largely takes place within the confines of the fig before the males chew a hole through the fig wall to the exterior to allow the females to escape. Pollinator females actively load up pollen from the ripe anthers before emerging from the fig to search for young receptive figs to complete the cycle. Most of the figs within a crop on a fig tree are usually at the same stage of development, with the consequence that emerging female fig wasps need to find another fig tree to continue the reproductive cycle. This may require a long distance flight to locate a tree with receptive figs for oviposition and pollination. These tiny wasps, averaging between one and two millimetres in length, achieve this remarkable feat by homing in on gaseous chemicals, released by the figs when they are receptive for pollination (van Noort *et al.* 1989, Hossaert-McKey *et al.* 1994).

Once the female fig wasps have left the fig, it ripens and becomes attractive to fruit-eating birds, bats and monkeys. Because figs are produced throughout the year a continual supply of food is provided through periods when there is a seasonal dearth of other fruits. As such, fig trees are considered to be keystone species in many tropical and subtropical ecosystems (Terborgh 1986, Lambert & Marshall 1992), but see Gautier-Hion & Michaloud (1989) and Basset *et al.* (1997). To complete the reproductive cycle of the mutualism, fruit-eating vertebrates play an important role in the propagation of fig trees, acting as the dispersal agents of the seeds, which, at least in the case of birds, are positively affected by passage through the digestive tract, resulting in increased germination viability (Compton *et al.* 1996).

Fig trees

Regional richness

Of the 105 fig tree species that occur in the Afrotropical region (Berg & Wiebes 1992) an estimated 39 species are found in Tanzania (Berg & Hijman 1989). Ten of these species are distributionally restricted (endemic) to east Africa. Tanzania has a higher fig tree species richness than Kenya, but a lower richness than Uganda (Berg & Hijman 1989) (Table 18.1). The higher Ugandan species richness is attributable to the presence of ten species that are typical elements of the Guinea-Congolian forest region and whose distribution does not reach as far east as Kenya or Tanzania. 28 fig species occur in all three countries, five are shared between Tanzania and Kenya, four between Tanzania and Uganda and one between Uganda and Kenya (Berg & Hijman 1989).

Fig tree species richness is considerably higher in east Africa than southern Africa, where 32 species occur in the whole southern African subregion (defined as including Namibia, Botswana, Zimbabwe, Mozambique south of the Zambezi River, South Africa, Swaziland and Lesotho). 22 of these species are present in

Table 18.1 Fig tree species richness by country.

	Tanzania	Kenya	Uganda	South Africa
Ficus species	39	34	43	22

South Africa (Berg 1990). The lower southern African species richness can be ascribed to the temperate climate of large areas of southern Africa, making most of the region unsuitable for fig trees which prefer a tropical climate.

Species richness and distribution within Mkomazi Game Reserve

Nine fig tree species were recorded within Mkomazi Game Reserve (Table 18.2). It is highly probable that further species await discovery, and because of this there is value in assessing which of the remaining 30 Tanzanian species may potentially be present in the reserve.

Five of the Tanzanian fig species are restricted to rainforest in the north-west region effectively excluding them from Mkomazi Game Reserve. *Ficus capreifolia* Delile, *F. verruculosa* Warburg, and *F. trichopoda* Baker are associated with riverine or swamp conditions (Berg 1990, Berg & Wiebes 1992) and therefore unlikely to be found in the seasonally dry conditions in Mkomazi Game Reserve. However, the habitat along the Umba River, the only permanent water body in the reserve, has not been comprehensively surveyed for fig trees, with only a single limited visit to one locality within this area. Conceivably, these three riverine fig species may be present along the eastern boundary of the reserve. A further riverine species that is also found in ground-water forest (Berg & Hijman 1989), *F. vallis-choudae* Delile, is common just outside Mkomazi at the base of the South Pare Mountains where it is present in riverine forest. It is feasible that this species remains undetected within the reserve, although no suitable habitats were identified. *Ficus sur* Forsskål is usually associated with riverine conditions or moist forest but also occurs in woodland (Berg & Hijman 1989) and because it is a common and widespread species it is likely to be present in Mkomazi.

A further seven Tanzanian species are associated with forest (Berg & Hijman 1989), two of which, namely *F. exasperata* Vahl and *F. tremula acuta* (De Wild), were recorded on the South Pare Mountains during this programme. These two species together with *F. mucosa* Ficalho, *F. c. cyathistipula* Warb., *F. s. scassellatii* Pamp., *F. polita brevipedunculata* Berg and *F. chirindensis* Berg may be present in the limited montane forest patches within the reserve on hill tops such as Ibaya Hill and Maji Kununua. To date only *F. thonningii* Bl. has been recorded in montane forest in Mkomazi. The montane forest habitat within the reserve may be too degraded or limited in extent to support these forest endemics. *Ficus lingua depauperata* (Sim) Berg, *F. ottoniifolia ulugurensis* (Mildbr. & Burr.) Berg and *F. t. tremula* Warb. are associated with lowland dry forest or coastal bushland. These three species have been recorded by Hawthorne (1993) in the east African coastal forests, but are probably not present within Mkomazi.

Of the rock-splitters (species that often germinate and grow in cracks in rocks), *F. glumosa* Delile is a very common species within Mkomazi, occurring on many of the rocky ridges on the hills in the western end of the reserve and on isolated

rock outcrops, such as Kamakota Hill in the central region. *Ficus ingens* (Miquel) Miquel is far less common, having only been recorded on Kamakota Hill, Kisima Hill and at Ngurunga Pools, but undoubtably occurs in other unsurveyed rocky areas as well. Further rock-splitters that were expected to be present, such as *F. cordata salicifolia* (Vahl) Berg, *F. abutilifolia* (Miquel) Miquel, *F. platyphylla* Delile, and *F. populifolia* Vahl, have not yet been recorded from Mkomazi.

A number of woodland species, *F. wakefieldii* Hutch., *F. n. natalensis* Hochst., *F. nigro-punctata* Mildbr. & Burr., *F. fischeri* Mildbr. & Burr., *F. amadiensis* De Wild, *F. faulkneriana* Berg, *F. usambarensis* Warburg and *F. ovata* Vahl may yet be recorded from the reserve. If they are present they are likely to be concentrated in the wetter western areas along perennial water courses, although this habitat in the vicinity of Ibaya Camp has been well surveyed for fig trees. *Ficus stuhlmannii* Warb., *F. s. sansibarica* Warb., *F. bubu* Warb. and *F. sycomorus* Linnaeus only occur along these seasonal river courses, such as the Mzukune River in Mbono Valley, or in wetter ravines on the slopes of hills such as the top of the valley north-west of Ibaya Camp leading up Ibaya Hill, where these species as well as *F. lutea* Vahl are present. *Ficus bussei* has only been recorded growing in rocky areas of the river course near Ngurunga Pools. The lower reaches of this river course, below the pools, have not yet been surveyed and promise to produce further records. The dryer central and eastern areas of Mkomazi appear to be unsuitable for these woodland species and apart from the concentrations of fig trees on the isolated rocky hills are relatively fig tree depauperate.

