COMPLEX INTERACTIONS INVOLVING THE CAPE FIG, *FICUS SUR* FORSSKÅL, AND ITS ASSOCIATED INSECTS

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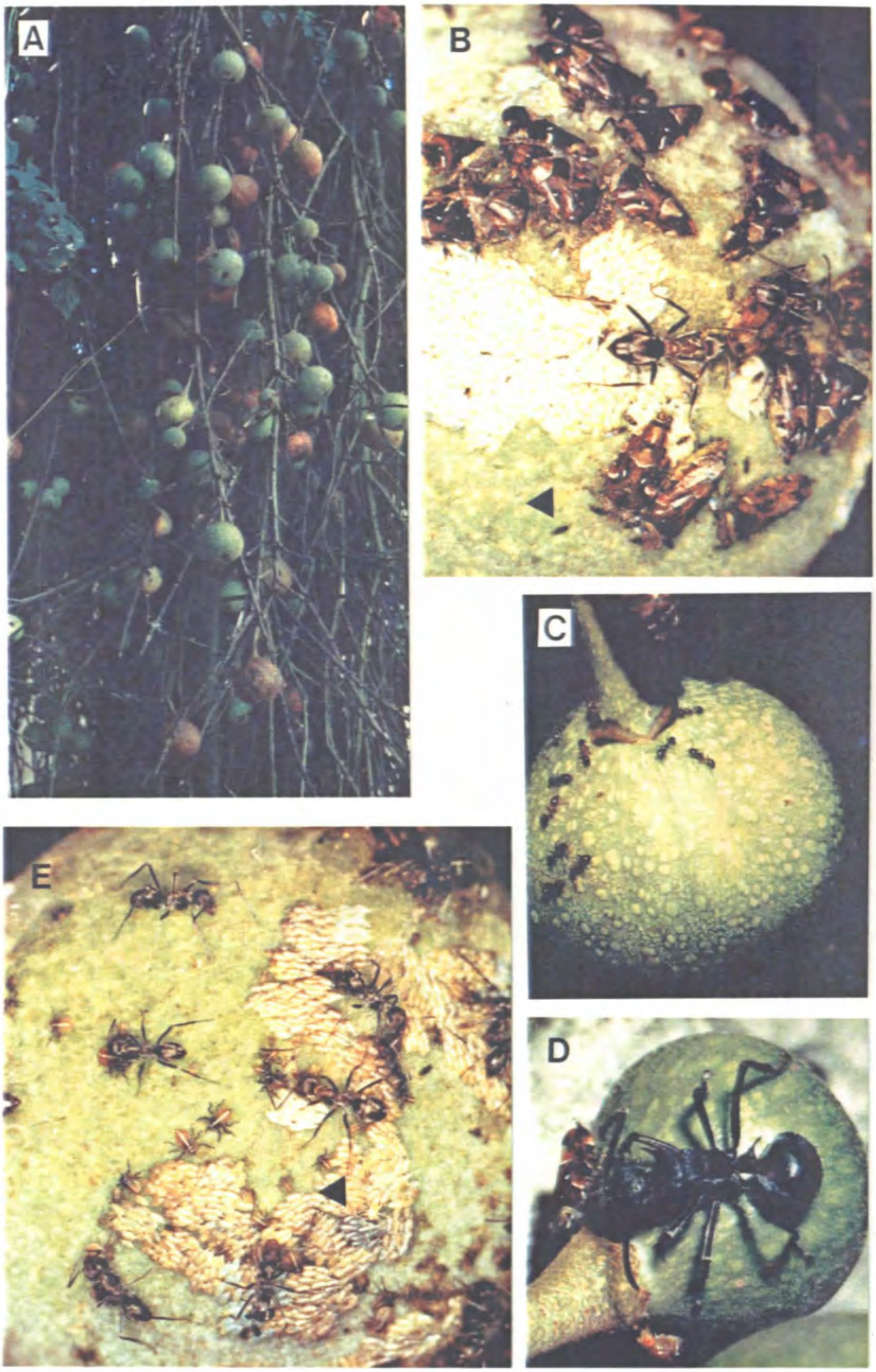
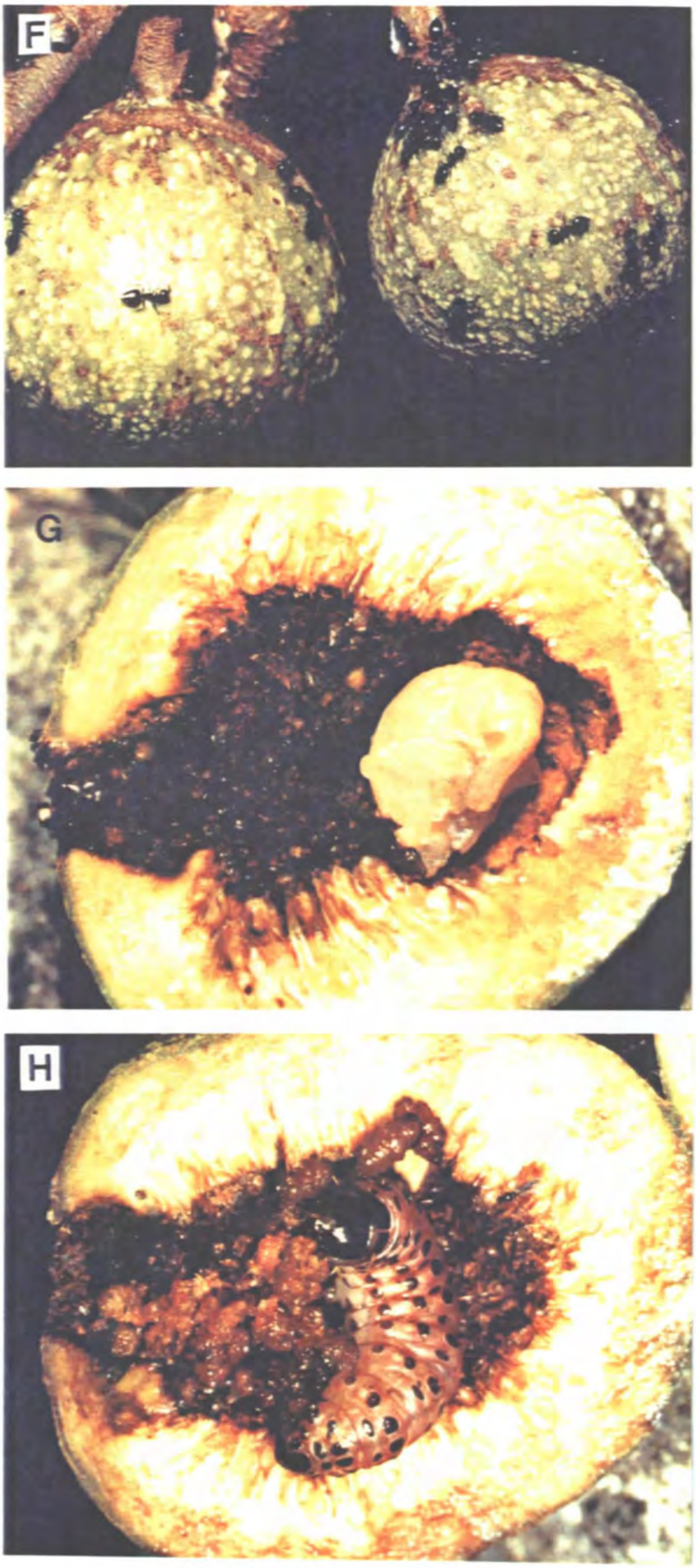
FOR JOHN



(A) *Ficus sur* fruiting branches. (B) *Anoplolepis custodiens* tending *Hilda patruelis* adults (*Psyllechthrus oophagus* adult arrowed). (C) *Pheidole megacephala.* (D) *Polyrhachis schistacea.* (E) *A. custodiens* tending *H. patruelis* nymphs (parasitised eggs arrowed).



(F) *Crematogaster liengmei*. (G) *Omophorus* sp. pupa. (H) *Botyodes hirsutalis* larva.

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ABSTRACT

The inadequacy of arbitrarily classifying interactions between species as antagonistic, neutral or mutualistic has become clear in recent years. Both direct and indirect interactions between species can vary between mutualism and antagonism, depending on the intrinsic and extrinsic contexts of the interaction.

This study investigated the characteristics of an ant-plant-homopteran interaction in southern Africa. The polyphagous homopteran *Hilda patruelis* (Tettigometridae) feeds primarily on the trunk-borne fruiting branches and figs of the Cape fig tree, *Ficus sur*, and produces honeydew which attracts tending ants. Ten of the sixteen ant species/species groups present on F. sur tended *H. patruelis*, with *Pheidole megacephala* the most frequent attendant. Ants attracted to *F. sur* by *H. patruelis* honeydew or other liquid food sources also preyed on insects on the tree, including adults of the small agaonid fig wasps whose larvae feed on the ovules in the developing figs. One fig wasp species (*Ceratosolen capensis*) is also the tree's only pollinator.

No benefits to *H. patruelis* from being tended by ants were detected, either in terms of reduced parasitism, or predation by a lycaenid caterpillar. A *P. megacephala* colony foraging on a *F. sur* tree was found to receive a high proportion of its likely energy requirements from the tree, mainly in the form of *H. patruelis* honeydew, during periods when it was bearing fruit. It is probable that the *H. patruelis-P. megacephala* interaction constitutes a direct mutualism at times, but that benefits to the homopteran are intermittent or weak.

Both *H. patruelis* and ants benefitted from *F. sur*, directly or indirectly, through the provision of food (and for some ants, nesting sites). The removal of phloem sap by *H. patruelis* did not detectably reduce the trees' reproductive output, either in terms of pollinator or viable seed production. The indirect effects of ant and *H. patruelis* presence on the *F. sur* trees were on average positive, as ants preyed disproportionately heavily on fig wasp species

parasitic on or competing with the pollinator, thus increasing pollinator production. Effects of ant presence on seed production were not investigated, but have been demonstrated as beneficial elsewhere. However, there is great variation both in the composition of the wasp fauna arriving to oviposit at different crops, and in ant densities per fig, on several temporal and spatial scales. This results in high variability in the effects of ants on the pollinator and, through it, the tree, from positive to zero and potentially even negative.

Despite this conditionality of beneficial outcomes for the tree, the mean effect of ants on the *F. sur* population studied was to increase pollinator production by up to nearly 20%. This study is among the few to have demonstrated an overall benefit to a plant of having homopteran-tending ants present on it.

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1 INTRODUCTION

Virtually no species of organisms exist without interacting with other species in some way. Species interact both within and between trophic levels: as herbivores on plants, as parasites or pathogens and hosts, as predators and prey, as competitors and as mutualists. Interactions between species may increase, decrease or have no effect on the fitness of the individuals and populations involved. Such interactions are fundamental in structuring communities, ecosystems, and the biological world.

MUTUALISM

A mutualistic interaction or mutualism is defined as one in which two or more species reciprocally benefit from the presence of the other species (Addicott 1984) - species are inherently selfish and act to increase their fitness, so no altruism is involved. Beyond this, many other factors define a mutualism; these include the obligacy of the mutualism, whether the species are physically a unit (symbiosis) and how many species are involved in the mutualism (Boucher *et al.* 1982; Addicott 1984). Mutualistic interactions often occur between taxonomically unrelated species and include those between algae and fungi forming a lichen, symbiotic microorganisms in the guts of larger animals, pollinators of plants, frugivores dispersing seeds, and ants providing services for tended insects and plants in return for nesting sites or food. In most mutualisms one species can be identified as a host for another species, providing food or shelter for the visitor (Thompson 1982). Although some mutualisms are highly specific and obligate, involving only two species, many are facultative and may involve more than two species (Howe 1984). Many mutualisms are thought to have evolved from initially antagonistic interactions between species or to have been driven by the presence of an antagonistic interaction between one mutualist and a third species (Thompson 1982). Some mutualisms, such as those involving ant-fed plants, appear to be driven by environmental stresses, however (Thompson 1982). Beattie (1985) points out, though, that antagonistic third species can be considered as biological stresses.

VARIABLE OUTCOMES OF INTERACTIONS, AND THEIR IMPLICATIONS

Many interactions between species are characterised by the variability in their outcomes (Thompson 1988). They may vary in magnitude or in sign - from mutualism to antagonism, for example. This variability in outcome is fundamental to the way in which interactions evolve (Thompson 1988) but the importance of considering variability in outcome rather than simply mean outcome has only been recognised recently, particularly in the context of mutualisms (Cushman & Addicott 1991).

Many factors contribute to the variability of an interaction - these may be intrinsic or extrinsic to the interaction. Only those interactions which are at least sometimes mutualistic (conditional mutualisms *sensu* Cushman & Whitham (1989)) will be considered here. Because mutualisms often derive from antagonistic interactions there are usually still costs involved for the mutualistic partners (Thompson 1982, 1988). Variation in the cost to benefit ratio and therefore the outcome of an interaction often occurs as a function of the relative or absolute densities of the mutualistic partners, with their sizes or ages, with the intensity of the requirements of a species or the problems which it faces and the ability of the mutualistic partner to solve them. Competition for mutualists within or between species, as well as the complexity of the mutualistic system, also results in variability in outcome (Addicott 1984, 1986; Thompson 1988; Cushman & Addicott 1989). Variation in all these parameters may occur in time and space - variability in time may result in intermittency of interaction on, for example, a seasonal basis.

While obligate and highly specific mutualisms, such as those between figs amd fig wasp pollinators or yuccas and their moth pollinators, must be considered highly coevolved, most mutualisms appear to involve little coevolution between fixed pairs of species. The variability in intensity and possibly sign of interactions over time and space results in great variation in selective pressures which, together with frequent genetic constraints, prevent the tight coevolution of mutualistic species pairs (Howe 1984). In fact, selection on hosts may often be to maximise visits by a number of species of mutualistic partners (Thompson 1982). Species are probably often preadapted by previous interactions to engage in mutualist interactions with novel partners in a new context or habitat (Boucher *et al.* 1982) - an apparently closely coadapted species pair does not necessarily indicate that they have coevolved (Janzen 1980). Any coadaptation that is present is typically broad, gradual and occurs at a higher taxonomic level than species (Howe 1984). However, this does not necessarily diminish the importance of the benefits gained by the species acting as mutualists (Beattie 1985).

MUTUALISM AT A POPULATION AND INDIVIDUAL LEVEL

Many studies of mutualism assess fitness gains by individuals by looking at, for example, increases in fecundity over fairly short time periods. The effects of mutualistic interactions at a population level have been assessed in a number of studies, including some that employ models (Addicott 1981; Keeler 1981). However, few link effects at an individual level with effects at a population level for a given interaction (Addicott 1986). Addicott (1986) has argued that effects at an individual level do not necessarily translate to population changes, and that if they do, they may affect a variety of possible parameters. A mutualism may affect the equilibrium density of a population or it may affect only population growth rate. Alternatively it may only be important at low population levels (e.g. the protection of homopterans by ants during the establishment phase of the former) in which case it may act to stabilise and buffer a population rather than determining equilibrium density. Populations of the mutualists may vary independently and never be at equilibrium densities (Addicott 1984). The likelihood that benefits to a species at an individual level will be reflected at the population level depends on how many life stages of the species are involved in the mutualism and in how many ways one partner benefits the other (Addicott 1986).

ANT-PLANT-HOMOPTERAN INTERACTIONS

Social insects, and particularly ants, interact mutualistically with a large number of species. It is suggested that this is both because they are very widespread and abundant in ecosystems, foraging on a wide variety of foods (Carroll & Janzen 1973) and thus coming into contact with a large number of species, and because of their social structure (Thompson 1982; Hölldobler & Wilson 1990). Ants can provide continual and diffuse protection to a partner and have a rich behavioural repertoire which can be transferred from nestmates to mutualists.

Ants interact mutualistically with species in three main ways. They disperse seeds with or without elaiosomes; they protect plants from herbivores or provide nutrients in return for food from nectaries or nesting sites; and they provide various services to homopterans, lepidopterans in the families Lycaenidae and Riodinidae, and cynipid wasps, in return for honeydew or attractive secretions (Way 1963; Beattie 1985; Buckley 1987a, b; Hölldobler & Wilson 1990; Abe 1992). Ants are thus often associated with plants when participating in mutualistic interactions. Ants may also be attracted to plants in low numbers as foragers of insect prey and they may remove large numbers of insects from a plant (Skinner 1980). Often ants are attracted to a plant (particularly if it is large) by a variety of sources: one or more species of honeydew-producing homopterans and/or lepidopterans, insect prey and nesting sites - they may thus be very important to the ecology of the plant (Whittaker & Warrington 1985; Whittaker 1991; but see Grant & Moran 1986; Mahdi & Whittaker 1993).

Ants benefit tended homopterans in one or more ways: they protect them from predators and parasitoids (Wood 1977; Bach 1991; Cudjoe *et al.* 1993), they remove honeydew which otherwise accumulates and fouls feeding sites, and often encourages the growth of mould (Buckley 1987b; Bach 1991), they provide shelters for certain homopterans (Way 1963; Weaving 1980), and they transport them to new feeding sites (Maschwitz & Hänel 1985). Many homopterans display behavioural or morphological adaptations which favour myrmecophily (Way 1963; Sudd 1987). Great variability exists in the characteristics of ant-homopteran mutualisms, depending on the species involved. Intensity varies from facultative and occasional to obligatory on either or both sides (Maschwitz & Hänel 1985; Buckley 1987a; Sudd 1987; Bristow 1991) although few studies have thus far rigorously assessed the obligacy of mutualisms (Cushman & Beattie 1991). Ants also sometimes prey on the homopterans they tend, which clearly represents a cost to the homopterans. Cushman (1991) proposes that variation in the nutritional content and quantity of honeydew determines whether ants act as tenders or predators. The costs of tending homopterans incurred by ants probably include protecting homopterans from their enemies, building shelters, and transporting individuals, but few studies have quantitatively examined fitness gains by the ant colonies whose workers are tending homopterans (Cushman & Beattie 1991). Ant species vary in the effectiveness of the services they provide to homopterans (Addicott 1979; Bristow 1984). In addition, some predator and parasitoid species are able to attack homopterans without disturbance from ants (Takada & Hashimoto 1985; Völkl & Mackauer 1993), and may even be protected by the ants from their enemies (Völkl 1992).

Within a given ant-homopteran interaction, ant and homopteran densities, as well as those of predators and parasitoids and the developmental stage of the homopteran, may affect the outcome in terms of cost to benefit ratios (Cushman & Whitham 1989). The presence of other mutualists, either of the same or different species (Buckley 1983; Cushman & Addicott 1989; Cushman & Whitham 1991), competing for the services of ants can also affect the outcome of the interaction. Variability in these various parameters may occur temporally and/or spatially, at different scales.

The plants on which ants and homopterans associate are affected by their presence in a number of ways. Ants tending homopterans often increase the persistence, growth rates or sizes of the homopteran populations (Cushman & Addicott 1989; Bach 1991; Rozario *et al.* 1993), resulting in increased phloem loss and pathogen transmission (Beattie 1985; Buckley 1987b). Ants and homopterans are therefore frequently both harmful to the plant. However, ants may also prey on other herbivores on the plant, resulting in reduced herbivory (Laine & Niemelä 1980; Messina 1981; Bach 1991; Ito & Higashi 1991). Whether the costs or benefits of ant presence on the plant are greater determines whether or not an indirect ant-plant mutualism is operating. At a further level of complexity, ants may promote other herbivores by preying on their predators (Fritz 1983). The outcome of these indirect ant-plant interactions will also be a function of herbivore, predator and ant numbers. Conversely, host plant factors may influence ant-homopteran interactions (Bristow 1991; Cushman 1991).

There are thus a large number of variable parameters in ant-plant-homopteran interactions. Many of these apply also to the mutualistic associations between ants and other insects. In consequence, great variability in outcomes of both direct and indirect interactions exists, with both the magnitude and sign of an interaction conditional upon context. The importance of this conditionality to the understanding of ant-plant-herbivore interactions has only been appreciated in recent years (Cushman & Addicott 1991).

FIG BIOLOGY

There are approximately 750 decribed *Ficus* (Moraceae) species worldwide (Berg 1989). They range in growth form from shrubs to large forest emergents and stranglers with a variety of fruiting habits, and occur mainly in the tropics and subtropics. Nearly all are pollinated by their own unique species of small wasp (Hymenoptera: Agaonidae). The fig-pollinator relationship represents a tightly coevolved mutualism which has been intensively studied (Galil 1977; Janzen 1979; Wiebes 1979; Bronstein 1992). The fig or syconium acts as a combined flowering and fruiting structure - it consists of an infolded hollow receptacle lined on its inner surface by hundreds or thousands of unisexual flowers (Verkerke 1989). The lumen is accessed by a bract-lined opening in the apex of the fig, the ostiole. Female flowers are distributed throughout the inner surface while male flowers are either dispersed around the wall of the lumen or in a circle surrounding the ostiole (Verkerke 1989). Figs vary in diameter from a few millimetres to about 15cm when ripe. Approximately 50% of species are monoecious while the rest are gynodioecious (Berg 1989).

Galil & Eisikowitch (1968) have divided the development of monoecious figs into five phases. An initial prefloral phase is followed by a short female phase when the female florets become receptive. The ostiole opens and the fig emits volatile attractants (van Noort *et al.* 1989). Female pollinators arrive at the tree and squeeze through the bracts of the ostiole, often losing their wings and antennal segments in the process. They pollinate a large number of the florets and lay eggs in some of those which they have pollinated - normally they die in the lumen. During the interfloral phase the fig increases in size, seeds mature in the fertilised ovules and wasp larvae develop in galled ovules - the larvae feed on the fertilised endosperm and pupate towards the end of the interfloral phase. Whereas in monoecious species there is a range of style lengths of florets, a mixture of seeds and wasps and a preponderance of female flowers, in gynodioecious figs some plants have figs in which only long-styled female flowers are present and nearly all florets produce seeds (functionally female), while others have figs in which only short-styled female flowers and male flowers are present and mainly wasps are produced (functionally male) (Verkerke 1989). During the male phase of fig development, pollen in the anthers ripens and the wingless male pollinators chew their way out of their galls and enter the lumen, where they locate galls containing female pollinators. They chew a hole in the gall, mate with the female inside and then bore one or more holes through the wall of the fig after which they emerge from the fig and die. Females emerge from their galls into the lumen, collect pollen, escape through the tunnel bored by the males and leave to find a female phase fig. The details of the male phase vary between fig species (Galil & Eisikowitch 1974; Frank 1984). The fig then enters its final, postfloral phase, in which it swells, softens and often changes colour. Many species are eaten by birds, bats, monkeys and other vertebrates and their seeds dispersed in this way (Jordano 1983; Breitwisch 1983; Lambert 1989). Ants (Roberts & Heithaus 1986; Kaufmann *et al.* 1991) and water (Ramirez 1989) may also act as dispersal agents.

Although most fig tree species have only one pollinator, a variable number of other chalcidoid wasp species are associated with each fig species too - up to 30 for a single fig species (Bronstein 1991). Many of these appear to be as species-specific as the pollinators (Bronstein 1991). These species do not pollinate, and they oviposit either by entering the lumen during the female phase like the pollinator, or from the outside of the fig, through its wall, using a long ovipositor. This latter mode allows a wider window of time in the fig's development during which to oviposit. The larvae of all the species develop in individual ovules and the progeny escape at the same time as those of the pollinator. The reproductive biology of most of these species is not well known (Bronstein 1991). They can apparently be divided into primary sycophiles, which oviposit in unfertilised florets and whose larvae feed on galled nucellar tissue, and secondary sycophiles or inquilines, which oviposit into ovules which have been oviposited in by other wasp species (Bronstein 1991) - it has not been proven that these species are parasitoids, but they may be entomophytophagous, eating first the galled plant tissue and later the larva (Compton *et al.* 1994). Some non-pollinators have males which may be winged, polymorphic and adapted for fighting, and may mate at various sites in and on the fig (Vincent 1991). The free-living adult stage of all wasp species is the least studied aspect of their biology (Bronstein 1992).

Besides the wasps, a large number of other insects, most of which are oligophagous, are associated with the genus *Ficus*. They vary from lygaeids feeding on fig seeds (Slater 1971, 1972), through drosophilids (Lachaise 1977; Lachaise *et al.* 1982) and phorids (Compton & Disney 1991) whose larvae develop in the figs and whose adults prey on adult fig wasps, to various lepidopterans and coleopterans which eat fruit, stems or leaves (Compton 1987, 1989; Perrin 1991). Ants are also ubiquitous on fig trees, nesting in branches and/or foraging for food on the tree. They tend homopterans or lycaenids, feed from exudates and prey on insects on the tree, including fig wasps (Frank 1984; Bronstein 1988; Compton & Robertson 1988, 1991).

THE SYSTEM STUDIED

Ficus sur Forsskål is a monoecious fig tree species in the section *Sycomorus*. It has a wide distribution throughout non-arid Africa, from the Cape Province of South Africa to West Africa and the Arabian peninsula. It is a freestanding or occasionally epiphytic tree 4-25m in height (Verkerke 1988) which grows primarily along the banks of rivers and streams and on forest margins. It produces figs of around 30mm in diameter containing up to 3000 flowers (Verkerke 1988) which turn from green to dark red when ripe. These are borne mainly on leafless branches on the major branches and trunks, although some figs are borne singly on smaller branches higher in the tree and others from subterranean fruiting branches - these geocarpic figs appear out of the soil up to a few metres from the tree. Several discrete crops per year may be borne, although they are sometimes produced asynchronously within a single tree. The richness and composition of the wasp fauna associated with the tree varies between regions. In West Africa two pollinators and nine other species are present (Compton *et al.* 1994), while in the eastern Cape Province of South Africa only six species are present in total. These are a single pollinator, *Ceratosolen capensis* Grandi, the primary sycophiles *Sycophaga cyclostigma* Waterston, which also enters the fig to oviposit, and three *Apocryptophagus* species which oviposit from the outside, and the secondary sycophile *Apocrypta guineensis* Grandi which also oviposits from outside the fig.

While many homopterans feed on the leaves and stems of *Ficus* species, gregarious polyphagous homopterans of the family Tettigometridae feed primarily on the figs themselves. They have been recorded in Africa and Madagascar from *Ficus sur*, *F. sycomorus* L., *F. sakalavarum* Baker, *F. botryoides* Baker (pers. obs.) and *F. ingens* (Miq.) Miq. (J.M. Greeff pers. comm.). These tettigometrids are invariably tended by ants, usually in large numbers, on both figs and other plant species (Bourgoin & Dejean 1994).

On *F. sur* a complex set of interactions involving ants, the tettigometrid *Hilda patruelis* Stal., the fig tree and its wasps, has been reported (Compton & Robertson 1988, 1991). Ants which tend *H. patruelis* on *F. sur* figs also disturb or prey on wasps arriving and leaving the tree. Compton & Robertson (1988, 1991) showed that figs on which ants were present produced lower numbers of externally ovipositing wasps (*A. guineensis* and *Apocryptophagus* spp.) and higher numbers of internal ovipositors. Thus ants interfered differentially with externally ovipositing female wasps, because they spend a longer time on the fig surface than internal ovipositors. In this way ants increase the male fitness of the tree (pollinator females) and also probably the female fitness (seeds - through decreased *Apocryptophagus* oviposition) and an indirect ant-plant mutualism is therefore potentially operating.

Compton & Robertson (1988) tested only two trees with a wide discrepancy in ant densities, while a wider range of ant densities and species was tested in a subsequent study (Compton & Robertson 1991). However, no assessment of other parts of the interaction, such as the effects of *H. patruelis* on the tree, ants on emerging wasps, or benefits to other parties, was made. No final conclusion on the presence or otherwise of a mutualism and the conditions under which it operated could thus be drawn. The objectives of this study were therefore to quantify and assess all the major interactions between ants, *H. patruelis*, the tree and its wasps in a population of *F. sur* trees. The relative importance of these interactions and their overall importance to the biology of the fig population were also assessed. Because each chapter has been written to stand on its own to a large degree, there is some duplication within the introductory and methodological sections between chapters.

Chapter 2 outlines characteristics of the study sites, while Chapter 3 considers the phytophagous insect fauna and major arthropod predators on *F. sur*. In particular the abundances of the different species or species groups, and their feeding sites and modes, as well as seasonality, are assessed. The fruiting and leafing phenology of the plants is then related to the insect patterns. This chapter therefore gives a measure of the relative importance of the different phytophagous and predatory species.

The ant fauna on *F. sur* forms the subject of Chapter 4. Species abundances, both relative and absolute, seasonal variation in species activity and numbers, and spatial variation in distribution at an inter-site, inter-tree and within-tree level are all considered. The behavioural activities of each species are also quantified. Finally, the mean numbers of ants and *H. patruelis* per fig, as well as spatial and temporal variation in these numbers, are calculated for the population of fig trees for the duration of the study. This gives a measure of the mean protection afforded figs and their occupants from externally ovipositing wasps by ants, and the variation therein.

Chapter 5 assesses the effects which *H. patruelis* feeding has on wasp progeny and seed production as well as on fig growth and abortion rates. In Chapter 6 the effects of the presence of tending ants on *H. patruelis* are evaluated, and particularly their effects on parasitism and predation rates, *H. patruelis* growth rates and changes in numbers. Chapter 7 investigates the benefits to, and patterns of, ants tending *H. patruelis* and foraging on a fruiting *F. sur* tree. In Chapter 8 the effects of ant predation of female internally ovipositing species on the numbers of these wasps entering the lumen is determined. More data are also presented on the effects of predation and disturbance by ants of wasps ovipositing externally on the numbers and proportions of progeny developing in the figs. Finally, Chapter 9 considers the effects of ants preying on wasp progeny emerging from figs, as well as describing the biology of emergence.

In the concluding discussion, Chapter 10, an assessment is made of the relative importance of the various effects that ant presence has on *Ficus sur* and thus whether and under what conditions an indirect ant-plant mutualism is operating. Consideration is also given to the other parties involved in the interaction, namely *H. patruelis* and ants, and to how important the effects of ants on the fitness and reproductive success of *F. sur* are in relation to other factors and the total biology of the tree.

2 STUDY SITES

The study was conducted in the eastern Cape region of South Africa, at three sites in and around the town of Grahamstown (33°19'S 26°31'E). Grahamstown lies at an elevation of 550m above sea level and receives an average of 690mm of rainfall *per annum* (Stone 1988), with peaks in November (spring) and March (autumn). However, rainfall is erratic in volume and timing from year to year, as the area lies on the summer/winter rainfall divide. The region is warm temperate and seasonal with mean monthly minima ranging from 4.3°C (July) to 14.4°C (February) and mean maxima from 18.9°C (July) to 26.8°C (February). The topography is hilly and soils are predominantly shale, sandstone and tillite (Hiller 1985). Floristically the eastern Cape is a transition region where a great number of vegetation types converge (Lubke & van Wijk 1988). The area around Grahamstown in which the study was conducted comprises bush clump savannah and heath/grassland (Jacot Guillarmod 1985). The *F. sur* trees used for this study ranged in height from 1.5-10m. Trees with and without fruiting branches were studied.

The first of the three sites was in the 1820 Settlers' Botanic Gardens and nearby, at about 580m altitude (Fig. 2.1a). A total of 12 trees was used here, of which three never bore fruit. The trees were scattered around the Gardens and most were fairly isolated from one another, with surrounding vegetation varying from thick bush to more open areas. Two trees were less than 5m from streams while three more grew within 20m of water.

The second study site was at a lower altitude to the first (500m), on Glenthorpe Farm, 5.5km from the first site (Fig. 2.1b). A total of eight trees was used here, all of which were fruit-bearing. Five trees were located next to streams and the other three in fields. Only two trees were surrounded by thick vegetation - the others were in fairly open pastureland.

The third site was at the lowest altitude of the three (380m), and was situated at the bottom of Howison's Poort, a set of valleys transecting the hills above which Grahamstown is situated (Fig. 2.1c). A total of 22 trees was used, seven of which never produced any figs. All trees were located along or near the banks of the Berg and Palmiet rivers and a third stream. Site 3 was the most natural of the three sites, although parts of it were overgrown with invasive tree species. Most *F. sur* trees were close to one another, and surrounded by thick bush. The site was 7km from site 1 and 3km from site 2.

Figure 2.1. Study sites. a) Site 1, 1820 Settler Botanical Garden, Grahamstown. b) Site 2, Glenthorpe Farm. c) Site 3, Howison's Poort. The arrowed tree at site 1 and the large trees in the foreground at sites 2 and 3 are *F. sur*.

3 A DIVERSE COMMUNITY: THE INSECTS ASSOCIATED WITH *FICUS SUR*

3.1 INTRODUCTION

The relationship between the genus *Ficus* and the chalcid wasps which utilise the fig florets is well documented (Ramirez 1970; Galil 1977; Janzen 1979; Wiebes 1979; Herre 1989; Bronstein 1992). Fig trees are also host to many other insects occupying several feeding guilds (*sensu* Root 1973) and interacting with the plant in different ways. They include phytophages feeding on all parts of the tree, predators, parasitoids, scavengers, an epiphyte-feeding fauna, "tourists" or incidentals (Moran & Southwood 1982) and ants. The insects which feed on fig trees vary in their degree of host specificity. Some are widely polyphagous (e.g. Pinhey 1975; Weaving 1980; Millar 1990) but a large number have only been recorded from one or more species in the genus *Ficus*, and could be termed oligophagous (e.g. Pettey 1924; Clark & Dickson 1971; Janzen 1979; Swain & Prinsloo 1986; Bronstein 1988; Perrin 1991).

Several groups of insects utilising African fig trees have received detailed attention: lygaeids (Carayon 1964; Slater 1971, 1972), drosophilids (Lachaise 1977; Tsacas & Lachaise 1979; Lachaise *et al.* 1982), phorids (Compton & Disney 1991), frugivorous weevils (Perrin 1991), some lepidopterans (Compton 1987, 1989), tettigometrids (Compton & Robertson 1988, 1991) and ants (Compton & Robertson 1988, 1991; Thomas 1988). Ueckermann (1991) has dealt with eriophyid mites feeding on Moraceae. In particular, many of the insects that feed on the edible fig, *Ficus carica*, have been studied (e.g. psyllids (Rapisarda 1989) and curculionids (Haines 1927)).