Fig wasps

Regional richness

On a world basis the Afrotropical fig wasps are probably the best documented, with systematics of two of the six subfamilies reasonably well known in the region: the Agaoninae, extensively studied by J.T. Wiebes, references in Berg & Wiebes (1992), and the Sycoecinae (van Noort 1993a, b, 1994a, b, c), although only an estimated 72% (Wiebes & Compton 1990) and 56% (van Noort 1994c) respectively of the total extant fauna of these two subfamilies is known. Additionally, the genus *Apocrypta* Coquerel (Sycoryctinae) has been revised on a world basis (Ulenberg 1985). Currently 230 fig wasp species have been described from the 105 Afrotropical species of *Ficus* (Moraceae) (Berg & Wiebes 1992, van Noort 1994c & 1998), a figure that probably represents about one third of the extant species, an estimation based on available undescribed material, host-specificity and extrapolation from host associations (van Noort & Rasplus 1997). Three of the remaining four subfamilies, the Epichrysomallinae (Rasplus, unpubl.), Sycophaginae (Rasplus & Kerdelhué, unpubl.) and the Otitesellinae (van Noort & Rasplus 1997, van Noort, unpubl.) are currently under revision.

Sampling biases

Fig crops are produced randomly throughout the year and individual trees produce crops at different times to each other, both essential traits to ensure the continued cycling of the mutualism. Because of this most of the fig trees that are located during field surveys either have no figs or have figs at the wrong stage of development for rearing of fig wasps. On average only one out of every 30 trees that is located during field work has a fig crop at the right stage of development. These sampling constraints in conjunction with the limited time spent in the reserve meant that fig wasps were not reared from three fig tree species (*F. lutea*, *F. thonningii* and *F. bussei*) recorded in Mkomazi. In addition, the single *F. ingens* tree that was sampled had a fig crop that had already released most of its wasps and hence produced an incomplete sample (Table 18.2).

Furthermore, not every fig wasp species associated with a particular fig tree species is reared from every sample of figs. There are two reasons for this. Firstly, not every fig crop borne by the tree has all the possible fig wasp species present. Some species normally associated with the tree may not have managed to located the fig crop, or alternatively some species may be absent from the local geographical area. Secondly, it is impossible to sample every fig in a particular crop and, because not all the fig wasp species associated with the fig crop will be breeding in every fig, some species which are rarer than others may be missed. To collect every fig wasp species associated with a fig tree species may require anything up to 23 samples from different trees at different times in a particular geographic area

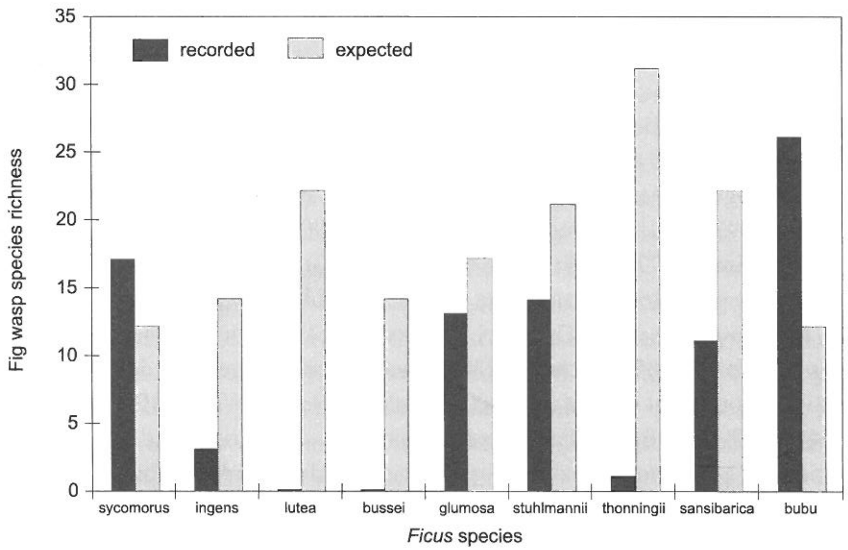

Figure 18.1 Recorded and expected species richness of the fig wasp assemblages associated with the nine fig tree species in Mkomazi Game Reserve.

(Compton and Hawkins 1992, Compton, *et al.* 1994, West *et al.* 1996). This is verified by an example from the New World where a single crop of *F. aurea* in Florida, USA produced four species of fig wasp, a sample of 12 crops over time from the same tree produced seven species, and a sample of 60 crops from 23 different trees produced a total of nine species (Bronstein & Hossaert-Mckey 1996), indicating that comprehensive sampling is required to collect the full compliment of the associated fig wasp assemblage. To be reasonably confident that all the associated fig wasp species have been collected from a fig tree species a species accumulation curve is plotted. This curve depicts the sequential acquisition of new fig wasp species associated with a fig tree species as the samples are collected. Once the curve starts levelling out to a plateau this indicates that the majority of species have been sampled. None of the fig tree species were sufficiently sampled in Mkomazi to attain a levelling off of the accumulation curves. One exception may be *F. bubu* where an excellent sample of figs was taken from a single tree with a large fig crop. This produced a record number of fig wasp species (25) reared from a single fig crop for *F. bubu*, and is likely to be close to the total number associated with this host species in the reserve. It is thus possible, but unusual, to sample the majority of fig wasps associated with a particular host through a single collection. This is verified by a single collection made from *F. thonningii* in Tanzania that produced 31 species of fig wasp (J.Y. Rasplus, pers. comm.), a total only achieved after 49 collections were made from this fig tree species in southern Africa.

There are thus two main reasons for the underestimation of fig wasp species richness in Mkomazi Game Reserve. Firstly, fig wasp species richness recorded from the host fig tree species in the reserve is currently an under representation, given the limited sampling effort, and secondly, it is likely that further species of *Ficus* still await to be recorded from Mkomazi Game Reserve each with its own host-specific fig wasp fauna.

Species richness within Mkomazi Game Reserve

Eighty-five species of fig wasp have been recorded from Mkomazi of which around three-quarters are undescribed (Tables 18.2 & 18.3). This is about half of the fig wasp species expected to be reared from the nine recorded fig tree species in Mkomazi (see under sampling biases for an explanation). However, because of the high host-specificity of fig wasps we can be reasonably confident that wasps previously recorded as being associated with the unsampled fig trees will probably also be present in Mkomazi Game Reserve (Figure 18.1). These previous records are from fig wasp collections made in other areas in eastern and southern Africa (Table 18.3). If these unrecorded fig wasps are taken into account the minimum total richness for the reserve is likely to be around 183 species. This total will still be an underestimate because it is probable that further fig tree species are present within the reserve. The unrecorded fig wasp species have been included in the

Table 18.2 Systematic composition of the fig wasp assemblages associated with each fig tree species in Mkomazi Game Reserve. Brackets enclose the expected species number (based on collections elsewhere in east and southern Africa). A dash (–) denotes instances where the subfamily or tribe is not associated with the host fig tree. * denotes where foundress female pollinating fig wasps were collected from immature figs.