Guild composition of the insect faunas of a number of tree species has been investigated in both temperate (Moran & Southwood 1982; Southwood *et al.* 1982) and tropical (Stork 1987; Basset 1990; Basset & Arthington 1992) regions, as have seasonal patterns in these insects (Lawton 1978; Basset 1991a, b). No quantitative data on guild structure in fig feeding insects has been published to date, however, although Carmin & Scheinkin (1931) documented the occurrence and seasonality of a few species on *F. sycomorus* in Palestine.

This chapter primarily describes the phytophagous insect species recorded on *Ficus sur* in the Grahamstown region of South Africa, in terms of their guild structure, seasonality and general biology. Generalist arthropod predators, epiphyte-feeding psocopterans and some parasitoids are also examined. Ants are excluded from this chapter as they are the subject of Chapter 4. Insects which were judged to be on the tree incidentally are not considered. The insect community on the tree is then examined within the context of the fruiting and leaf phenology of the tree population.

3.2 MATERIALS AND METHODS

Ficus sur trees were monitored at the three sites described in Chapter 2 for 80 weeks, between April 1989 and October 1990. Trees were sampled at two to four week intervals. Each of the three sites was sampled on 27 dates in total. Sampling dates were divided into two periods. During the first period (50 weeks) both trees with and without fruiting branches were sampled (Table 3.1). On all trees during this first period the terminal 30cm of approximately five (mean = 4.84) leafy branches and a similar number of fruiting branches (where a "fruiting branch" is defined as one which has the potential to bear fruit, but may be without fruit at a given time) were examined. Only fruiting branches, and therefore only trees possessing these, were examined during the second (30 weeks) period. A mean of 4.44 fruiting branches per tree was examined over the whole 18 months. Variability in the number of trees sampled on each date (Table 3.1), particularly at site 3, was due to several factors: floodwaters rendered some trees temporarily inaccessible, while flooding or herbicides destroyed three trees.

The numbers of figs and the developmental stages of leaves were recorded on the branches examined, and the developmental stages of figs present on whole trees were also recorded. The species and numbers of insects present on both fruiting and leafy branches were recorded, as were certain types of feeding damage. The feeding habits of phytophagous species were noted. Where necessary, insects were collected for identification. The trunks and main branches of the trees were also examined for the presence of insects, particularly ants.

Mean monthly temperatures and monthly rainfall totals for the whole monitoring period were calculated from Rhodes University Weather Station records.

Because the lengths of the monitoring periods for fruiting and leafy branches were different, seasonal effects result in overall insect incidences on the two branch types not being entirely quantitatively comparable. In addition, intervals between sample dates in summer were greater and result in a bias in incidences toward winter levels on both branch types.

3.3 RESULTS AND DISCUSSION

3.3.1 Temperatures and rainfall over the monitoring period

At the beginning of the sampling period, in April 1989, the region had been under drought conditions for more than five years. These were broken by flooding in November 1989 (Fig. 3.1), so that the total rainfall received in 1989 was 760mm, which was above the average annual rainfall of 690mm recorded for the period 1960-1980 (Stone 1988). However, rainfall in the following year (493mm) was again below average.

Table 3.1. The number of *F. sur* trees examined, sampling dates, and "sample points" over 80 weeks at three sites around Grahamstown, for fruiting and leafy branches. Each sample point represents the data from one tree on one date.

branch type	sample period	monitoring period	no. of sample dates			no. trees examined			total "sample points"		
			site			site			site		
			1	2	3	1	2	3	1	2	3
fruiting	1	April 1989-March 1990	17	17	16	7-8	5-6	9-14	134	101	182
	2	March 1990-October 1990	10	10	11	7	6	7-8	70	60	87
leafy	1	April 1989-March 1990	17	17	16	10-11	5-6	13-21	187	101	290

Mean temperatures were declining from a January peak of 23.1°C (16.8-29.4°C minimum and maximum monthly means) when monitoring commenced in April 1989, and reached a minimum of 10.1°C (2.9-17.4°C) in June (Fig. 3.1). The following season temperatures reached a mean monthly maximum of 20.3°C (13.5-27.1°C) (January 1990) followed by a minimum of 11.8°C (4.5-19.1°C) (July 1990).

3.3.2 Tree phenology

Among the population of fig trees studied, most leaf-fall occurred during July and August, and was followed by a period of growth (September to December) (Fig. 3.2). Individual trees showed considerable variation in the timing of leaf loss. Trees varied in their sequence of phenological events from leaf loss prior to bud burst to leaf loss after bud burst. Only a few trees experienced total leaf loss before bud burst and here the interval between the two events was short (Fig. 3.2). Most trees possessed green leaves throughout the year. Occasional localised within-tree leaf loss and production events occurred through the year.

A large proportion of the trees with fruiting branches possessed some fruit for much of the monitoring period (80.6% of sampling points, Fig. 3.3) although often in small crops. Trees often possessed figs at two developmental stages, and on some trees crop initiation occurred almost continually, resulting in the simultaneous presence of figs of all developmental stages. Crop sizes, both within and between trees, varied from just one fig to several thousands. Of the 21 trees monitored for the entire 18 months, six bore figs continually, while the minimum number of crops borne was three, in two of the trees.

Mean crop duration for 26 distinct crops over the whole monitoring period was 129 ± 36

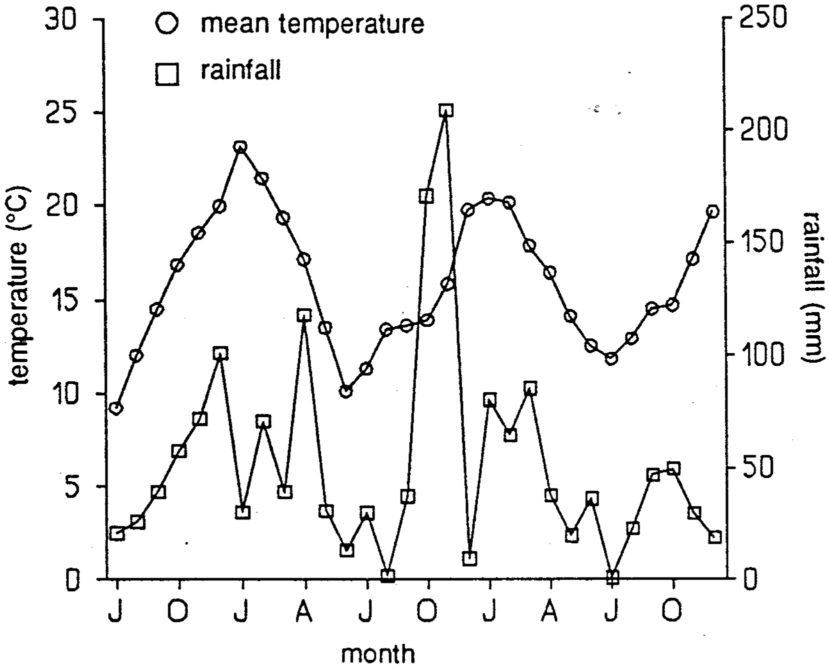


Figure 3.1. Monthly rainfall and mean monthly temperatures in Grahamstown between July 1988 and December 1990.

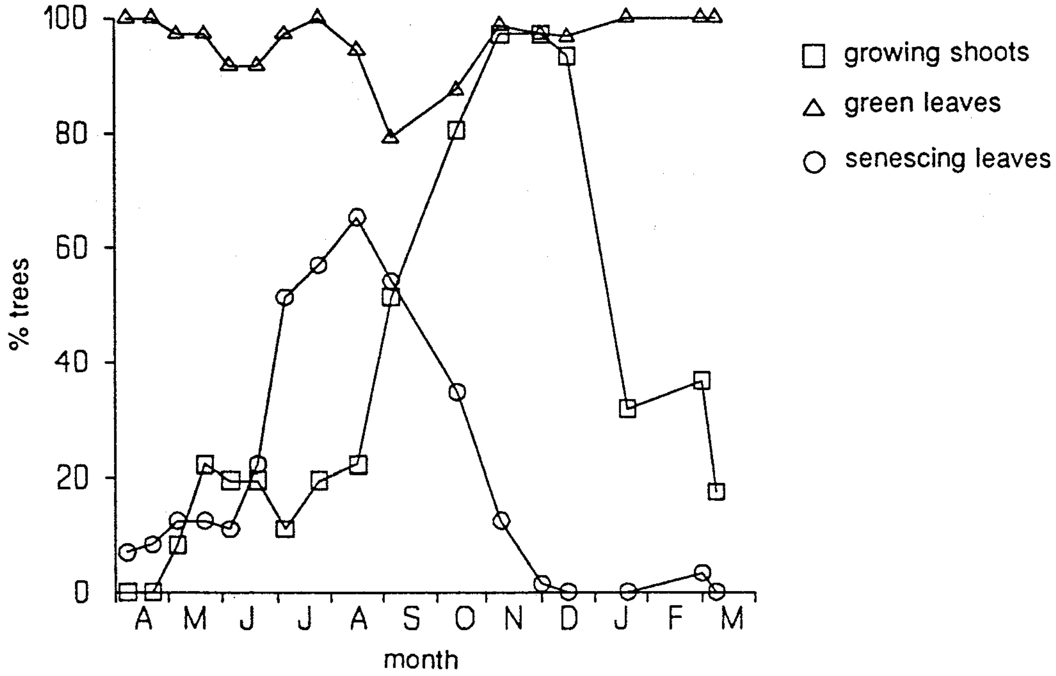


Figure 3.2. Leaf phenology of *F. sur* between April 1989 and March 1990, showing the percentage of monitored trees possessing green leaves, senescing leaves and young growing shoots on each sample date. More than one phenological stage could be present on a single tree on each date. Between 29 and 38 trees were monitored on each date.

days (18.5 weeks) with a range of 65 to 205 days. If 50% or more of a crop's developmental time fell between the beginning of April and the end of September, it was classified as a winter crop. Crop duration over winter (155 ± 25 days, n = 14) was highly significantly longer than in summer (100 ± 19 days, n = 12) (Mann-Whitney U: $Z = -4.140$, $p = 3.47 \times 10^{-5}$). No clear seasonal trends were evident in the total percentage of trees with figs, or in the percentage with pre- or interfloral figs (Fig. 3.3).

In Natal, which is wetter and more tropical than Grahamstown, *F. sur* trees ranged from being evergreen to shedding their leaves fairly regularly (Baijnath & Ramcharun 1983). Most other studies on leafing phenology have been conducted on tropical *Ficus* species (Milton *et al.* 1982; Corlett 1984, 1987; Milton 1991). In these studies, phenology varied with species from continual leaf production to several flushes per year, often with a scatter in phenological events at an inter-tree level.

Compton *et al.* (1994) recorded a mean of 58.9% of fruit-bearing *F. sur* trees per sample date in Grahamstown (which included some of the trees in this sample), a considerably lower figure than in this study. Both Baijnath & Ramcharun (1983) and Compton *et al.* (1994) also found great asynchrony in fruit production within crops on individual trees. An extremely short developmental time of 60 days was recorded by Baijnath & Ramcharun (1983). However, this was for only a single tree at an unspecified time of year. Clear seasonal patterns in the frequency of crop production were also absent from Compton *et al.*'s (1994) *F. sur* population, but Baijnath & Ramcharun (1983) found a slight increase in frequency during summer in Natal. Other studies on fruiting phenologies in *Ficus* usually show continual asynchronous production within a population, but often with peaks and lows through the year (Milton *et al.* 1982; Corlett 1984, 1987; Milton 1991). Within tree synchrony of crop production also varies between species (Corlett 1987; Bronstein & Patel 1992).

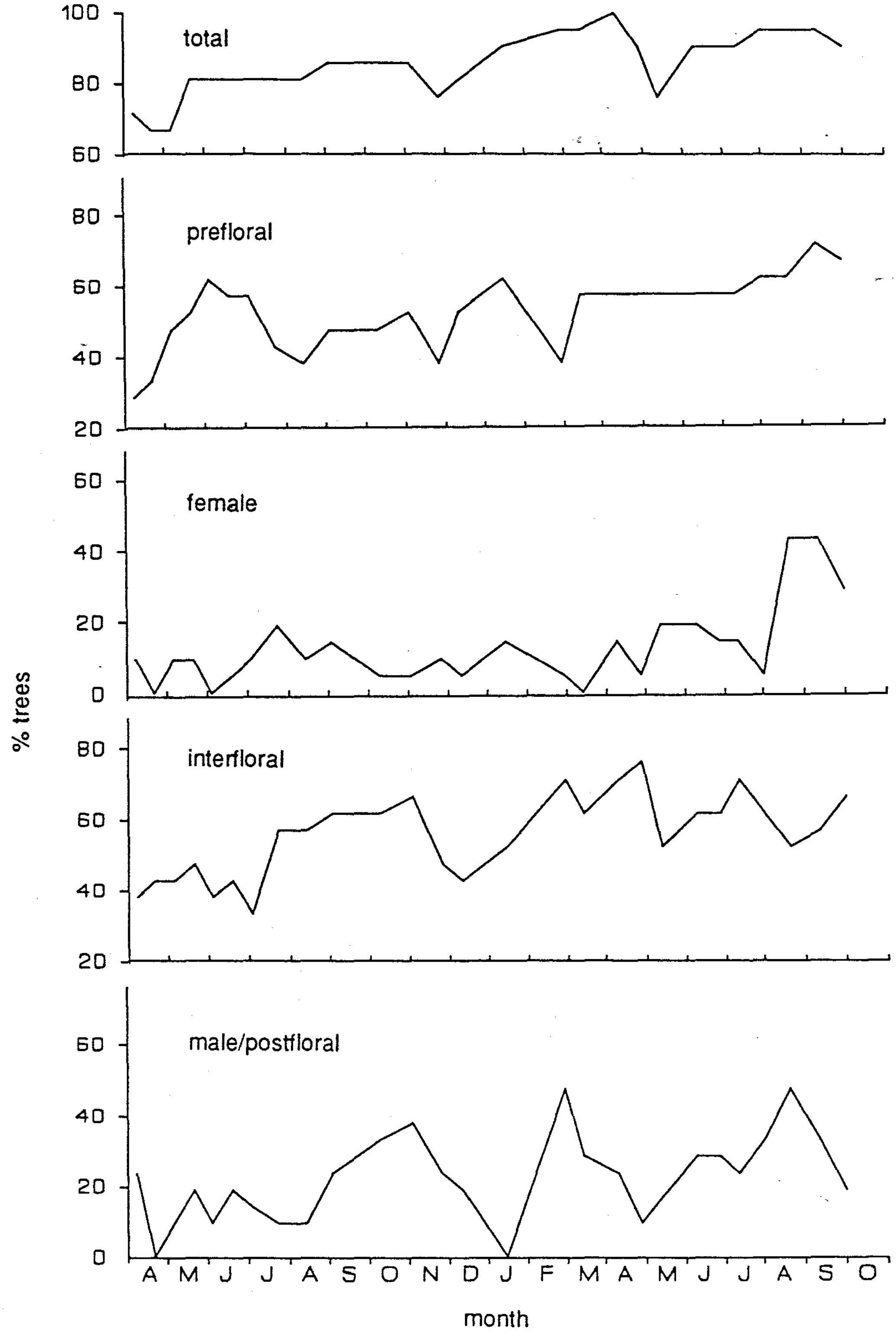


Figure 3.3. Fruiting phenology of *F. sur* between April 1989 and March 1990, showing the percentage of monitored trees possessing prefloral-, female-, interfloral- and postfloral-phase figs on each date. More than one phenological stage could be present on a single tree on each date. 21 trees were monitored on each date.

3.3.3 Insect feeding guilds

The insects found on *F. sur* were categorised into twelve guilds (Table 3.2), where guilds I to VII were phytophagous on living F. sur tissue, guild VIII on dead wood, guild XII on epiphytic flora on *F. sur*, and guilds IX and X were carnivorous. Guild II, the fig galling species, were all agaonid wasps, and are not discussed in this chapter, as they are considered in detail in later chapters. Species considered to have occurred as "tourists" or incidentals (Moran & Southwood 1982) are not dealt with further, while ants (guild XI) are discussed in Chapter 4.

Guilds I-VII. Insects phytophagous on living *F. sur* tissue

I. Fruit/fruiting branch chewers (Table 3.3)

Botyodes hirsutalis Walker (Lepidoptera: Pyraustidae) and *Omophorus* sp. (Coleoptera: Curculionidae) were recorded on figs only on 0.78% and 1.41% of the sample points (i.e. the number of trees over the whole monitoring period) respectively), but caused the most conspicious damage to fruit; they were capable of destroying entire crops. Both species oviposited soon after pollination. *Omophorus* sp. adults fed on the exterior of the fig (as well as on leafy branches) and oviposited into the ostiole, covering the egg with a plug of frass. *B. hirsutalis* adults laid clusters of eggs on stems near the figs, and larvae bored into the fig through the ostiole and other damaged areas. The larvae of both species bored into the interfloral fig lumen and destroyed most of the fig interior, including wasps and seeds. No more than one *Omophorus* sp. larva was ever found in a fig. Larvae utilised only one fig during development, pupating in the fig and eclosing during or after other figs in the crop were at the male phase of development. Several young *B. hirsutalis* larvae were recorded

Table 3.2. Insect species collected on *Ficus sur*. Guilds: I.fruit/fruiting branch chewers; II.fruit gallers; III.fruit/fruiting branch piercers; IV.leaf/stem chewers; V.leaf miners; VI.leaf/stem piercers; VII.leaf gallers; VIII.dead wood feeders; IX.predators; X.parasitoids; XI.ants; XII.epiphytic fauna.

Order	Family	Species	Guild
(Acari)	Eriophyidae	?*Aceria suri* Ueckermann	IX
	Tydeidae	*Tydeus spathatus* Meyer & Rodrigues	VII
Coleoptera	Chrysomelidae	*Hemiphracta livida*	IV
		Monolepta congener (Jacoby)	I,IV
		Monolepta nigrotibialis (Jacoby)	I,IV
		Monolepta sp.	I,IV
	Coccinellidae	various, incl. *Cheilomenes lunata* (Fabricius)	IX
	Curculionidae	*Omophorus* sp.	I,IV
	Scarabaeidae	*Hypopholis sommeri* (Burmeister)	IV
	Scolytidae	*Diamerus* sp.	VIII
	unidentified	CZ29	I
Diptera	Drosophilidae	*Lissocephala* sp.	I
		Zaprionus sp.	I
	Lonchaeidae	*Dasiops* sp.	I
	Tachinidae	*Afrolixa macula* Curran	X

Table 3.2 *continued*

Order	Family	Species	Guild
Heteroptera	Coreidae	various, incl. *Elasmopoda valga* (Linnaeus)	III,VI
	Lygaeidae	*Appolonius quadratus* Scudder	III
		Dinomachellus maculatus Scudder	III
		Dinomachus marshalli Distant	III
	Pentatomidae	various	III,VI
	Reduviidae	various	IX
Homoptera	Aphididae	various, incl. *Aphis gossypii* Glover	III,VI
		Sitobion halli (Eastop)	III,VI
		Toxoptera aurantii (Boyer de Fonscolombe)	III,VI
	Cercopidae	*Locris sanguinipes* Walker	VI
	Cicadellidae	various, incl. CZ24 (Typhlocybinae)	III,VI
	Coccidae/ Diaspididae	various, incl. *Hemiberlesia lataniae* (Signoret)	III,VI
	Lecanodiaspididae	various	III,VI
	Margarodidae/ Pseudococcidae	various, incl. *Icerya purchasi* Mask.	III,VI
	Psyllidae	?*Pauropsylla trichaetae* Pettey /*Trioza* sp.	VII
	Tettigometridae	*Hilda patruelis* Stal.	III,VI

Table 3.2 *continued*

Order	Family	Species	Guild
Hymenoptera	Agaonidae	*Apocrypta guineensis* Grandi	X
		Apocryptophagus sp.1-3	II
		Ceratosolen capensis Grandi	II
		Sycophaga cyclostigma Waterston	II
	Braconidae	CZ27	X
		CZ33	X
		CZ34	X
		CZ36	X
		CZ37	X
	Encyrtidae	*Copidosoma* sp. indescr.	X
		Psyllechthrus oophagus Ghesquiére	X
	Eulophidae	?*Euderus* sp.	X
		Pediobius sp.	X
	Formicidae	*Acantholepis capensis* Mayr	XI
		Anoplolepis custodiens (F. Smith)	XI
		Camponotus maculatus Fabricius	XI
		Camponotus natalensis (F. Smith)	XI
		Camponotus nr *postoculatus* Forel	XI
		Camponotus sp.1	XI
		Cataulacus intrudens (F. Smith)	XI
		Crematogaster nr *delagoensis* Forel	XI
		Crematogaster liengmei Forel	XI
		Monomorium sp.-*boerorum* complex	XI
		Pheidole megacephala (Fabricius)	XI
		Plagiolepis fuscula Emery	XI
		Plagiolepis sp.1	XI
		Polyrhachis schistacea (Gerstaecker)	XI
		Smithistruma transversa (Santschi)	XI
		Technomyrmex albipes (F. Smith)	XI
		Technomyrmex sp.1	XI

Table 3.2 *continued*

Order	Family	Species	Guild
Lepidoptera	Bombycidae	*Ocinara ficicola* Westwood & Ormerod	IV
	Brachodidae	*Phycodes mochlophanes* Meyrick	IV
	Choreutidae	*Brenthia* sp.	IV
		Choreutis aegyptiaca Zollar	IV
	Galleriidae	*Lamoria imbella* (Walker)	I
	Geometridae	*Ascotis selenaria reciprocaria* (Walker)	I,IV
	Gracillariidae	*Acrocercops ficina* Vári	V
	Hypsidae	*Aganais speciosa* (Drury)	IV
	Lycaenidae	*Lachnocnema bibilus* (Fabricius)	IX
		Myrina silenus ficedula Trimen	I,IV
	Noctuidae	*Bareia incidens* Walker	IV
		Celama sp.	IV,IX
	Pyraustidae	*Botyodes hirsutalis* Walker	I
		Cirrhochrista convoluta Hampson	I
	Sphingidae	*Pseudoclanis postica* (Walker)	IV
Neuroptera	Chrysopidae	various	IX
	Hemerobiidae	various	IX
Psocoptera		various	XII

together in single figs, and individual larvae utilised more than one fig. Pupation probably occurred in the ground. Haines (1927) recorded *O. stomachosus* Boh. larvae developing in figs and adults feeding on the fig surface on *F. carica* L..

Cirrhochrista convoluta Hampson (Lepidoptera: Pyraustidae) larvae bored into the bases of prefloral figs and consumed the pericarp. A single larva was capable of destroying a large number of figs, and despite being recorded on only three occasions was the most obvious invertebrate fig herbivore besides *Omophorus* sp. and *B. hirsutalis*. *C. convoluta* has also been reared from *F. burtt-davyi* Hutch. (S. Ross pers. comm.) and *F. lutea* Vahl (pers. obs.). Pyralid (pyraustid) and curculionid species are commonly found in the figs of many species (Haines 1927; Janzen 1979; Bronstein 1988; Perrin 1991; pers. obs.), where they may destroy a large percentage of the crop.

Adults of the leaf-beetles *Monolepta nigrotibialis* (Jacoby), *M. congener* (Jacoby) and *Monolepta* sp. (Coleoptera: Chrysomelidae) and the larvae of the lepidopterans *Ascotis selenaria* ssp. *reciprocaria* (Walker) (Geometridae) and *Myrina silenus* ssp. *ficedula* Trimen (Lycaenidae) were occasionally recorded feeding on the surface of figs (Table 3.3). *A. reciprocaria* has previously been recorded on a large number of tree species (Pinhey 1975), while *M. ficedula* feeds on the fruit and leaves of a number of African fig species, including *F. sur*, *F. cordata* Thunb., *F. natalensis* Hochst. (Clark & Dickson 1971) and *F. burtt-davyi* (S. Ross pers. comm.). Most of these species were also recorded feeding on leafy branches. Four *Lamoria imbella* (Walker) (Lepidoptera: Galleriidae) larvae were recorded boring into interfloral geocarpic figs from the ground on one occasion. A small unidentified beetle (CZ29) was discovered in the vicinity of wasp exit holes on postfloral figs on a number of occasions.

Adult drosophilids of the genera *Lissocephala* (two species) and *Zaprionus* (one species) were found walking on the surface of figs on 12.3% of the sample points, and drosophilid larvae were observed in figs which had been opened. The genus *Lissocephala* is specific to

Ficus (Lachaise *et al.* 1982). In West Africa, six *Lissocephala* species replace one another between the female and late interfloral phases of *F. sur* fig development (Lachaise *et al.* 1982). The eggs are laid in the ostiole and larvae feed in the lumen. *Zaprionus* species are more polyphagous (Lachaise *et al.* 1982) and in *Ficus*, their larvae develop in the outer wall of post-emergent figs. Adults of *Dasiops* sp. (Diptera: Lonchaeidae) were also observed on the fig surface. Lonchaeid larvae have been recorded in figs previously (Janzen 1979); they usually feed on living or injured plant tissue (D. Barraclough pers. comm.).

III. Fruit/fruiting branch piercers (Table 3.4)

The polyphagous (Weaving 1980) bug *Hilda patruelis* (Homoptera: Tettigometridae) was present on 30.6% of sample points, making it the most common species on fruiting branches, both in terms of the number of trees on which it was present and, if a persistent large infestation of scale insects on one tree is excluded, in total numbers of individuals. Numbers of *H. patruelis* on fruiting branches varied from isolated adults with small egg batches to large aggregations of adults and nymphs with communally-laid egg batches. *H. patruelis* fed on both figs and stems; when disturbed, both adults and nymphs tended to walk towards the base of the fruiting branch which they were on. *H. patruelis* was almost invariably tended by ants. Seasonal patterns in *H. patruelis* are examined in a later section of the chapter.

Scale insects (Homoptera: Coccidae/Diaspididae) were also fairly widespread, appearing on 16.1% of sample points, usually in low numbers but sometimes as large permanent infestations. The only species identified on the tree was the diaspidid *Hemiberlesia lataniae* (Signoret). Some species were ant-tended. Three aphid (Homoptera: Aphididae) species were identified on *F. sur*, namely *Aphis gossypii* Glover, *Sitobion halli* (Eastop) and *Toxoptera aurantii* (Boyer de Fonscolombe), although they were not recorded separately in the field. Aphids were present in lower numbers on fruiting than on leafy branches, and are therefore dealt with in more detail below.

The heterogastrine bugs *Dinomachus marshalli* Distant and *Dinomachellus maculatus* Scudder and the rhyparochromine bug *Appolonius quadratus* Scudder (Heteroptera: Lygaeidae) fed on seeds in developing figs on the trees. These species have also been recorded on other figs, and the subfamily Heterogastrinae is apparently specific to the genus *Ficus* in South Africa (Slater 1972). Observations on their biology agree with those of Slater (1971). *D. maculatus* was the most common species, being present on 9.3% of sample points, and large aggregations of nymphs and adults were found feeding on figs or hiding under pieces of bark near fruiting branches. These latter records were included when calculating abundance; therefore only trees with fruiting branches in the first period were used (n = 417). A number of other lygaeid species have been recorded from *F. sur* (Slater 1972), but these feed on mature seeds in figs that have fallen beneath the tree.

Homopterans of the families Pseudococcidae, Margarodidae (including the Australian Bug *Iceryia purchasi* Mask.) and Lecanodiaspididae were occasionally found on the fruiting branches of *F. sur*, as were heteropterans of the families Cicadellidae, Pentatomidae and Coreidae. The only species to be identified was the coreid *Elasmopoda valga* (L.).

IV. Leaf/stem chewers (Table 3.5)

The larvae of *Brenthia* sp. and *Choreutis aegyptiaca* Zollar (Lepidoptera: Choreutidae) were the most widespread leaf chewers, and were recorded on 3.7% and 4.7% of sample points respectively. *Brenthia* sp. usually fed on the surface of mature, green leaves and occurred throughout the year in low numbers. It has also been recorded on *F. burtt-davyi* (S. Ross pers. comm.). *C. aegyptiaca* was confined to a large outbreak in spring. It fed by spinning a web over a shoot terminal and chewing the young leaves under the web. Numbers of *C. aegyptiaca* individuals could not be accurately assessed (Table 3.5) as they were concealed in leaf-sheaths

Table 3.3. Guild I. Fruit/fruiting branch chewers on *Ficus sur* trees. Species or species groups in the guild, the number of sample points on which they were recorded, their percentage contribution to the guild (no. sample points on which species was recorded/no. sample points on which sum of species were recorded), and total numbers of individuals recorded. Total no. sample points = 640.

species/group	no. sample points present	% contribution to guild	total no. individuals
Drosophilidae	79	69.7	234
Omophorus sp.[1]	9	8.0	12
Botyodes hirsutalis	5	4.42	5
Dasiops sp.	4	3.54	5
CZ29 (Coleoptera)	4	3.54	8
Ascotis reciprocaria[1]	3	2.66	3
Cirrhochrista convoluta	3	2.66	3
Lamoria imbella	1	0.88	4
Monolepta congener[1]	1	0.88	1
Monolepta nigrotibialis[1]	1	0.88	2
Monolepta sp.[1]	1	0.88	1
Myrina ficedula[1]	1	0.88	1
Phycodes mochlophanes[1]	1	0.88	1

1: a member of more than one guild.

Table 3.4. Guild III. Fruit/fruiting branch piercers on *Ficus sur* trees. Species or species groups in the guild, the number of sample points on which they were recorded, their percentage contribution to the guild, and total numbers of individuals recorded. Total no. sample points = 640.

species/group	no. sample points present	% contribution to guild	total no. individuals
Hilda patruelis[1]	196	44.0	3036
Coccidae/Diaspididae[1]	103	23.2	4950
Dinomachus marshalli[2]	39	13.5	287
Aphididae[1]	36	8.10	641
Dinomachellus maculatus/ *Appolonius quadratus*[2]	15	5.18	24
Pseudococcidae/Margarodidae[1]	12	2.70	62
Cicadellidae[1]	5	1.12	8
Lecanodiaspididae[1]	4	0.91	4
Coreidae[1]	3	0.68	3
Pentatomidae[1]	3	0.68	3

1: a member of more than one guild
2: total no. sample points = 417

which were not opened.

Gregarious larvae of the beetle *Hemiphracta livida* (Coleoptera: Chrysomelidae) fed on *F. sur* leaves, while adults fed both on leaves and stems. *H. livida* was recorded only on 2.1% of sample points, but the large number of gregarious larvae present on these trees caused considerable damage to mature leaves. The adults of another chrysomelid, *Monolepta nigrotibialis*, fed on young leaves and leaf-sheaths, while adults of the weevil *Omophorus* sp. were occasionally recorded feeding on green stems. Haines (1927) has observed *O. stomachosus* feeding on young twigs on *F. carica*.

The larvae of several other species of Lepidoptera, most of which were larger than those of *Brenthia* sp. and *C. aegyptiaca*, were recorded in low numbers, feeding on *F. sur* leaves and stems. *Ocinara ficicola* Westwood & Ormerod (Bombycidae) has been recorded from other fig species and recently appeared in the western Cape (Cochrane 1989). This species, together with *Ascotis reciprocaria* (Geometridae) and *Myrina ficedula* (Lycaenidae) fed on young leaves. *Pseudoclanis postica* (Walker) (Sphingidae), which has been recorded feeding on several fig species as well as other Moraceae, such as mulberry trees, fed on mature leaves, as did the noctuid *Bareia incidens* Walker. *Aganais speciosa* (Drury) (Hypsidae) fed on both young and mature leaves and has also been found feeding on *F. burtt-davyi* (Compton 1987). *P. postica* and mature *A. speciosa* sabotage the latex defenses of leaves by cutting through veins prior to eating (Compton 1987, 1989). Most *Phycodes mochlophanes* Meyrick (Lepidoptera: Brachodidae) larvae bored into young green stems. The congener *P. punctata* Walsingham has been recorded on *F. burtt-davyi* (S. Ross pers. comm.) and *F. natalensis* (Swain & Prinsloo 1986). Adults of the beetles *Monolepta congener*, *Monolepta* sp. (Chrysomelidae) and *Hypopholis sommeri* (Burmeister) (Scarabaeidae) were occasionally recorded feeding on *F. sur* leafy branches. *H. sommeri* has been recorded on *F. sur* previously (Swain & Prinsloo 1986).

V. *Leafminers*

Acrocercops ficina Vári (Lepidoptera: Gracillariidae) larvae mined young green leaves, forming a narrow convoluted track. Usually only one mine per leaf was present, and remained visible through the season. In the first monitoring season 18 leaves on seven of the 37 trees were mined. During the second season this increased to 36 leaves on 17 trees. The species has been recorded previously on *F. natalensis* (Swain & Prinsloo 1986). Another species that formed more circular mines may also have been present but no adults were obtained to confirm this.

VI. *Stem/leaf piercers (Table 3.6)*

This guild had a large number of species in common with guild III, although they often occurred at greatly different relative frequencies. The most widespread species was an unidentified typhlocybine (Homoptera: Cicadellidae) recorded on 43.2% of sample points. Adults and nymphs of this species were usually found on the undersides of mature leaves. The subfamily Typhlocybinae feed on mesophyll cells, and were also recorded by Claridge & Wilson (1976) and Basset (1991b) feeding on mature leaves. The species was present throughout the year - patterns of seasonality are examined in a following section - and has also been recorded on *F. burtt-davyi* (S. Ross pers. comm.).

The most abundant insects in the stem/leaf piercing guild were aphids, which were found on 15.7% of sample points at a mean of 20.5 per point. The three species identified on the tree, *Aphis gossypii*, *Sitobion halli* and *Toxoptera aurantii*, were not recorded separately in the field. The aphids fed mainly on young and growing shoots and were present in large numbers in spring. The aphids *Toxoptera aurantii* and *Aphis gossypii* are both highly polyphagous cosmopolitan species whereas *Sitobion halli* has only been recorded feeding on plants in five families, including Moraceae (*Ficus*) (Millar 1990).