Ficus sp.	no. of samples	Agaoninae	Epichryso-mallinae	Otitesellinae	Sycoecinae	Sycophaginae	Sycoryctinae	Eurytomidae	Ormyridae	total
F. sycomorus	5	2 (2)	1 (0)	–	–	4 (4)	7 (6)	3 (0)	0 (0)	17 (12)
F. ingens	1 (poor)	1 (1)	0 (1)	1 (2)	–	–	1 (4)	0 (6)	0 (0)	3 (14)
F. lutea	0	0 (1)	0 (6)	0 (2)	0 (1)	–	0 (5)	0 (7)	0 (0)	0 (22)
F. bussei	0	0 (1)	0 (3)	0 (0)	0 (1)	–	0 (6)	0 (3)	0 (0)	0 (14)
F. glumosa	7	1 (1)	2 (2)	2 (2)	2 (3)	–	3 (4)	2 (4)	1 (1)	13 (17)
F. stuhlmannii	1	1 (1)	3 (3)	2 (2)	2 (3)	–	6 (8)	0 (4)	0 (0)	14 (21)
F. thonningii	0*	1 (1)	0 (4)	0 (2)	0 (2)	–	0 (9)	0 (10)	0 (3)	1 (31)
F. sansibarica	3	1 (1)	1 (2)	1 (2)	1 (1)	–	6 (8)	1 (7)	0 (1)	11 (22)
F. bubu	2	1 (1)	4 (2)	2 (2)	1 (1)	–	9 (4)	9 (1)	0 (1)	26 (12)
total	19	8 (10)	11 (23)	8 (14)	6 (12)	4 (4)	32 (54)	15 (42)	1 (6)	85 (165)

checklist (but clearly marked as such), because this provides a more realistic interpretation of local fig wasp species richness.

18 more fig wasp species were recorded from Mkomazi fig trees than were expected based on fig wasp collections made in southern Africa (Table 18.2). These additional species were reared from *F. sycomorus* and *F. bubu* illustrating the higher species richness of the fig wasp assemblages associated with these two species in east Africa as compared to southern Africa (Figure 18.2). However, all families and subfamilies of fig wasps as well as the fig wasp assemblages from many of the fig trees are under-represented in Mkomazi Game Reserve (Table 18.2). This is simply because of the insufficient sampling that has been undertaken within reserve. Once the fig wasps and fig trees have been comprehensively surveyed a very different picture of actual species richness is likely to emerge.

Many of the undescribed fig wasp species collected in Mkomazi have already been collected from their hosts elsewhere in Africa and await taxonomic revisions, but a number of new, previously uncollected species of fig wasp were sampled. For example this was the first record of a third *Sycoscapter* species from *F. stuhlmannii*, and the first record of a third *Sycoryctes* species and a second *Watshamiella* species from *F. s. sansibarica*. The *Ficus bubu* collections produced 14 additional species to those previously recorded in southern Africa, although six of these have previously been recorded from Tanzania (Rasplus, pers. com.). Material collected from *F. ingens* contributed to the description of a new species of Otitesellinae: *Otitesella longicauda* van Noort (van Noort & Rasplus 1997).

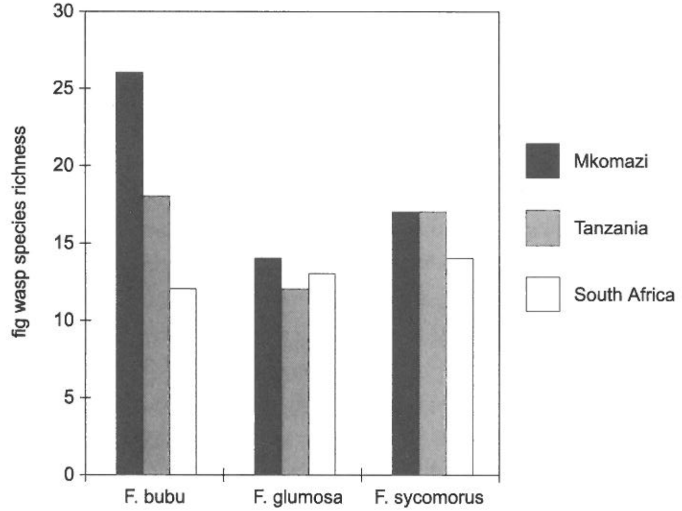

Figure 18.2 Comparative regional species richness of the three most common *Ficus* species in Mkomazi Game Reserve. The Tanznaian figure excludes Mkomazi and respresents collections made by J.Y. Rasplus and C. Kerdelhué.

The fig wasp assemblages associated with each fig species are listed in Table 18.3. For comparison fig wasps recorded from outside the reserve around Kisiwani and on the South Pare Mountains are listed in Table 18.4.

Comparative species richness and similarity

An assessment of fig tree species richness represented in Mkomazi Game Reserve can be achieved by comparing the number of recorded species with floral surveys carried out in other east African areas. A study of indigenous trees and shrubs of Bura, in the Tana River district (Kenya), a semi-arid region that is floristically similar to Mkomazi, identified four *Ficus* species (Gachathi *et al.* 1994). Two of the three identified species occur in Mkomazi and the remaining *F. capreifolia* could potentially be present along the Umba River. The *Ficus* species count in a similar habitat, but one-tenth the area of Mkomazi, Ol Ari Nyiro Ranch on the Laikipia Plateau (Kenya), totalled six species (Muasya *et al.* 1994). Based on the floral diversity recorded, an estimated 10% of the Kenyan flora, Ol Ari Nyiro is touted as one of the most diverse non-forest areas in east Africa (Muasya *et al.* 1994). In a study of species richness and endemism of the Usambara Mountain forests, 12 *Ficus* species were identified (Rodgers & Homewood 1982), only three more than occur in Mkomazi from an area which constitutes one of the richest biological communities in Africa (Rodgers & Homewood 1982). Five of the Usambara species are shared with Mkomazi, but all five are fairly widespread savanna species that are not typically associated with montane forest. Hawthorne (1993) recorded 16 fig tree species occurring in the east African coastal forests. However, this survey encompassed a wide area and hence elevated species richness. Six of these species also occur in Mkomazi. From these comparisons Mkomazi appears to have a high fig tree species richness (Table 18.5), but all of these studies are likely to have underestimated species richness in their respective areas. A more