Table 3.5. Guild IV. Leaf/stem chewers on *Ficus sur* trees. Species or species groups in the guild, the number of sample points on which they were recorded, their percentage contribution to the guild, and total numbers of individuals recorded. Total no. sample points = 574.

species/group	no. sample points present	% contribution to guild	total no. individuals
Choreutis aegyptiaca	27	26.3	-
Brenthia sp.	21	20.8	28
Hemiphracta livida	12	11.9	80
Monolepta nigrotibialis[1]	9	8.94	10
Bareia incidens	7	6.95	8
Aganais speciosa	6	5.98	8
Ascotis reciprocaria[1]	5	4.96	5
Omophorus sp.[1]	3	2.98	3
Phycodes mochlophanes[1]	3	2.98	6
Monolepta sp.[1]	2	1.98	2
Pseudoclanis postica	2	1.98	2
Hypopholis sommeri	1	0.99	1
Monolepta congener[1]	1	0.99	1
Myrina ficedula[1]	1	0.99	1
Ocinara ficicola	1	0.99	1

1: a member of more than one guild

Table 3.6. Guild VI. Leaf/stem piercers on *Ficus sur* trees. Species or species groups in the guild, the number of sample points on which they were recorded, their percentage contribution to the guild, and total numbers of individuals recorded. Total no. sample points = 574.

species/group	no. sample points present	% contribution to guild	total no. individuals
CZ24 (Typhlocybinae)	248	53.7	749
Aphididae[1]	90	19.5	1848
Coccidae/Diaspididae[1]	53	11.5	170
Pseudococcidae/Margarodidae[1]	25	5.41	34
other Cicadellidae[1]	18	3.90	20
Locris sanguinipes	10	2.16	16
Coreidae[1]	6	1.30	6
Pentatomidae[1]	6	1.30	7
Hilda patruelis[1]	2	0.43	12
Lecanodiaspididae[1]	2	0.43	2
Psyllidae[1] (adult)	2	0.43	3

1: a member of more than one guild

Locris sanguinipes Walker (Homoptera: Cercopidae) adults were present on leaves for a few months in early summer. A number of species of cicadellid adults and nymphs were recorded on leaves, but at much lower frequencies than the typhlocybine discussed above. Coccoidea were less common than on fruiting branches, both in terms of the number of trees on which they were found and the numbers of individuals present. *Hilda patruelis* was also rare on leafy branches (0.35% of sample points). Finally, coreids and pentatomids were found on leafy branches occasionally, the coreids causing tip-wilting in growing shoots.

VII. Leaf gallers

The nymphs of an unidentified psyllid (Homoptera: Psyllidae) species developed in galls on the underside of young fig leaves. The number of galls per leaf varied from one to more thanten, and galls remained visible throughout the season. Leaves on 70.2% of the 37 monitored trees were galled in the first monitoring season and on 70.4% in the second season. Pettey (1924) recorded *Pauropsylla trichaeta* Pettey forming galls on a native *Ficus* species in the eastern Transvaal, and Swain & Prinsloo (1986) listed *P. trichaeta* and *Trioza* sp. on *F. sur*. Carmin & Scheinkin (1931) discussed the lifecycles of two *Pauropsylla* species on *F. sycomorus* L. in the Middle East. Their description of the galls of these species is identical to those found on *F. sur* in this study.

Unidentified eriophyid mites created small white blisters on young *F. sur* leaves. The extent of the damage varied from a few blisters per leaf to leaves covered with blisters and, again, the damage remained visible throughout the summer. Damage was not recorded in the first season. In the second season 67.6% of the 37 monitored trees had some blistering on their leaves. *Aceria suri* Ueckermann has been recorded previously on *F. sur*, where it caused leaf blisters (Ueckermann 1991).

Relative contributions of phytophage orders and guilds

An estimated 59 species of phytophagous insects were recorded on *Ficus sur* over the monitoring period, most of which were homopterans or lepidopterans (Fig. 3.4). Coleoptera, Heteroptera, Diptera and Hymenoptera were also represented by a number of species. Most species fell into piercing and chewing guilds on fruiting and leafy branches (Fig. 3.5).

The number of sample points (i.e. the number of trees over the whole monitoring period) on which a species was present was calculated for each species (see above), except for guilds V and VII, where only damage was recorded. These values were then added together for all species within a guild and standardised for total sampling effort on the different parts of the tree, in order to give an indication of how widespread the individuals of a guild were in time and space (Fig. 3.6a). The piercing guilds (III and VI) were present on 74% of sampling points while leaf gallers (VII) achieved the same status as fruit (I) and leaf (IV) chewers. This indicates that there were fewer species but higher per-species abundance for leaf gallers. The fruit and especially the leaf chewing guilds were species rich, but most species were rare. However, because persistent damage was recorded for leaf gallers and miners but only insect presence for the other guilds, the former two guilds are probably relatively over-represented in Fig. 3.6. In terms of total numbers of individuals in each guild (Fig. 3.6b) the piercing guilds were proportionally even larger, accounting for 96% of all individuals. Numbers of individuals in guild VII were not included, while numbers of damaged leaves were used for guild V.

Guild VIII. Dead wood feeders

A number of adults of *Diamerus* sp. (Coleoptera: Scolytidae) were found on one occasion

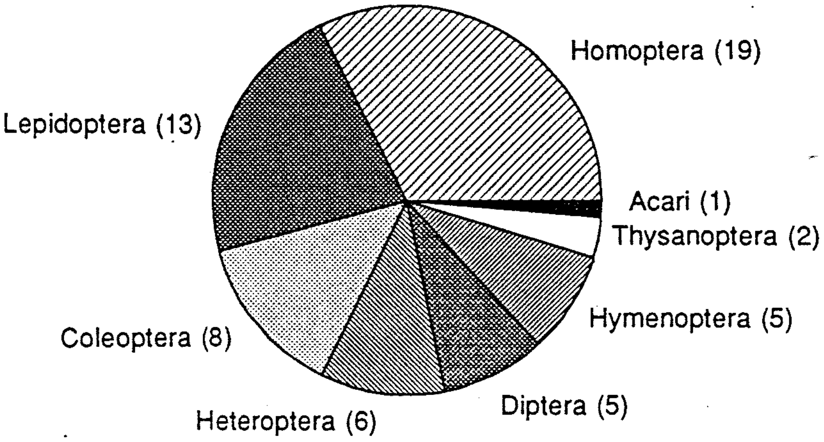


Figure 3.4. Number of phytophagous species in each order on *F. sur*. Numbers of species are indicated on the pie chart.

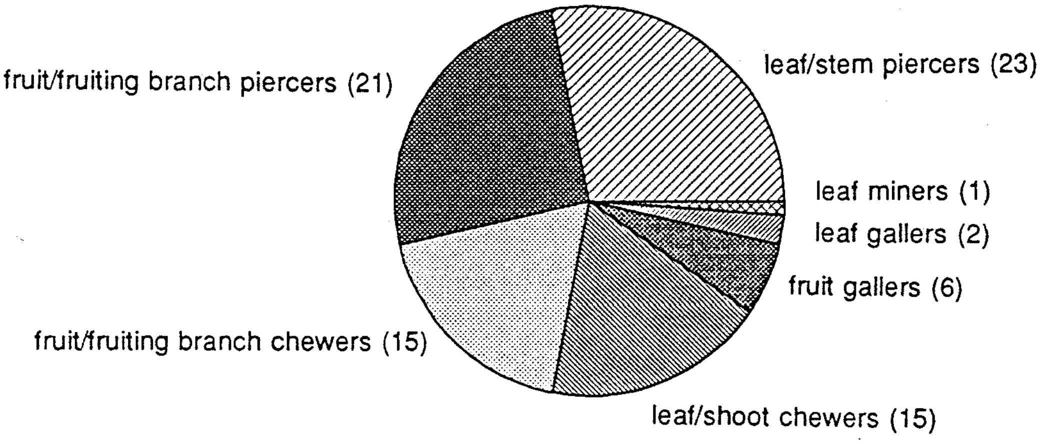
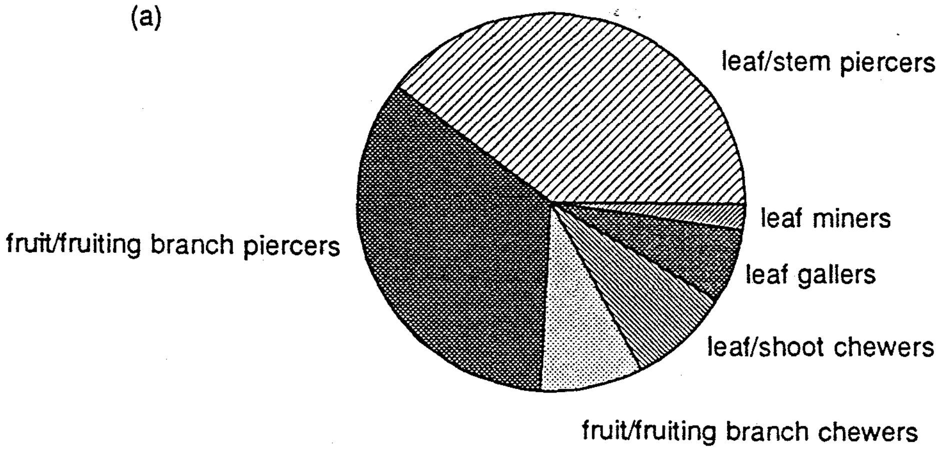


Figure 3.5. Number of species in each phytophagous guild on *F. sur*. Numbers of species are indicated on the pie chart.

(a)



(b)

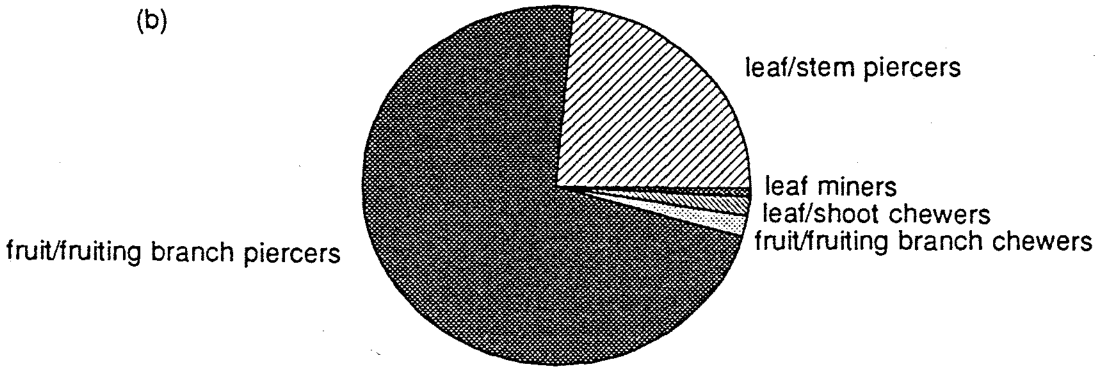


Figure 3.6. a) Total number of sample points on which individuals in each guild were recorded over the monitoring period on *F. sur*. Values are corrected for differences in sampling effort between guilds. For guilds V and VI numbers of trees with feeding damage were used. b) Total number of individuals recorded in each guild over the monitoring period. Values are corrected for differences in sampling effort between guilds. For guild V the number of damaged leaves was used. Guild VII was omitted as no data were available.

boring into a dead branch. *D. pulverulentus* has previously been recorded on *F. sur* (Swain & Prinsloo 1986) and adults of a *Diamerus* species were found locally in dead wood on *F. burtt-davyi* (S. Ross pers. comm.).

Guilds IX and X. Carnivorous insects

IX. Predators (Table 3.7)

A large number of unidentified species of spiders were widespread both on the leafy branches, where they were present on 29.6% of sample points, and on fruiting branches (8.1% of sample points). Very little predation by spiders was observed - a few insects caught in webs and a single salticid carrying an *H. patruelis* adult.

Adult beetles of the family Coccinellidae were observed feeding on aphids. Elsewhere, the coccinellid *Cheilomenes lunata* (Fabricius) has been recorded as preying on the aphid *Toxoptera aurantii* (Fürsch 1985), and Weaving (1980) recorded a coccinellid adult of the genus *Hyperaspis* feeding on *H. patruelis* eggs. Predatory larvae, most of which were neuropterans (Chrysopidae and Hemerobiidae), were observed feeding on aphids and, on one occasion, *H. patruelis* eggs. Eggs, possibly of these species, were found near groups of aphids. Reduviids (Heteroptera) were occasionally found on fruiting and leafy branches.

The predatory caterpillar *Lachnocnema bibilus* (Fabricius) (Lepidoptera: Lycaenidae) was found only on fruiting branches on which *H. patruelis* was present. This species was found to be an important predator of *H. patruelis* eggs and nymphs, and its biology is discussed further in Chapter 6.

The mite *Tydeus spathatus* Meyer & Rodrigues (Tydeidae) was common on the leaves, although its abundance was not measured, and may prey on the eriophyid mite *A. suri*, as tydeids have been recorded preying on *A. ficus* (Cotte) (Baker & Wharton 1952). On one occasion several mites were observed feeding on a leafhopper exuvium. Phorids were not recorded in this study, but are known to prey on fig wasps both inside and on the surface of figs. *Megaselia ficaria* Disney and *M. surophila* Disney have been recorded from *F. sur* (Compton & Disney 1991). 82% of the 351 predatory individuals recorded in total were found on leafy branches.

X. *Parasitoids*

A number of parasitoids were reared from identified lepidopteran, coleopteran and homopteran hosts (Table 3.8). *Omophorus* sp. egg parasitism by the eulophid *Euderus* sp. as well as *Brenthia* sp. larval parasitism by an unidentified braconid (Table 3.8) appeared common. Clusters of parasitoid cocoons from larger lepidopteran larvae such as *B. incidens* and *A. speciosa* were found on leaves and trunks. Another, orange-coloured, species of braconid (Table 3.8) was seen searching and ovipositing through the ostiole of figs infested with *Omophorus* sp. or *B. hirsutalis* on a number of occasions, but it was not clear which species was being parasitised. *Psyllechthrus oophagus* Ghesquiére was the only parasitoid species recorded for *H. patruelis*. Its biology is discussed further in Chapter 6.

Guild XII. Epiphyte-feeding fauna

The eggs, nymphs, adults and webs of an unknown number of species of Psocoptera were found mainly on the undersides of leaves. On leafy branches adults, nymphs and/or eggs were present on 15.5% of the total of 574 sample points, but on fruiting branches they were only recorded on 1.7% of the 640 sample points. Seasonal patterns are discussed below.

Table 3.7. Guild VI. Predators on *Ficus sur* trees. Species or species groups in the guild, the number of sample points on which they were recorded, their percentage contribution to the guild, and total numbers of individuals recorded. Total no. sample points = 574 for leafy branches and 640 for fruiting branches.

branch type	species/group	no. sample points present	% contribution to guild	total no. individuals
leafy	spiders	170	79.4	234
	Coccinellidae (adults)	20	9.35	22
	Neuroptera (larvae)	15	7.01	17
	Neuroptera (adults)	5	2.34	5
	Reduviidae	4	1.87	4
fruiting	spiders	52	80.0	56
	Lachnocnema bibilus	4	6.15	4
	Neuroptera (larvae)	4	6.15	4
	Coccinellidae (adults)	3	4.61	3
	Neuroptera (larvae)	1	1.54	1
	Reduviidae	1	1.54	1

Table 3.8. Parasitoid species from insect herbivores on *F. sur*. Only parasitoids reared from host species identified at least to genus level are listed.

Host species	Parasitoid sp./accession no. (Family)	stage parasitised
Hemiphracta livida	*Afrolixa macula* (Tachinidae)	larva
Omophorus sp.	?*Euderus* sp. (Eulophidae)	egg
Omophorus sp./*Botyodes hirsutalis*	CZ27 (Braconidae)	larva
Hilda patruelis	*Psyllechthrus oophagus*	egg
Choreutis aegyptiaca	(Encyrtidae)	larva
Brenthia sp.	CZ36 (Braconidae)	larva
Bareia incidens	CZ37 (Braconidae)	larva (hyperparasitoid
	Pediobius sp. (Eulophidae)	via braconids)

3.3.4 Seasonal patterns in species occurrence

The total number of sample points on which a species was recorded and the total numbers of individuals of that species recorded over the monitoring period gives no indication of spatial versus temporal distribution. Thus a species appearing in high numbers for a short period may have the same overall values as one which is present in low numbers throughout the year. When these factors are considered, the most seasonal species were generally those feeding only on young shoots or leaves (Fig. 3.7) - the majority of these were Lepidoptera, but included Homoptera and Coleoptera. Species feeding on mature leaves were either present through most of the year (*Brenthia* sp., *H. livida*, typhlocybine species) or appeared later in spring or summer (*B. incidens*, *P. postica*). The number of species of phytophages increased to a maximum of 24 in November and December (Fig. 3.8), due mainly to an increase in the number of species feeding on leafy branches. The number of species utilising fruiting branches varied less with season than did the leaf feeders (Fig. 3.8), probably due to their more stable year-round phenology. The November-December peak corresponded to the peak in growth activity of *F. sur* (Fig. 3.2) and occurred about one month before the peak in summer temperature (Fig. 3.1).

A number of insect species were present in sufficient numbers to warrant analysis of seasonal population patterns. The most important of these in the context of this study was *H. patruelis*, but population patterns in the typhlocybine species, aphids and psocopterans are also examined below.

Seasonal changes in *H. patruelis* in this study are in agreement with those observed by Weaving (1980) in Zimbabwe. In Weaving's study a gradual increase in winter was followed by a rapid increase in breeding rate in spring and subsequently dispersal onto new host plants and continued breeding. The trend after this, in summer, depended on rainfall. In years of

Figure 3.7. Temporal patterns of phytophagous species recorded on *F. sur* between April 1989 and March 1990. Species presence on fruiting and leafy branches is combined for each sampling date, and is indicated by a solid bar.

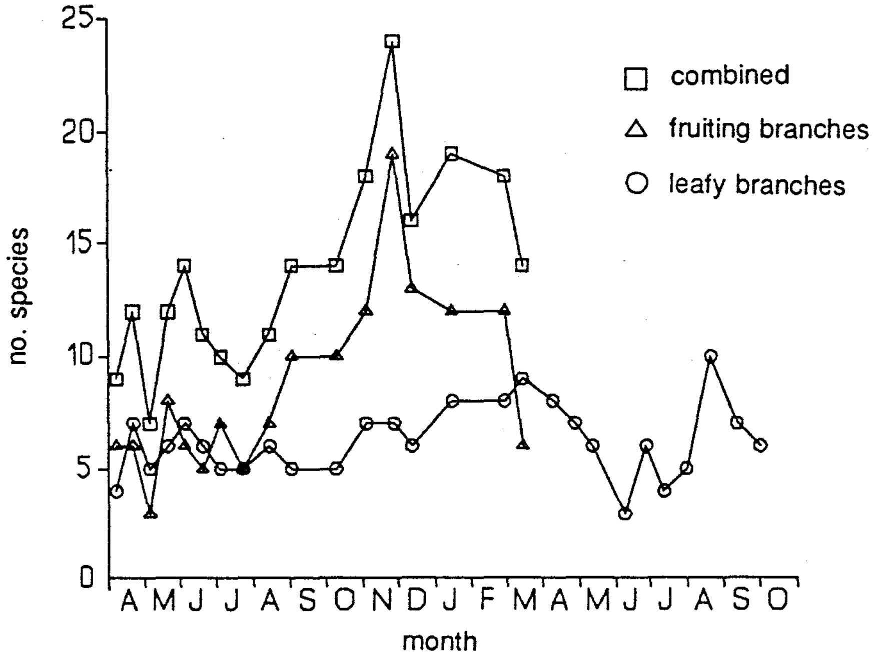


Figure 3.8. Total numbers of species recorded on *F. sur* on each date, recorded separately on fruiting branches and leafy branches, and combined.

high rainfall subterranean infestations became waterlogged and a decrease in population sizes occurred.

Fig. 3.9a and b illustrate the trends in the populations of *H. patruelis* in this study. *H. patruelis* gradually disappeared from trees during the 1989 winter, and on trees on which they were present they decreased in numbers. A slight increase at the end of August in the percentage of trees on which bugs were found and a large increase in the density of nymphs per tree may indicate that breeding had occurred. This was followed, in December, by an increase in the number of trees with adults, probably reflecting dispersal. A subsequent large increase in the number of trees with nymphs and number of nymphs per tree in January may have been due to egg-laying by adults which had dispersed in December. In the meantime, adult distribution had decreased, possibly because they had died or dispersed to other host plants. The number of trees with adults increased dramatically in late February, again due possibly to the eclosion of developing nymphs, the numbers of which had decreased. That the density of adults per tree did not increase at this stage possibly implies continued dispersal. The numbers of adults per tree slowly increased until the end of summer. The percentage of trees with nymphs and adults remained high until the end of May, after which it decreased, together with the numbers of adults and nymphs per tree. At the end of August, as in the previous year, there was a slight increase in the percentage of trees with nymphs and a large increase in the numbers of nymphs per tree, possibly indicating breeding.

In Zimbabwe *H. patruelis* is extremely polyphagous and has been recorded on 42 plant species - it transfers from one weed species to another as they succeed each other (Weaving 1980). The number of plant species utilised by *H. patruelis* in the Grahamstown area is unknown, and therefore the importance of *F. sur* in the population dynamics of the bug cannot be predicted. The fig trees probably represent a stable food source for adults as most trees have some figs at most times; however, *H. patruelis* requires young figs to complete a

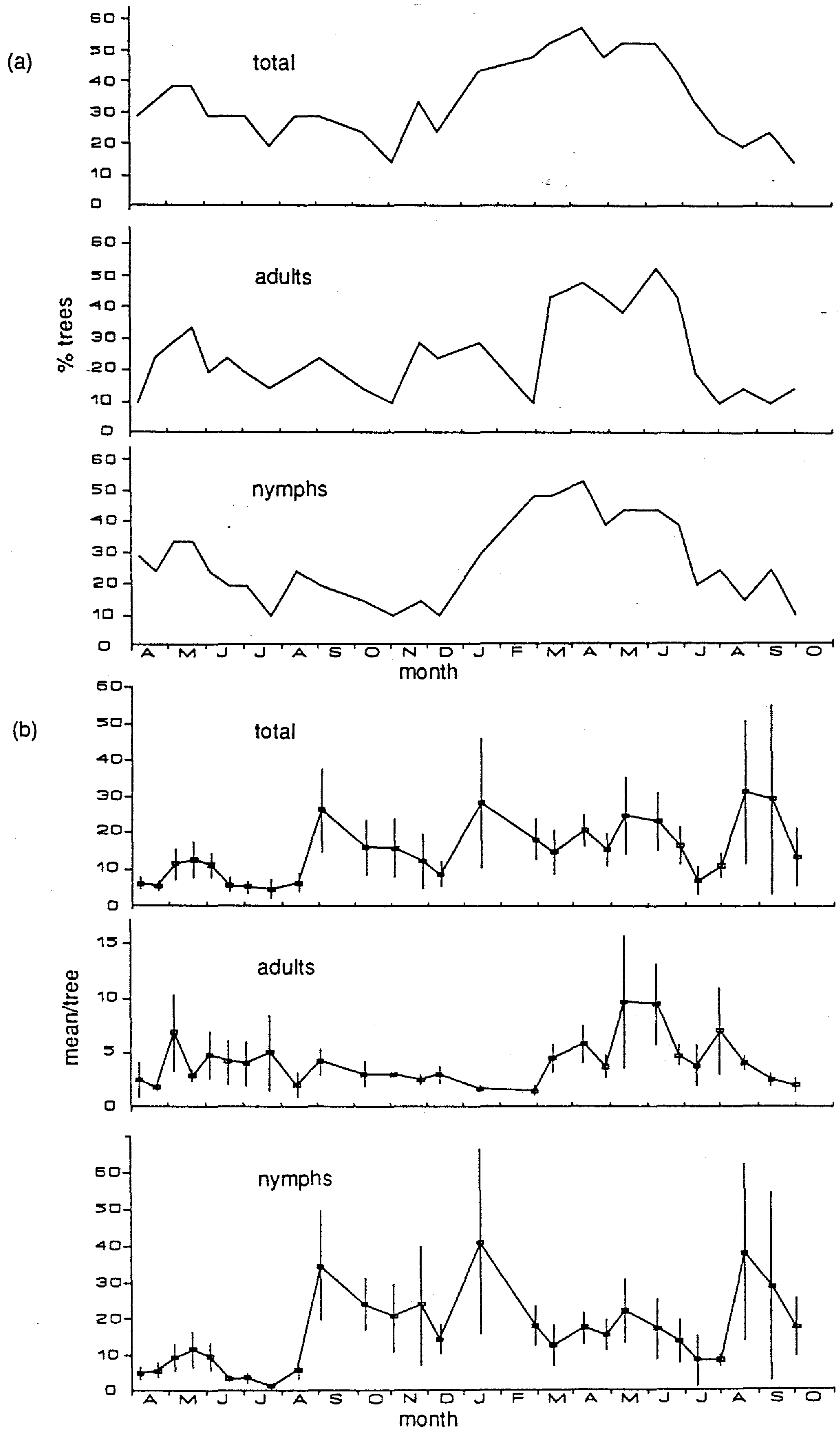


Figure 3.9. *H. patruelis* numbers on fruiting branches. a) Percentage of 21 monitored trees on which *H. patruelis* was present on each sampling date. b) Mean number of *H. patruelis* per tree ± 1SE, for trees on which they were present. Nymphs and adults presented separately, and combined.

generation on a crop. Peaks in young fruit production (Fig. 3.3) correspond with peaks in the numbers of nymphs per tree (Fig. 3.9b), but probably do not explain the amplitudes of these peaks, as the percentage of trees with young figs only ranged from 30 to 65% over the monitoring period.

The percentage of trees with the typhlocybine species present decreased towards the end of winter and increased during late spring and during summer (Fig. 3.10a). Nymphs decreased in winter so that on most trees only adults were present. At the end of winter the number of trees on which adults were present decreased; adults probably laid eggs and died or dispersed. The large increase in the number of trees on which nymphs were present in spring was probably due to the hatching of eggs layed the previous winter. It was followed by an increase in the number of trees on which adults were present, due to eclosion and/or dispersal. Claridge and Wilson (1976) found that typhlocybine species on British trees either overwintered as eggs or as adults which layed eggs in spring. Mean numbers per tree of the cicadellid were low in this study (Fig. 3.10b); during winter there were more adults than nymphs per tree and adults accounted for most fluctuation in abundance. During spring and summer the situation was reversed, possibly reflecting the dispersal of adults.

Aphid species were not routinely recorded separately and therefore their relative abundances are unknown. However, the one or more species which contribute to seasonal population changes on the leafy branches of *F. sur* (Fig. 3.11) appear to be heteroecious (host alternating) as all aphids disappeared from the trees in mid-summer, possibly dispersing onto secondary, herbaceous host species for the duration of the summer (Dixon 1973; Millar 1990). An increase in the percentage of trees with aphids in winter was possibly a reflection of a return movement from secondary host species to figs, the primary hosts. The aphids may have then overwintered as adults or eggs, but at least *Toxoptera aurantii* appears to be entirely anholocyclic (parthenogenetic reproduction only) (Millar 1990). The large, rapid increase in

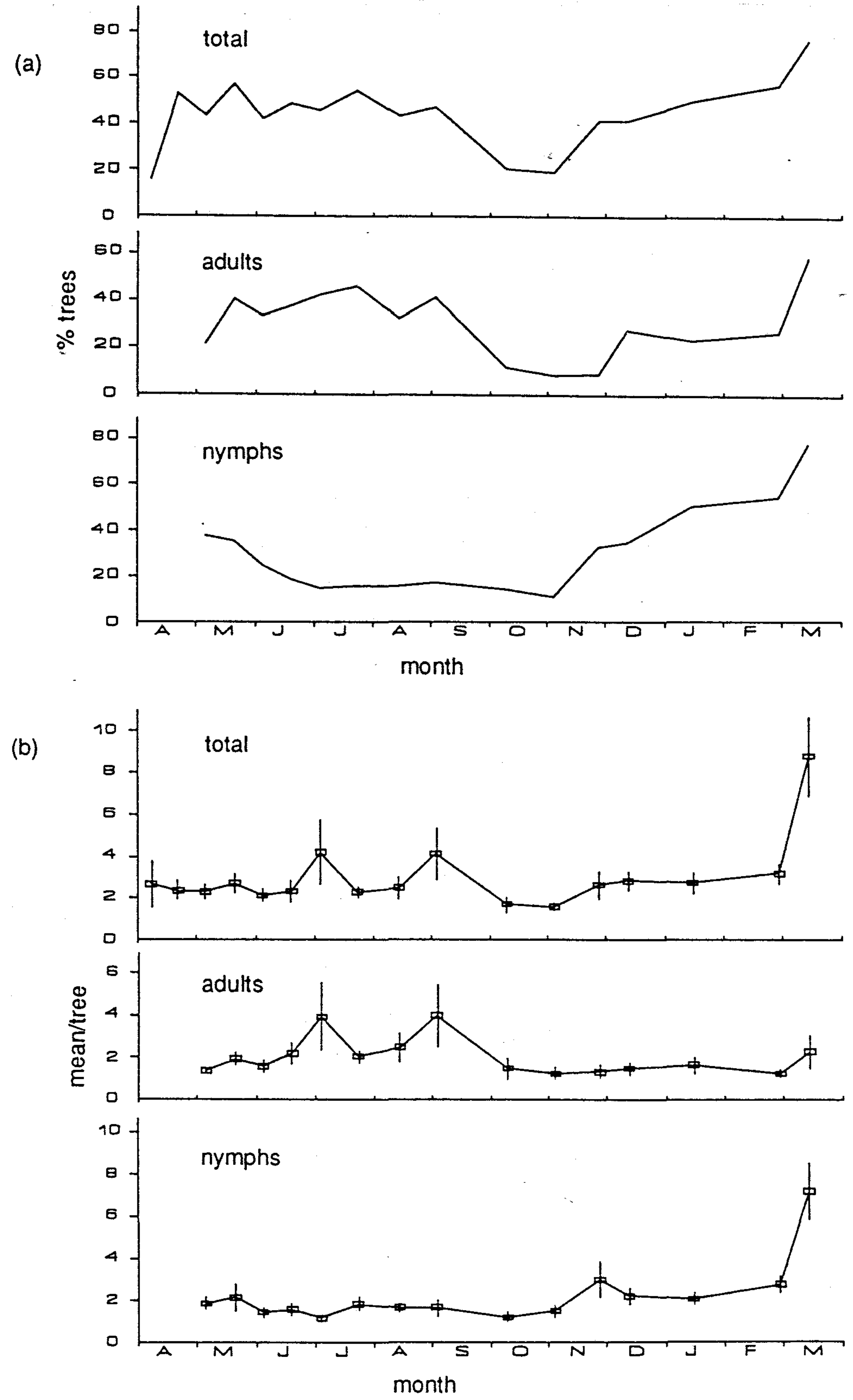


Figure 3.10. Typhlocybine (cicadellid) species (CZ24) numbers on leafy branches. a) Percentage of 29-38 monitored trees on which the typhlocybine was present on each sampling date. b) Mean number of typhlocybines per tree ± 1SE, for trees on which they were present. Nymphs and adults presented separately, and combined.

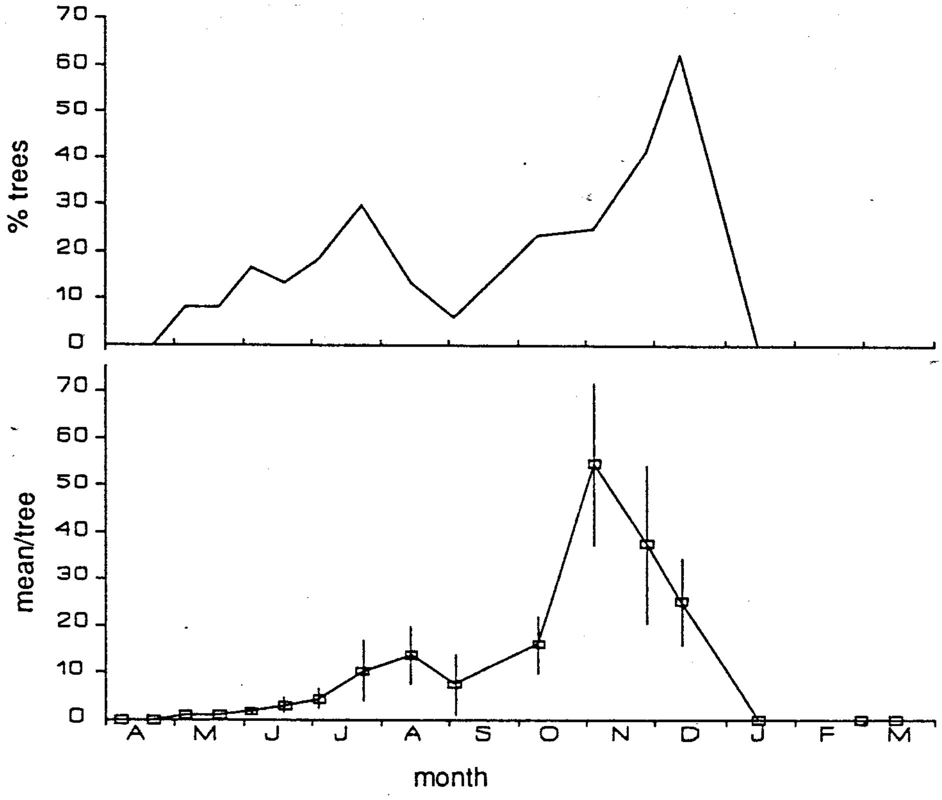


Figure 3.11. Aphid numbers on leafy branches. Percentage of 29-38 monitored trees on which aphids were present, and mean number of aphids per tree ± 1SE, for trees on which they were present, on each sample date.