F. sycomorus	*F. ingens*	*F. lutea*	*F. bussei*	*F. glumosa*
Ceratosolen arabicus	*Platyscapa soraria*	**Allotriozoon heterandromorphum*	**Elisabethiella* sp.	*Elisabethiella glumosae*
Ceratosolen galili	*Otitesella longicauda*	**Philocaenus silvestrii*	**Philocaenus zambesiacus*	*Philocaenus warei*
Sycoscapteridea sp. 1	**Otitesella rotunda*	**Sycoryctes* sp. 4	**Philotrypesis* sp. 7	*Crossogaster stigma*
Sycoscapteridea sp. 2	*Philotrypesis* sp. 2	**Sycoryctes* sp. 5	**Sycoryctes* sp. 6	**Crossogaster quadrata*
Sycoscapter sp. 1	**Sycoryctes* sp. 2	**Sycoscapter* sp. 3	**Sycoryctes* sp. 7	*Sycoryctes* sp. 8
Watshamiella sp. 1	**Sycoryctes* sp. 3	**Philotrypesis selenitica*	**Sycoscapter* sp. 4	*Sycoryctes* sp. 9
Watshamiella sp. 2	**Sycoscapter* sp. 2	**Philotrypesis* sp. 8	**Sycoscapteridea* sp.	**Sycoscapter* sp. 5
Apocrypta longitarsus	**Camarothorax* sp. 1	**Otitesella* sp. 1	**Watshamiella* sp. 3	*Philotrypesis* sp. 5
Apocrypta sp. 1	**Sycophila* sp. 4	**Otitesella* sp. 2	**Camarothorax* sp. 8	*Otitesella* sp. 3
Sycophaga sycomori	**Sycophila* sp. 5	**Camarothorax* sp. 2	**Camarothorax* sp. 9	*Otitesella* sp. 4
Eukoebelea sycomori	**Sycophila* sp. 6	**Camarothorax* sp. 3	**Camarothorax* sp. 10	*Camarothorax* sp. 11
Apocryptophagus gigas (Mayr)	**Sycophila* sp. 7	**Camarothorax* sp. 4	**Sycophila* sp. 16	*Camarothorax* sp. 12
Apocryptophagus sp.1	**Sycophila* sp. 8	**Camarothorax* sp. 5	**Sycophila* sp. 17	*Sycophila* sp. 19
Camarothorax sp. 22	**Acophila* sp. 1	**Camarothorax* sp. 6	**Sycophila* sp. 18	*Sycophila* sp. 20
Sycophila sp. 1		**Camarothorax* sp. 7		**Sycophila* sp. 21
Sycophila sp. 2		**Sycophila* sp. 9		**Sycophila* sp. 22
Sycophila sp. 3		**Sycophila* sp. 10		*Ormyrus* sp. 1
		**Sycophila* sp. 11		
		**Sycophila* sp. 12		
		**Sycophila* sp. 13		
		**Sycophila* sp. 14		
		**Sycophila* sp. 15		

F. stuhlmannii	*F. thonningii*	*F. sansibarica*	*F. bubu*
Alfonsiella binghami	*Elisabethiella stuckenbergi*	*Courtella armata*	*Courtella michaloudi*
Philocaenus liodontus	**Philocaenus barbarus*	*Seres solweziensis*	*Seres wardi*
**Philocaenus barbarus*	**Crossogaster odorans*	*Otitesella* sp. 8	*Sycoryctes* sp. A
Crossogaster odorans	**Philotrypesis parca*	**Philosycus* sp.	*Sycoryctes* sp. B
Otitesella sp. 5	**Philotrypesis* sp. 1	*Sycoryctes* sp. 12.	*Sycoryctes* sp. C
Otitesella sp. 6	**Sycoscapter cornutus*	*Sycoryctes* sp. 13	*Sycoryctes* sp. D
Sycoryctes sp. 10	**Sycoryctes remus*	*Sycoryctes* sp. 14	*Sycoryctes* sp. E
Sycoryctes sp. 11	**Sycoryctes hirtus*	**Sycoscapteridea* sp. 4	*Sycoryctes* sp. F
**Sycoryctes* sp. 21	**Sycoryctes* sp. 1	**Sycoscapter* sp. 9	*Sycoscapter* sp. 10
Sycoscapter sp. 6	**Watshamiella alata*	*Watshamiella* sp. 6	*Watshamiella* sp. 8
Sycoscapter sp. 7	**Watshamiella* sp. 4	*Watshamiella* sp. 7	*Watshamiella* sp. 9
Sycoscapter sp. 8	**Watshamiella* sp. 5	*Philotrypesis* sp. 6	*Otitesella* sp. 9
Philotrypesis sp. 3	**Otitesella tsamvi*	**Camarothorax* sp. 16	*Philosycus* sp. 2
**Philotrypesis* sp. 4	**Otitesella* sp. 7	*Camarothorax* sp. 17	*Camarothorax* sp. 18
Camarothorax sp. 13	**Camarothorax brevimucro*	**Sycophila* sp. 27	*Camarothorax* sp. 19
Camarothorax sp. 14	**Camarothorax equicollis*	**Sycophila* sp. 28	*Camarothorax* sp. 20
Camarothorax sp. 15	**Camarothorax longimucro*	**Sycophila* sp. 29	*Camarothorax* sp. 21
**Sycophila* sp. 23	**Sycotetra serricornis*	**Sycophila* sp. 30	*Ficomila* sp. 1
**Sycophila* sp. 24	**Ficomila curtivena*	**Sycophila* sp. 31	*Sycophila* sp. 34
**Sycophila* sp. 25	**Ficomila gambiensis*	**Sycophila* sp. 32	*Sycophila* sp. 35
**Sycophila* sp. 26	**Eurytoma ficusgallae*	*Sycophila* sp. 33	*Sycophila* sp. 36
	**Syceurytoma ficus*	**Ormyrus* sp. 2	*Sycophila* sp. 37
	**Sycophila flaviclava*		*Sycophila* sp. 38
	**Sycophila kestraneura*		*Sycophila* sp. 39
	**Sycophila modesta*		*Sycophila* sp. 40
	**Sycophila naso*		*Sycophila* sp. 41
	**Sycophila punctum*		**Ormyrus* sp. 3
	**Sycophila sessilis*		
	**Ormyrus flavipes*		
	**Ormyrus subconicus*		
	**Ormyrus watshami*		

Table 18.3 *Ficus* species and their associated fig wasps in Mkomazi Game Reserve. * denotes fig wasp taxa not yet recorded from the reserve, but recorded from the *Ficus* species elsewhere in east and southern Africa. The majority of the fig wasps listed below are undescribed species.

useful comparison may be provided by examination of local species richness in southern Africa, where the presence of host fig trees and collections of fig wasps is better documented.

An assessment of local species richness in South Africa was achieved by demarcating a comparative region (in size and habitat) to that of Mkomazi Game Reserve. This region was centred around Mkuze Game Reserve (Kwazulu Natal) and encompassed four sixteenth degree squares contained between 27°–28°S and 32°–32°15'E, with an altitudinal variation of 80–700 m, and an area of 3,250 km^2. The vegetational types comprised Natal Lowveld Bushland, Lebombo Arid Mountain Bushland and Sweet Lowveld Bushland (Low & Rebelo 1996). Overall this is a similar habitat to that found within Mkomazi, although the species composition is disparate between the two locations. Twelve fig tree species have been recorded within this demarcated area, including five of the species recorded in Mkomazi. Ninety fig wasp species have been reared from seven of these host species. Based on collections from elsewhere in southern Africa, the remaining five fig tree species should produce at least a further 27 wasp species. The recorded fig wasp species richness from Mkuze is thus comparable with that from Mkomazi (Table 18.6). However, the Mkomazi count will undoubtably increase with further surveys in the region and *Ficus* species richness is expected to be higher than currently recorded, whereas the Mkuze region is well surveyed for fig trees. Once Mkomazi is completely surveyed the reserve will probably be shown to protect a higher species richness than is found in a comparable savanna area in South Africa.