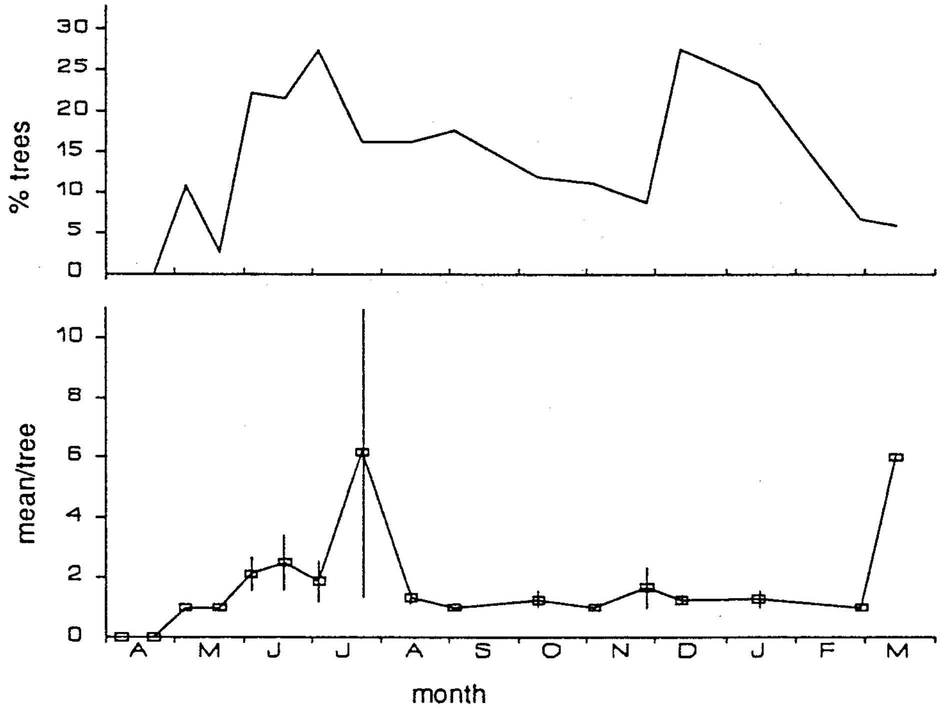


Figure 3.12. Psocopteran numbers on leafy branches. Percentage of 29-38 monitored trees on which psocopterans were present, and mean number of psocopterans per tree ± 1SE, on each sample date.

numbers per tree in spring (Fig. 3.11) may have been due to breeding or the hatching of eggs. This was followed by a dramatic increase in the number of trees on which aphids were present, which may have reflected colonising dispersal flights. The aphids then disappeared completely. Aphids on fruiting branches displayed the same population patterns and reappeared in autumn 1990 (unpubl. data).

The number and identities of psocopteran species contributing to the observed seasonal population changes (Fig. 3.12) is not known. A sharp winter increase in the number of trees on which psocopterans were present (Fig. 3.12), followed by a brief peak in the numbers per tree, may reflect dispersal and breeding. The decrease in distribution at the end of winter and in spring may have been due to leaf loss, as most psocopterans were found under leaves. Psocoptera may have preferred older leaves, as these carry higher epiphyte loads (Basset 1991b). A second increase in the percentage of trees with psocopterans in summer, followed by an increase in the numbers per tree may have been caused by dispersal and breeding of the same or additional species.

3.3.5 Conclusions

A large number of arthropod species, and particularly insects, feed on the stems, leaves and figs of *Ficus sur*, on its epiphytic flora, and on each other. Phytophages range in their degree of host specificity from monophagous in the case of the gall-forming fig wasps *C. capensis*, *S. cyclostigma* and *Apocryptophagus* spp., to broadly polyphagous in the case of *H. patruelis* and the aphids *T. aurantii* and *A. gossypii*. Several species are oligophages, feeding on a number of *Ficus* species, or on Moraceae in general. In terms of numbers of individuals, homopterans are by far the most abundant taxa, although their individual sizes are often far lower than that of the much rarer lepidopteran species. Leaf-feeding species tended to be more seasonal than frugivores due to differences in the seasonality of leafing versus fruiting phenological events.

Monitoring an insect fauna during a single year gives a better indication of total guild and species composition and abundance than data gathered on a single occasion (Basset 1991b), but does not reflect variation in the composition of the fauna over several years, as relative abundances of insect species vary from year to year (Wolda 1992). In addition, the insect fauna may vary between localities (Lawton 1978; Strong *et al.* 1984). The species composition and relative abundances recorded in this study are therefore not necessarily completely representative of a wider temporal and spatial scale, but nevertheless give an indication of the dynamics and interactions occurring on the tree.

4 THE ANT COMMUNITY ON *FICUS SUR*

4.1 INTRODUCTION

Ants (Hymenoptera: Formicidae) form an important component of most terrestrial ecosystems, in terms of their species, biomass, numbers and activities (Hölldobler & Wilson 1990). They are important particularly as predators, scavengers and collectors of liquid nutrients - plant sap and nectar and insect honeydew (Carroll & Janzen 1973). Ants therefore enter into a wide variety of interactions with both plants and other arthropods. They can form mutualistic associations with plants in several ways, e.g. in return for harvesting sap and nectar from extrafloral nectaries and other plant parts they provide protection against herbivores (Beattie 1985; Hölldobler & Wilson 1990). Some highly species-specific mutualisms have been recorded in which plants provide specialised nesting structures for ants, receiving nutrients or protection from herbivores in return (Beattie 1985; Hölldobler & Wilson 1990). Ants rarely pollinate plants, but use various parts for nesting and sometimes food; they may also remove and consume large numbers of seeds, acting as both seed-predators and dispersers (Hölldobler & Wilson 1990).

Ants are important predators of a wide variety of insects, including other ants, and engage in mutualistic associations with some homopterans and lepidopterans, acquiring honeydew and other substances in exchange for providing protection from their enemies (Beattie 1985; Buckley 1987a, b). Through these interactions they have often been shown to influence the composition or abundance of insects in the ecosystems in which they are present (Stork 1987).

Ants are a diverse group, with species that vary greatly in their habitat preferences, food requirements, colony sizes and nesting requirements, aggressiveness, territoriality and foraging strategies (Traniello 1989). Some ants are ground nesters while others nest in dead wood or specialised structures arboreally. Some species are highly specialised in their feeding habits (Hölldobler & Wilson 1990) but most engage in a variety of activities, in particular scavenging and honeydew and seed collecting (Carroll & Janzen 1973). However, they often display preferences towards one or the other food type, and this preference may vary seasonally (Carroll & Janzen 1973; Sudd & Sudd 1985; Rico-Gray & Sternberg 1991).

In most habitats a number of ant species usually co-occur, their spatial and temporal distibution patterns dictated not only by the ecological tolerances and preferences of the individual species but also by interactions with other ants of the same and other species. Although the role of competition in the structuring of many animal communities is still very controversial (Savolainen & Vepsäläinen 1988; Fellers 1989), its role in structuring ant communities is widely recognised (Savolainen & Vepsäläinen 1988; Hölldobler & Wilson 1990; Andersen 1992). Spatial and temporal patterns in ant communities have been investigated in a large number of studies. Spatial patterns were extensively studied in tropical fruit tree plantations, mainly in the 1970s (e.g. Greenslade 1971a; Room 1971, 1975; Majer 1972, 1976a, b; Taylor 1977). Ant temporal variation and community structure has been investigated in terrestrial arid-zone communities (Whitford 1978; Briese & Macauley 1980; Andersen 1983) and in temperate ecosystems (Brian *et al.* 1976; Andersen 1986; Fellers 1989). Ant community structures in tropical and subtropical rainforests have recently also received considerable attention (Torres 1984; Wilson 1987; Majer 1990). Many ant communities comprise a minority of numerically and behaviourally dominant species, which are often negatively associated, and a majority of subordinate and often less common species coexisting with dominants through behavioural and other strategies (Greenslade 1971a; Room 1971; Majer 1972, 1976 a, b; Leston 1978; Jackson 1984; Andersen 1986, 1992; Savolainen & Vepsäläinen 1988; Samways 1990). Ants in tropical fruit-tree plantations often form "ant mosaics", with each dominant species monopolising individual trees and resulting in a patchwork across the plantation. The mosaic is formed and maintained by both competition and environmental heterogeneity in combination with nesting and feeding preferences of the individual species (Majer 1972, 1976a). Many ant communities are also characterised by high temporal and spatial heterogeneity (e.g. Greenslade 1971a; Whitford 1978; Samways 1990; Andersen 1992). Ant communities are often much richer and form a larger component of the total arthropod faunas in tropical and arid ecosystems than in temperate ecosystems (Taylor 1977; Andersen 1983, 1986; Stork 1987; Basset *et al.* 1992).

The frequency with which a particular tree species is visited or inhabited by ants can be expected to depend on the food and nesting resources offered by that tree. Ants have been observed tending homopterans or acting as predators on a number of species of fig tree (Bronstein 1988; Compton & Robertson 1988, 1991; Thomas 1988; pers. obs.). They also disperse fig seeds (Kaufmann *et al.* 1991). In Africa, it is on the section *Sycomorus* however, a group with large figs often borne on specialised fruiting branches growing on old wood, that ants occur at their highest densities (Cushman *et al.* in prep). This may be a result of higher phloem flow which attracts homopterans with a high honeydew production, such as tettigometrids, which in turn attract the ants. Because of their active local photosynthesis, figs in some other *Ficus* groups may be much less dependent on an inflow of nutrients (A. Herre pers. comm.).

Aspects of the ant fauna of the Cape Fig, *Ficus sur*, have been investigated by Thomas (1988) (as *F. capensis* Thunb.), Compton & Robertson (1988, 1991) and Kansky (1988). Compton & Robertson (1988, 1991) found that ants on the tree mainly tended homopterans, in particular the tettigometrid *Hilda patruelis* on developing figs. High ant densities on *F. sur* figs (Compton & Robertson 1988) affect the fitness of the tree: ants prey on wasps which parasitise the pollinators developing inside the fig. An indirect mutualism between ants and the tree is thus established.

This chapter describes an investigation of the ant community on *F. sur* in the Grahamstown district - the species present, their abundances and feeding habits, as well as seasonal variation and spatial patterns at an inter- and within-tree level. In turn these patterns are related to the tending of *H. patruelis* by the ants and their consequent "protection" of figs from parasitoids and herbivores by ants (Chapter 8).

4.2 MATERIALS AND METHODS

Trees were sampled for ants at the same times as for other insects and for tree phenology studies (Chapter 3). The numbers and species of ants were recorded on fruiting branches during the day at each of the three study sites on 27 sample dates over 18 months (April 1989 to October 1990). A total of 634 "sample points" (the number of trees sampled on each date x the number of sample dates) was obtained. Ant numbers were also recorded on leafy branches between April 1989 and March 1990, on 17 sample dates for sites 1 and 2 and 16 for site 3. A total of 574 such sample points were obtained. In addition, the trunks and main branches were examined for the presence of ants and their numbers were recorded for both trees with and without fruiting branches in the first period (April 1989 to March 1990) and with fruiting branches only in the second period (April to October 1990) (n = 795 trees). Where ants formed a trail along a trunk, the number of ants passing a point on the trunk over a two minute interval was recorded. The behavioural activities of individual ants were recorded on fruiting and leafy branches. Where necessary, ants were collected to establish their identities. Several species were difficult to distinguish in the field and were recorded together - two *Crematogaster* species, *C.* nr *delagoensis* Forel and *C. liengmei* Forel, as well as the small yellow ants *Monomorium* sp.-*boerorum* complex, *Plagiolepis* sp.1 and

Technomyrmex sp.1, which were classed as "small ant spp.".

In order to assess variation in ant, *H. patruelis* and fig numbers from the base of the trunk to the crown of individual trees, three medium to large (6-9m high) trees bearing figs were selected. The number of figs as well as the proportion of figs on which ants were present was counted in 1m sections from ground level to the top of the tree. For practical reasons the top two to three metres of each tree were combined as a single unit. At each level three fruiting branches with figs and ants were also selected and the numbers and stages of figs, the species and numbers of ants and the numbers of *H. patruelis* recorded.

4.3 RESULTS

4.3.1 Ant incidences, distributions and activities

Nineteen ant species were recorded on *F. sur* during the 18 month sampling period (Chapter 3, Table 3.2; Table 4.1), almost all of which were recorded on fruiting branches, with fewer species present on leafy branches (Fig. 4.1a, b; Table 4.2, 4.3). Ants were present on 76.5% of the 795 tree sample points and on the fruiting branches of 56.8% of the 634 fruiting branch-bearing tree sample points, with a mean of 23.9 ants per fruiting branch sample. Ants were present on 13.9% of 574 leafy branch sample points at a density of 2.31 ants per sample. Ants usually occurred on those fruiting branches where figs were present. Ant abundance varied with species, tree, site and time. The most widely occurring species on trees as a whole (fruiting branches, leafy branches and trunks) (Table 4.1) and on fruiting branches (Fig. 4.1a; Table 4.2) were *Pheidole megacephala*, the two *Crematogaster* species and *Acantholepis capensis* Mayr. For tree sample points on which they were present, however, *Anoplolepis custodiens* (F. Smith) and *Polyrhachis schistacea* (Gerstaecker) were present in

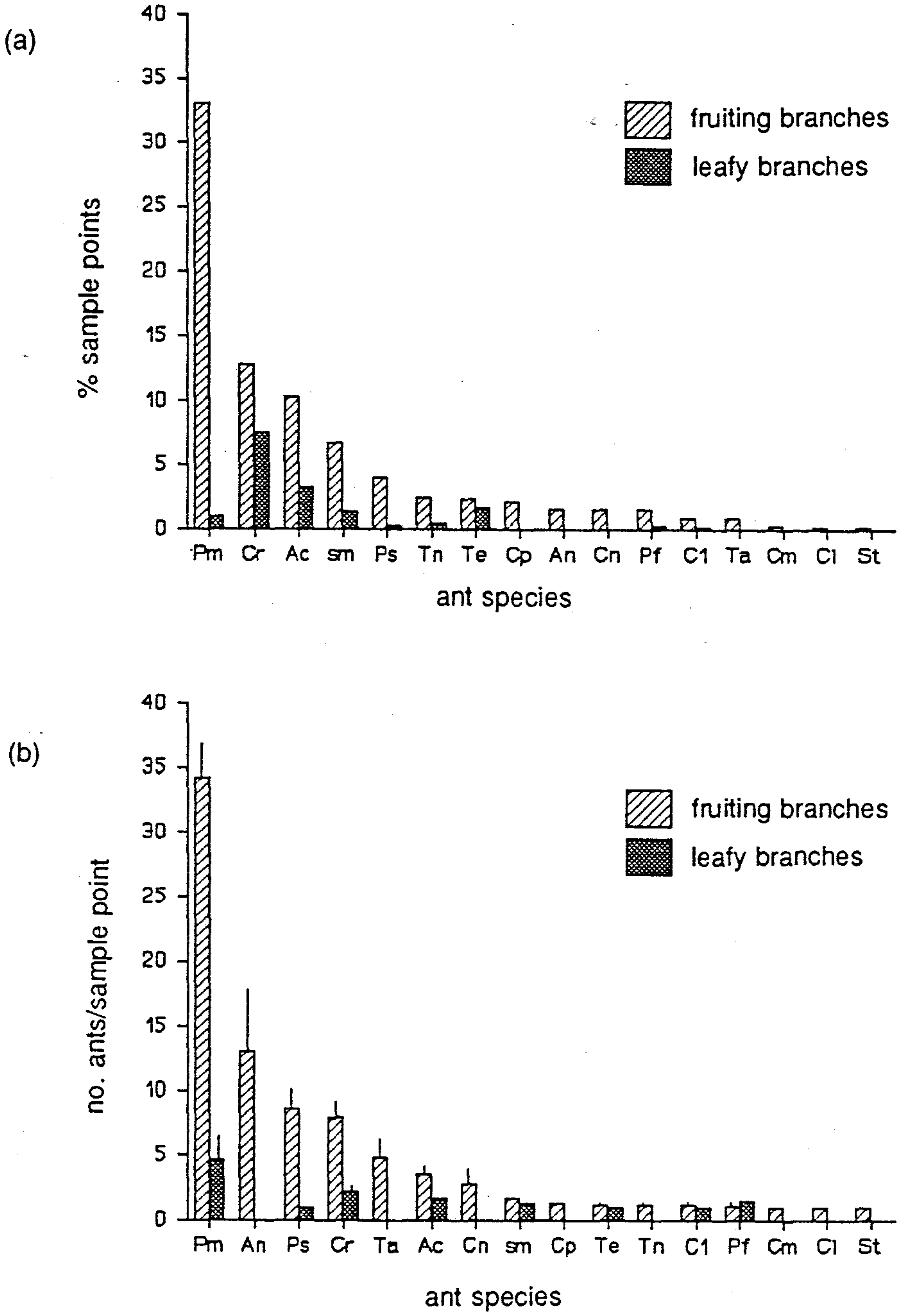


Figure 4.1. a) Percentage of sample points on which each ant species was present on fruiting branches and leafy branches. b) Mean number of ants of each species + 1SE per sample point on fruiting branches and leafy branches. Ac = *Acantholepis capensis*, An = *Anoplolepis custodiens*, Ci = *Cataulacus intrudens*, Cr = *Crematogaster* spp., Cm = *Camponotus maculatus*, Cn = *C. natalensis*, Cp = *C.* nr *postoculatus*, C1 = *Camponotus* sp.1, Pf = *Plagiolepis fuscula*, Pm = *Pheidole megacephala*, Ps = *Polyrhachis schistacea*, sm = small spp., St = *Smithistruma transversa*, Ta = *Technomyrmex albipes*, Te = *Tetraponera emeryi*, Tn = *T. natalensis*.