Although Mkomazi Game Reserve lies within the Somalia-Masai regional centre of floral endemism (White 1983), the reserve is close to the transition point between this centre, the Zambezian regional centre of endemism and the Zanzibar-Inhambane regional mosaic, which extends down the coast into southern Mozambique (White 1983). These three systems have shared affinities. As a result many of the *Ficus* species occurring within Mkomazi would be expected to be shared with the southern African subregional flora and in fact all nine of the *Ficus* species from Mkomazi enjoy a wide distribution that extends into southern Africa (Berg & Wiebes 1992). However, a number of these species are nearer the centre of their distribution in east Africa, whereas in southern Africa they are at the extreme of their range and relatively rare. This has important ramifications for species richness of the associated fig wasp assemblages, which become increasingly depauperate towards the periphery of their host species distribution (Compton *et al.* 1994). This is a trend exemplified by *Ficus bubu*, from which fig wasp fauna was previously only known from a few collections in South Africa and Tanzania, although the species is widespread, extending from eastern South Africa up to Kenya and across to the Ivory Coast, but supposedly rare or overlooked (Berg & Wiebes 1992). *Ficus bubu* is relatively common in Mkomazi in the vicinity of Ibaya Camp. This is a species that sometimes persists in disturbed areas (Berg & Hijman 1989) and this ability may explain the continued existence of this forest species in fire encroached areas in the Mbono Valley and in the valley north-west of Ibaya Camp. Prior to the Mkomazi collections, 12 species of fig wasp were recorded from *F. bubu* in southern Africa and 18 species (J.Y. Rasplus, pers. comm.) from this host in Tanzania. An exceptional 26 species were reared from this host species in Mkomazi Game Reserve (Figure 18.2). A record 25 of these species were collected from a single fig crop produced by a tree between Dindira Dam and Viteweni Ridge. *Ficus sycomorus* similarly produced three more species than the 13 species recorded from southern African samples (Compton & Hawkins 1992) and one less than the 17 species previously recorded from this host in Tanzania (J.Y. Rasplus, pers. comm.). By contrast *F. glumosa*, *F. stuhlmannii* and *F. s. sansibarica* produced less species than expected. This is likely to be the result of under sampling and is supported by collections made from *F. s. sansibarica* from just outside the reserve, where an additional 10 species over those collected from within the reserve were recorded. With further sampling these species will

Table 18.4 *Ficus* species and their associated fig wasps from areas adjacent to Mkomazi Game Reserve (Kisiwani and South Pare Mountains).

F. exasperata	*F. vallis-choudae*	*F. sycomorus*	*F. lutea*	*F. thonningii B*	*F. thoninngii C*	*F. tremula acuta*	*F. sansibarica*	
Kradibia gestroi afrum *Sycoryctes* sp. 21 *Philotrypesis* sp. 9	*Ceratosolen megacephalus* *Apocrypta robusta* *Sycoscapteridea* sp.5 *Eukoebelea* sp. 1 *Camarothorax* sp.23 *Sycophila* sp. 42 *Sycophila* sp. 43	*Ceratosolen arabicus* *Ceratosolen galili* *Sycoscapteridea* sp.1 *Sycoscapteridea* sp.2 *Sycoscapter* sp. 1 *Watshamiella* sp. 1 *Apocrypta longitarsus* *Apocrypta* sp. 1 *Sycophaga sycomori* *Apocryptophagus gigas* *Apocryptophagus* sp. 1	*Allotriozoon heterandromorphum* *Philocaenus silvestrii* *Sycoryctes* sp. 4	*Alfonsiella brongersmai* *Philocaenus medius* *Philocaenus barbarus* *Crossogaster vansomereni* *Sycoscapter* sp. 11 *Sycophila* sp. 43 *Sycophila* sp. 44	*Elisabethiella socotrensis* *Otitesella* sp. 7 *Sycoryctes* sp. 22	*Courtella* sp. 1 *Philotrypesis* sp. 8	*Courtella armata* *Sycoryctes* sp. 12 *Sycoryctes* sp. 13 *Sycoscapter* sp. 9 *Watshamiella* sp. 6 *Philotrypesis* sp. 6 *Otitesella* sp. 8 *Philosycus* sp. 1 *Camarothorax* sp. 16	*Camarothorax* sp. 17 *Ficomila* sp. 1 *Sycophila* sp. 27 *Sycophila* sp. 28 *Sycophila* sp. 29 *Sycophila* sp. 30 *Sycophila* sp. 31 *Sycophila* sp. 32

undoubtably be recorded from within Mkomazi as well. Tanzanian data is available for three of the fig tree species that were not, or were poorly sampled in Mkomazi. Thirty-one, nine and eight species of fig wasp have previously been recorded from limited collections of *F. thonningii*, *F. bussei* and *F. ingens* respectively in Tanzania (J.Y. Rasplus, pers. comm.). A similar species richness can be expected for Mkomazi although based on southern African collections the richness is an underestimate for the latter two species and a figure of 14 species associated with *F. bussei* and *F. ingens* is probably more representative of real richness.

Table 18.5 Comparative local fig tree and fig wasp species richness. Numbers represent fig wasp species and * indicates fig tree presence but where no data is available on the associated fig wasps.

Ficus sp.	Mkomazi	Mkuze (S. Africa)	Bura (Kenya)	Ol Ari Nyiro (Kenya)	S. Pare Mtns.	Usambara Mtns.
F. exasperata					3	
F. capreifolia		*	*			
F. mucosa						*
F. vallis-choudae					7	*
F. sycomorus	16	11	*	*	10	*
F. sur		7				*
F. ingens	3	12		*		
F. c. salicifolia		*				
F. lutea	*				3	*
F. ?vasta				*		
F. abutilifolia		12				
F. glumosa	13	14		*		
F. stuhlmannii	14	14				
F. bussei	*		*			*
F. craterostoma		*				
F. n. natalensis				*		
F. n. leprieurii						*
F. usambarensis						*
F. burtt-davyi		*				
F. thonningii	*	20		*		*
F. "thonningii" B					7	
F. "thonningii" C					3	
F. scassellati						*
F. c. cyathistipula						*
F. tremula acuta					2	
F. bubu	26					
F. p. polita		*				
F. sansibarica	11				17	*
Ficus sp.			*			
total	9	12	4	6	8	12

Data from collections of the common species *F. glumosa* could be analysed in more detail because of the repetitive samples obtained in Mkomazi Game Reserve. An analysis of a comparative area in South Africa (a 45 km radius around Jozini in northern Kwazulu/Natal, which approximates the extent of the area in Mkomazi that was sampled for this fig tree species) illustrates that local species richness is comparable between the two areas: 13 fig wasp species were reared from *F. glumosa* in Mkomazi compared to 14 in the Jozini area. Previously 12 species had been recorded from three collections of *F. glumosa* in Tanzania (J.Y. Rasplus, pers. comm.). To evaluate whether the recorded fig wasp species richness from *F. glumosa* represented real species richness a species accumulation curve was produced for *F. glumosa* from each area. An accumulation curve plots the sequential addition of new species for each subsequent sample that is collected. When the curve starts levelling off, it indicates that the majority of the fig wasp species have been collected. As can be seen from Figure 18.3, only Jozini has been well sampled, whereas the Mkomazi curve is still rising. The data were further analysed using the program *EstimateS* (Version 4, R.K. Colwell, unpublished), which uses the incidence of species in each sample to estimate the number of uncollected species, and hence estimates the total fig wasp species richness associated with *F. glumosa* in each area. The resultant estimated local species richness for Mkomazi marginally exceeds that of Jozini by 15 to 14 species (Figure 18.3). The regional estimate for southern African fig wasp species richness associated with *F. glumosa* totals 20 species and if combined with the Mkomazi data the total increases to an estimated 24 fig wasp species associated with *F. glumosa* in east and southern Africa (Figure 18.3).

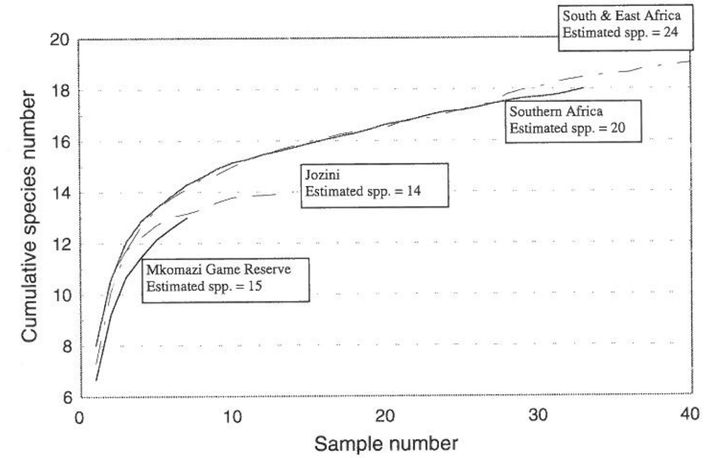

Figure 18.3 Species accumulation curves, including local and regional species richness estimates, for the fig wasp assemblage associated with *Ficus glumosa*.

Table 18.6 Comparative richness of fig trees and fig wasps between Mkomazi and a comparably demarcated area in South Africa, centred on Mkuze Game Reserve.

	Mkomazi	Mkuze
Fig tree species	9	12
Fig wasp species	85	90
Potential wasp species	183	117

The species accumulation curve from a particular host depends to a large extent on timing of samples and size of the fig crop. A large fig crop sampled at optimum development, i.e. just before the wasps emerge, will produce a high species count from a single sample. By contrast the same species count may only be achieved after 15 or 20 samples if the crop or sample sizes (due to non-optimum development) are small. These factors compound assessments of natural geographical or ecological variation of fig wasp species assemblage richness.

Conclusions

This study has shown that a typical savanna fig tree and fig wasp species richness is protected within Mkomazi Game Reserve. However, *Ficus bubu*, a fig tree that is generally assumed rare or overlooked in the Afrotropical region (Berg & Wiebes 1992) is locally abundant in Mkomazi and has a high associated fig wasp species richness. Although savanna fig tree species are well represented in the reserve, forest fig trees appear under-represented. The high fig tree and fig wasp species richness that is likely to be present on the mountains surrounding Mkomazi appears to be poorly represented in the isolated montane forests within the reserve. This is borne out by the four species of fig tree recorded on the South Pare Mountains during this programme that were absent within the reserve (Table 18.5).

Conservation and management

Fig trees are likely to be keystone species with many invertebrates and vertebrates depending on the presence of the resources provided by these trees. Since each species of fig tree is pollinated by its own species of fig wasp, an understanding of this complex obligate mutualism is critical for the future conservation and management of tropical ecosystems. The continued presence of many insects and vertebrates in Mkomazi therefore potentially hinges on the preservation of the fig trees within the reserve. Mature fig trees are probably not adversely affected by fire, given their habitat preference and resistance to burning by a fast moving grass fire. Nevertheless, too frequent burning will affect young trees, which even along the perennial watercourses are susceptible to fire destruction in their early years of growth. Although only one species, *F. thonningii*, has currently been recorded from the montane forests, it is probable that other forest species are present in these isolated patches and hence degradation of this habitat will adversely affect fig tree and fig wasp species richness within the reserve.

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Checklist: Fig wasps of Mkomazi

85 species recorded; 183 potential species. Potential species are those which have not yet been recorded in Mkomazi but are thought likely to occur there due to the presence of their host fig trees. **Potential species are included in the list, but are indented to distinguish them from the recorded species.** Species determinations by S. van Noort.

Class INSECTA

Order HYMENOPTERA

Superfamily CHALCIDOIDEA

Family Agaonidae

Subfamily Agaoninae

- *Ceratosolen arabicus* Mayr (ex *Ficus sycomorus*)
- *Ceratosolen galili* Wiebes (ex *F. sycomorus*)
- *Platyscapa soraria* Wiebes (ex *F. ingens*)
    - *Allotriozoon heterandromorphum* Grandi (ex F. *lutea*)
- *Elisabethiella glumosae* Wiebes (ex *F. glumosa*)
- *Elisabethiella stuckenbergi* Grandi (ex *F. thonningii*)
    - *Elisabethiella* sp. (ex *F. bussei*)
- *Alfonsiella binghami* Wiebes (ex *F. stuhlmannii*)
- *Courtella armata* (Wiebes) (ex *F. sansibarica sansibarica*)
- *Courtella michaloudi* (Wiebes) (ex *F. bubu*)

Subfamily Sycoryctinae

Tribe Apocryptini

- *Apocrypta longitarsus* (Mayr) (ex *F. sycomorus*)
- *Apocrypta* sp. 1 (ex *F. sycomorus*)

Tribe Philotrypesini

    - *Philotrypesis selenitica* Grandi (ex *F. lutea*)
    - *Philotrypesis parca* Wiebes (ex *F. thonningii*)
    - *Philotrypesis* sp. 1 (ex *F. thonningii*)
- *Philotrypesis* sp. 2 (ex *F. ingens*)
- *Philotrypesis* sp. 3 (ex *F. stuhlmannii*)
    - *Philotrypesis* sp. 4 (ex *F. stuhlmannii*)
- *Philotrypesis* sp. 5 (ex *F. glumosa*)
- *Philotrypesis* sp. 6 (ex *F. s. sansibarica*)
    - *Philotrypesis* sp. 7 (ex *F. bussei*)
    - *Philotrypesis* sp. 8 (ex *F. lutea*)

Tribe Sycoryctini

    - *Sycoryctes remus* Wiebes (ex *F. thonningii*)
    - *Sycoryctes hirtus* Wiebes (ex *F. thonningii*)
    - *Sycoryctes* sp. 1 (ex *F. thonningii*)
    - *Sycoryctes* sp. 2 (ex *F. ingens*)
    - *Sycoryctes* sp. 3 (ex *F. ingens*)
    - *Sycoryctes* sp. 4 (ex *F. lutea*)
    - *Sycoryctes* sp. 5 (ex *F. lutea*)
    - *Sycoryctes* sp. 6 (ex *F. bussei*)
    - *Sycoryctes* sp. 7 (ex *F. bussei*)
- *Sycoryctes* sp. 8 (ex *F. glumosa*)
- *Sycoryctes* sp. 9 (ex *F. glumosa*)
- *Sycoryctes* sp. 10 (ex *F. stuhlmannii*)
- *Sycoryctes* sp. 11 (ex *F. stuhlmannii*)
- *Sycoryctes* sp. 12 (ex *F. sansibarica sansibarica*)
- *Sycoryctes* sp. 13 (ex *F. sansibarica sansibarica*)
- *Sycoryctes* sp. 14 (ex *F. sansibarica sansibarica*)
- *Sycoryctes* sp. 15 (ex *F. bubu*)
- *Sycoryctes* sp. 16 (ex *F. bubu*)
- *Sycoryctes* sp. 17 (ex *F. bubu*)
- *Sycoryctes* sp. 18 (ex *F. bubu*)
- *Sycoryctes* sp. 19 (ex *F. bubu*)
- *Sycoryctes* sp. 20 (ex *F. bubu*)
    - *Sycoryctes* sp. 21 (ex *F. stuhlmannii*)
    - *Sycoscapter cornutus* Wiebes (ex *F. thonningii*)
- *Sycoscapter* sp. 1 (ex *F. sycomorus*)
    - *Sycoscapter* sp. 2 (ex *F. ingens*)
    - *Sycoscapter* sp. 3 (ex *F. lutea*)
    - *Sycoscapter* sp. 4 (ex *F. bussei*)
    - *Sycoscapter* sp. 5 (ex *F. glumosa*)
- *Sycoscapter* sp. 6 (ex *F. stuhlmannii*)
- *Sycoscapter* sp. 7 (ex *F. stuhlmannii*)
- *Sycoscapter* sp. 8 (ex *F. stuhlmannii*)
    - *Sycoscapter* sp. 9 (ex *F. sansibarica sansibarica*)
- *Sycoscapter* sp. 10 (ex *F. bubu*)
- *Sycoscapteridea* sp. 1 (ex *F. sycomorus*)
- *Sycoscapteridea* sp. 2 (ex *F. sycomorus*)
    - *Sycoscapteridea* sp. 3 (ex *F. bussei*)
    - *Sycoscapteridea* sp. 4 (ex *F. sansibarica sansibarica*)
    - *Watshamiella alata* Wiebes (ex *F. thonningii*)
- *Watshamiella* sp. 1 (ex *F. sycomorus*)
- *Watshamiella* sp. 2 (ex *F. sycomorus*)
    - *Watshamiella* sp. 3 (ex *F. bussei*)
    - *Watshamiella* sp. 4 (ex *F. thonningii*)
    - *Watshamiella* sp. 5 (ex *F. thonningii*)
- *Watshamiella* sp. 6 (ex *F. sansibarica sansibarica*)
- *Watshamiella* sp. 7 (ex *F. sansibarica sansibarica*)
- *Watshamiella* sp. 8 (ex *F. bubu*)
- *Watshamiella* sp. 9 (ex *F. bubu*)

Subfamily Otitesellinae

- *Otitesella longicauda* van Noort (ex *F. ingens*)
    - *Otitesella rotunda* van Noort (ex *F. ingens*)
    - *Otitesella tsamvi* Wiebes (ex *F. thonningii*)
    - *Otitesella* sp. 1 (ex *F. lutea*)
    - *Otitesella* sp. 2 (ex *F. lutea*)
- *Otitesella* sp. 3 (ex *F. glumosa*)
- *Otitesella* sp. 4 (ex *F. glumosa*)
- *Otitesella* sp. 5 (ex *F. stuhlmannii*)
- *Otitesella* sp. 6 (ex *F. stuhlmannii*)
    - *Otitesella* sp. 7 (ex *F. thonningii*)
- *Otitesella* sp. 8 (ex *F. sansibarica sansibarica*)
- *Otitesella* sp. 9 (ex *F. bubu*)
    - *Philosycus* sp. 1 (ex *F. sansibarica sansibarica*)
- *Philosycus* sp. 2 (ex *F. bubu*)

Subfamily Sycoecinae

    - *Philocaenus silvestrii* (Grandi) (ex *F. lutea*)
    - *Philocaenus zambesiacus* van Noort (ex *F. bussei*)
- *Philocaenus warei* van Noort (ex *F. glumosa*)
- *Philocaenus liodontus* (Wiebes) (ex *F. stuhlmannii*)
    - *Philocaenus barbarus* Grandi (ex *F. thonningii & F. stuhlmannii*)
- *Crossogaster stigma* van Noort (ex *F. glumosa*)
    - *Crossogaster quadrata* van Noort (ex *F. glumosa*)
- *Crossogaster odorans* Wiebes (ex *F. thonningii & F. stuhlmannii*)
- *Seres solweziensis* van Noort (ex *F. sansibarica sansibarica*)
- *Seres wardi* van Noort (ex *F. bubu*)

Subfamily Sycophaginae

- *Sycophaga sycomori* (Linnaeus) (ex *F. sycomorus*)
- *Eukoebelea sycomori* Wiebes (ex *F. sycomorus*)
- *Apocryptophagus gigas* (Mayr) (ex *F. sycomorus*)
- *Apocryptophagus* sp. 1 (ex *F. sycomorus*)

Subfamily Epichrysomallinae

    - *Camarothorax brevimucro* Boucek (ex *F. thonningii*)
    - *Camarothorax equicollis* Boucek (ex *F. thonningii*)
    - *Camarothorax longimucro* Boucek (ex *F. thonningii*)
    - *Camarothorax* sp. 1 (ex *F. ingens*)
    - *Camarothorax* sp. 2 (ex *F. lutea*)
    - *Camarothorax* sp. 3 (ex *F. lutea*)
    - *Camarothorax* sp. 4 (ex *F. lutea*)
    - *Camarothorax* sp. 5 (ex *F. lutea*)
    - *Camarothorax* sp. 6 (ex *F. lutea*)
    - *Camarothorax* sp. 7 (ex *F. lutea*)
    - *Camarothorax* sp. 8 (ex *F. bussei*)
    - *Camarothorax* sp. 9 (ex *F. bussei*)
    - *Camarothorax* sp. 10 (ex *F. bussei*)
- *Camarothorax* sp. 11 (ex *F. glumosa*)
- *Camarothorax* sp. 12 (ex *F. glumosa*)
- *Camarothorax* sp. 13 (ex *F. stuhlmannii*)
- *Camarothorax* sp. 14 (ex *F. stuhlmannii*)
- *Camarothorax* sp. 15 (ex *F. stuhlmannii*)
    - *Camarothorax* sp. 16 (ex *F. sansibarica sansibarica*)
- *Camarothorax* sp. 17 (ex *F. sansibarica sansibarica*)
- *Camarothorax* sp. 18 (ex *F. bubu*)
- *Camarothorax* sp. 19 (ex *F. bubu*)
- *Camarothorax* sp. 20 (ex *F. bubu*)
- *Camarothorax* sp. 21 (ex *F. bubu*)
- *Camarothorax* sp. 22. (ex *F. sycomorus*)
    - *Sycotetra serricornis* Boucek (ex *F. thonningii*)

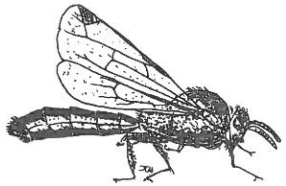
Family Eurytomidae

    - *Acophila* sp. 1 (ex *F. ingens*)
    - *Ficomila curtivena* Boucek (ex *F. thonningii*)
    - *Ficomila gambiensis* Boucek (ex *F. thonningii*)
- *Ficomila* sp. 1 (ex *F. bubu*)
    - *Eurytoma ficusgallae* Boucek (ex *F. thonningii*)
    - *Syceurytoma ficus* Boucek (ex *F. thonningii*)
    - *Sycophila flaviclava* Boucek (ex *F. thonningii*)
    - *Sycophila kestraneura* (Masi) (ex *F. thonningii*)

Sycophila modesta Boucek (ex *F. thonningii*)
Sycophila naso Boucek (ex *F. thonningii*)
Sycophila punctum Boucek (ex *F. thonningii*)
Sycophila sessilis Boucek (ex *F. thonningii*)
Sycophila sp. 1 (ex *F. sycomorus*)
Sycophila sp. 2 (ex *F. sycomorus*)
Sycophila sp. 3 (ex *F. sycomorus*)
Sycophila sp. 4 (ex *F. ingens*)
Sycophila sp. 5 (ex *F. ingens*)
Sycophila sp. 6 (ex *F. ingens*)
Sycophila sp. 7 (ex *F. ingens*)
Sycophila sp. 8 (ex *F. ingens*)
Sycophila sp. 9 (ex *F. lutea*)
Sycophila sp. 10 (ex *F. lutea*)
Sycophila sp. 11 (ex *F. lutea*)
Sycophila sp. 12 (ex *F. lutea*)
Sycophila sp. 13 (ex *F. lutea*)
Sycophila sp. 14 (ex *F. lutea*)
Sycophila sp. 15 (ex *F. lutea*)
Sycophila sp. 16 (ex *F. bussei*)
Sycophila sp. 17 (ex *F. bussei*)
Sycophila sp. 18 (ex *F. bussei*)
Sycophila sp. 19 (ex *F. glumosa*)
Sycophila sp. 20 (ex *F. glumosa*)
Sycophila sp. 21 (ex *F. glumosa*)
Sycophila sp. 22 (ex *F. glumosa*)
Sycophila sp. 23 (ex *F. stuhlmannii*)
Sycophila sp. 24 (ex *F. stuhlmannii*)
Sycophila sp. 25 (ex *F. stuhlmannii*)
Sycophila sp. 26 (ex *F. stuhlmannii*)
Sycophila sp. 27 (ex *F. sansibarica sansibarica*)
Sycophila sp. 28 (ex *F. sansibarica sansibarica*)
Sycophila sp. 29 (ex *F. sansibarica sansibarica*)
Sycophila sp. 30 (ex *F. sansibarica sansibarica*)
Sycophila sp. 31 (ex *F. sansibarica sansibarica*)
Sycophila sp. 32 (ex *F. sansibarica sansibarica*)
Sycophila sp. 33 (ex *F. sansibarica sansibarica*)
Sycophila sp. 34 (ex *F. bubu*)
Sycophila sp. 35 (ex *F. bubu*)
Sycophila sp. 36 (ex *F. bubu*)
Sycophila sp. 37 (ex *F. bubu*)
Sycophila sp. 38 (ex *F. bubu*)
Sycophila sp. 39 (ex *F. bubu*)
Sycophila sp. 40 (ex *F. bubu*)
Sycophila sp. 41 (ex *F. bubu*)

Family Ormyridae

Ormyrus flavipes Boucek (ex *F. thonningii*)
Ormyrus subconicus Boucek (ex *F. thonningii*)
Ormyrus watshami Boucek (ex *F. thonningii*)
Ormyrus sp. 1 (ex *F. glumosa*)
Ormyrus sp. 2 (ex *F. sansibarica sansibarica*)
Ormyrus sp. 3 (ex *F. bubu*)



Ants (Hymenoptera: Formicidae) of Mkomazi

Hamish G. Robertson

Introduction

Ants are a conspicuous and important component in the structure and functioning of terrestrial ecosystems (Hölldobler & Wilson 1990). The abundance of many animals is strongly influenced by the persistent predatory pressure of ants. Ants also influence plant survival through seed predation and protection of plant sucking bugs. They are also important in soil turnover although their effects are dwarfed by the much greater amounts of soil brought to the ground surface by termites (White 1983). Besides their ecological importance, ants are of great value as biological indicators not only because they are so abundant and found in a wide range of ecological niches but also because adult workers occur all year round so that short duration surveys can provide an adequate sample of the total diversity.

Termites are frequently confused with ants as both groups are social with reproductive and worker castes and with the capability of building up nests that in some species can persist for decades. However, there are obvious differences between them. Whereas termites are the sister group to the cockroaches and mantids (Thorne & Carpenter 1992), ants evolved from wasps (Baroni Urbani *et al.* 1992). Termites therefore have a hemimetabolous life cycle where the immatures become steadily more adult-like with each moult whereas in ants the immatures are grub-like and pass through a pupal stage to become adults. In both ants and termites, winged reproductives are released on a dispersal flight but whereas in ants the males mate and die, in termites the male ('king') joins the female ('queen') in starting a nest and they mate periodically through their lives (Watson & Gay 1991). In termites, workers can be of either sex whereas in ants all workers are female. Queen ants share with the rest of the Hymenoptera the ability to control the sex of their offspring, fertilised eggs usually producing females and unfertilised eggs producing males. Lastly, many of the higher termites (subfamily Termitinae) form mounds of soil whereas mound building by African ants is rare (no mound builders in Mkomazi Game Reserve).

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