Table 4.1. The number of sample points on which each ant species/group was present on the whole *F. sur* tree (fruiting branches, leafy branches or main trunks and branches) over the sample period, at the three sites and in total.

ant species	no. sample points (no. sample points at each site)							
	site 1 (n = 257)	%	site 2 (n = 161)	%	site 3 (n = 377)	%	total (n = 795)	%
Pheidole megacephala	150	58.4	66	41.0	97	25.7	314	39.4
Crematogaster spp.	21	8.17	114	70.8	166	44.0	303	37.9
Acantholepis capensis	73	28.4	26	16.2	124	32.9	223	28.0
small ant spp.	2	0.78	17	10.6	70	18.6	89	11.2
Tetraponera emeryi	3	1.17	27	16.8	21	5.57	51	6.42
Camponotus nr *postoculatus*	28	10.9	9	5.59	9	2.39	46	5.78
Tetraponera natalensis	11	4.28	7	4.35	24	6.63	42	5.28
Camponotus sp.1	3	1.17	15	9.31	16	4.24	34	4.27
Polyrhachis schistacea	0	0	0	0	30	7.96	30	3.78
Plagiolepis fuscula	9	3.50	1	0.62	10	2.65	20	2.52
Anoplolepis custodiens	6	2.33	0	0	9	2.12	15	1.76
Cataulacus intrudens	0	0	8	4.97	5	1.33	13	1.63
Camponotus natalensis	0	0	0	0	11	2.92	11	1.38
Technomyrmex albipes	0	0	0	0	11	2.92	11	1.38
Camponotus maculatus	1	0.39	2	1.24	3	0.80	5	0.76
Smithistruma transversa	0	0	0	0	1	0.27	1	0.13

Table 4.2. Ants on fruiting branches. The number of sample points on which they were present at the three sites, and mean numbers per sample point on which the species was present (SEs shown on Fig. 4.1b). Ant species arranged in order of decreasing total number of sample points.

ant species	no. sample points (total no. sample points)				mean no. ants/sample point			
	site 1 (204)	site 2 (161)	site 3 (269)	total (634)	site 1	site 2	site 3	total
P. megacephala	103	37	70	210	41.6	37.7	20.7	33.9
Crematogaster spp.	2	30	48	81	3.50	13.8	4.42	7.90
A. capensis	18	1	46	65	5.39	1.0	2.89	3.55
small ant spp.	1	3	39	43	1.0	1.33	1.67	1.63
P. schistacea	0	0	26	26			8.58	8.58
T. natalensis	4	1	11	16	1.0	1.0	1.27	1.19
T. emeryi	3	5	7	15	1.33	1.0	1.29	1.20
C. nr *postoculatus*	7	1	6	14	1.14	1.0	1.50	1.29
A. custodiens	4	0	6	10	21.8		7.17	13.0
C. natalensis	0	0	10	10			2.80	2.80
P. fuscula	5	0	5	10	1.20		1.0	1.10
Camponotus sp.1	0	2	4	6		1.0	1.25	1.17
T. albipes	0	0	6	6			4.83	4.83
C. maculatus	1	0	1	2	1.0		1.0	1.0
C. intrudens	0	1	0	1		1.0		1.0
S. transversa	0	0	1	1			1.0	1.0

Table 4.3. Ants on leafy branches. The number of sample points on which they were present at the three sites, and mean numbers per sample point on which the species was present (SEs shown on Fig. 4.1b). Ant species arranged in order of decreasing total number of sample points.

ant species	no. sample points (total no. sample points)				mean no. ants/sample point			
	site 1 (183)	site 2 (101)	site 3 (290)	total (574)	site 1	site 2	site 3	total
Crematogaster spp.	5	10	28	43	1.60	1.70	2.50	2.21
A. capensis	5	2	12	19	1.20	3.0	1.58	1.63
T. emeryi	0	4	6	10		1.0	1.0	1.0
small ant spp.	0	0	8	8			1.25	1.25
P. megacephala	2	1	3	6	2.0	1.0	7.67	4.67
T. natalensis	0	1	2	3		1.0	1.50	1.33
P. fuscula	1	0	1	2	2.0		1.0	1.50
P. schistacea	0	0	2	2			1.0	1.0
Camponotus sp.1	0	1	3	4		1.0	1.0	1.0

Table 4.4. Comparison of a) numbers of fruiting branch sample points versus numbers of leafy branch sample points on which each ant species was recorded, for ant species found on both, b) numbers of whole-tree sample points on which each ant species was recorded at each site, c) numbers of whole-tree sample points versus fruiting branch sampling points on which each ant species was recorded. The ratio of the percentage sample points is presented, together with chi-square contingency statistics on numbers of sample points.

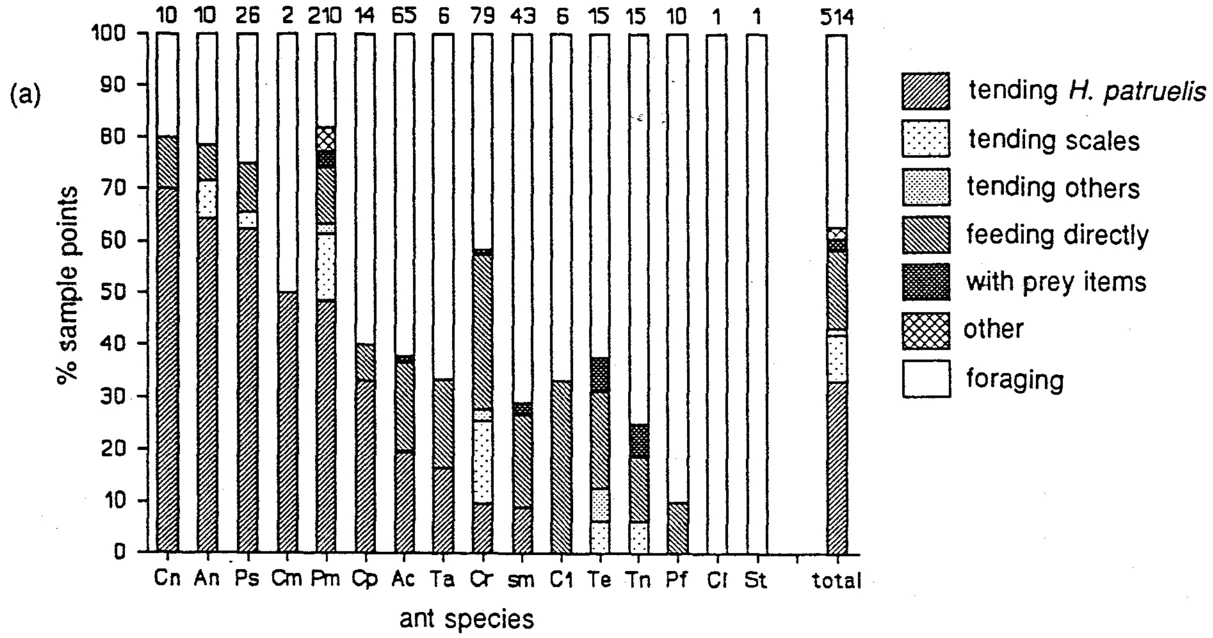
ant species	a) fruiting (fb) vs leafy branches (lb)			b) sites		c) whole tree (wt) vs fruiting branches (fb)		
	ratio %fb:%lb	X^2	p	X^2	p	ratio %wt:%fb	X^2	p
A. capensis	3.11	22.4	***	15.7	***	2.72	69.4	***
A. custodiens	-	9.13	**	3.88	NS	1.12	0.195	NS
C. maculatus	-	1.81	NS	0.978	NS	2.45	1.22	NS
C. natalensis	-	9.13	**	12.4	**	0.88	0.091	NS
C. nr *postoculatus*	-	12.8	***	20.3	***	2.62	11.2	***
Camponotus sp.1	5.59	0.228	NS	16.1	***	4.49	14.4	***
C. intrudens	-	0.906	NS	15.6	***	10.2	7.94	**
Crematogaster spp.	1.68	9.13	**	176.7	***	3.01	115.2	***
P. megacephala	31.5	211.1	***	68.4	***	1.19	6.17	*
P. fuscula	4.49	4.63	*	3.40	NS	1.61	1.51	NS
P. schistacea	11.7	18.7	***	34.6	***	0.92	0.10	NS
small ant spp.	4.88	21.6	***	48.7	***	1.65	8.19	**
S. transversa	-	0.906	NS	1.11	NS	0.81	-	-
T. albipes	-	5.46	*	12.4	**	0.45	0.574	NS
T. emeryi	1.36	0.578	NS	41.0	***	2.72	13.1	***
T. natalensis	4.85	7.79	**	1.68	NS	2.10	6.90	**

p: NS ≥ 0.05, * < 0.05, ** < 0.01, *** < 0.001

higher numbers on the fruiting branches than the *Crematogaster* spp. and *A. capensis* (Fig. 4.1b; Table 4.2), i.e. the former species were less widely distributed, but occurred at higher local densities. Most ant species were recorded on significantly fewer leafy branch sample points than fruiting branch sample points (Fig. 4.1a, b; Table 4.4). *P. megacephala*, *P. schistacea* and *A. custodiens* were relatively far more abundant on fruiting branches than leafy branches in contrast to species such as *Crematogaster* spp., *Plagiolepis fuscula* Emery and *Camponotus* sp. A. The *Crematogaster* spp. were the most common species on leafy branches, followed by *A. capensis*. In terms of the total number of 8789 individuals recorded on fruiting and leafy branches during the monitoring period, *P. megacephala* comprised 81.9%, *Crematogaster* spp. 8.37% and *A. capensis* 2.98% - these four species together accounted for more than 93% of the ant individuals on *F. sur*.

Ant activities on fruiting branches and leafy branches could be divided into several broad categories. Ants commonly tended the tettigometrid *H. patruelis* and removed sap from punctures in figs caused by its feeding. They also tended other homopterans such as scale insects, mealy bugs and aphids, and the lycaenids *Lachnocnema bibilus* and *Myrina silenus ficedula*. Ants were frequently recorded feeding from sap exudates - these were sometimes from fig ostioles but more often from areas of insect damage such as lygaeid feeding punctures or weevil bites - and in split or fig wasp-exited figs. On a few occasions ants were recorded with prey items - mainly fig wasps but also *H. patruelis* eggs (small ant species) and aphids (*P. megacephala*) on one occasion each. Ants observed walking on fruiting branches and leafy branches were classified as foragers. Finally, *P. megacephala* built auxilliary/satellite nests around fruiting branches on some occasions.

Ants on fruiting branches most frequently tended *H. patruelis* and foraged (Fig. 4.2a). Scale-tending, the main activity on bare fruiting branches, and exudate feeding were also fairly common. On leafy branches most ants were tending scales and foraging (Fig. 4.2b). Different



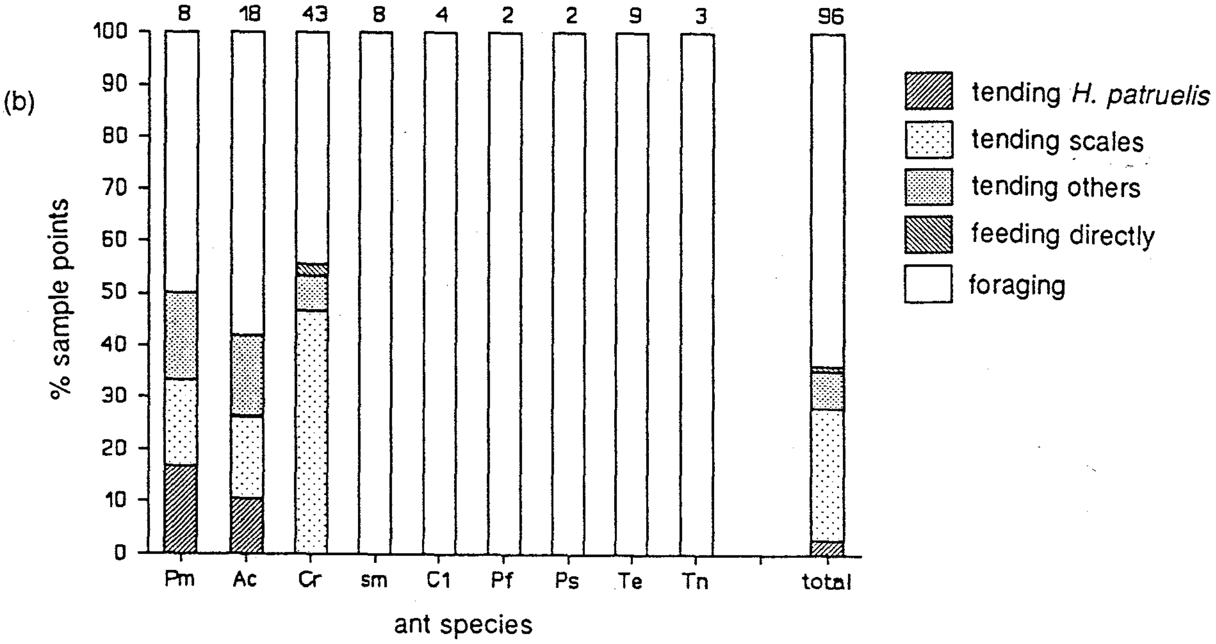


Figure 4.2. Ant activities on a) fruiting branches and b) leafy branches. The total number of sample points on which the species was recorded is indicated above each bar. The total percentage of "activity" sample points was greater than 100 for some species because ants were engaged in more than one activity on a sample point. In these cases the total was adjusted to 100.

ant species varied in their most common activity on the fruiting branches. *P. megacephala*, *A. custodiens* and *P. schistacea* were usually found tending *H. patruelis*. On leafy branches, apart from foraging, *Crematogaster* spp. mainly tended scales, while on fruiting branches they also commonly fed from exudates. *A. capensis* was usually present in low numbers and displayed diverse activities. *Tetraponera emeryi* (Forel) and *T. natalensis* (F. Smith) were the most exclusively predatory species in comparison to other species (Fig. 4.2a), although *P. megacephala* accounted for more predation in absolute terms. On eight of the total of 283 "activity" sample points (if a species was engaged in two activities on a sample point two "activity" sample points were counted) *P. megacephala* was carrying prey items, in comparison to two of 44 for the *Tetraponera* species - the difference in prey removal by the two genera was non-significant ($X^2 = 0.379$, $p = 0.538$). The three small ant species *Monomorium* sp.-*boerorum* complex, *Plagiolepis* sp.1 and *Technomyrmex* sp.1 were commonly foraging, but sometimes fed from exudates.

Most ant species were present on significantly more whole-tree sampling points than on sampling points from fruiting branches alone (Table 4.4). This can be partially explained by greater sampling effort on the whole tree; however the ratio varies considerably between species. *Crematogaster* spp. and *A. capensis*, as well as *Cataulacus intrudens* (F. Smith), *Camponotus* sp.1 and *T. emeryi* have the highest whole tree to fruiting branch ratio. They were thus found on trees far more commonly than can be explained by their attraction to the fruiting branches. In most cases they are arboreally nesting ants. This point is discussed more fully in the following section.

Considering individual trees rather than sample points, the distribution of each ant species can be considered to vary between individual trees in three ways: the total number of trees on which they ever appeared (i.e. distribution), the number of dates they were present on those trees on which they were found (i.e. frequency), and their mean numbers on the occasions when they were present (i.e. density) (Table 4.5). This analysis gives similar results to that using only sample points, i.e. some species were localised but in high numbers while others were widespread but in low numbers, and so on. The correlation between the frequency of appearance of a species on a tree and the ant density per tree for that species was highly significant (Spearman Rank: $r = 0.896$, $p = 0.0005$), and that between distribution and frequency was nearly significant ($r = 0.487$, $p = 0.0591$). However, no significant correlation was present between distribution and density ($r = 0.425$, $p = 0.10$). These results indicate that species which appeared frequently on a particular tree generally did so in high numbers, and that those which were widespread on trees appeared more frequently. However, species appearing on only a few trees could do so in high or low numbers.

4.3.2 Spatial incidences: between-site and -tree variability

Significant inter-site differences were present for 11 of the 16 species/species groups in terms of the number of whole-tree sample points on which they were recorded (Table 4.1, 4.4). Eleven species were present at each of sites 1 and 2 and 16 at site 3; ten species were common to all three sites. *P. megacephala* was present on only 25.7% of sample points at site 3, compared to 58.4% at site 1 and 41.0% at site 2. Of the species which differed significantly between sites, two occurred at their highest frequencies at site 1, three at site 2 and six at site 3 while eight were least common or absent at site 1, three at site 2 and two at site 3 (Table 4.1). Site 1 was therefore the most species-poor and site 3 the most species-rich. If we consider individual trees rather than sample points, there was a significant difference between sites 1 and 2 in the mean number of species per tree (number of species per tree: site 1: 3.27 ± 2.15, $n = 11$; site 2: 6.33 ± 1.86, $n = 6$; site 3: 5.0 ± 2.47, $n = 20$) (1-way ANOVA: $df = 2,34$; $F = 3.81$; $p = 0.032$) but this disappeared when only trees with

Table 4.5. Ant species on the fruiting branches of individual trees. The number of trees each species was recorded on over the monitoring period (distribution), the mean number of times they were recorded on each tree (frequency), and the mean number of individual ants per occurrence (density). The total number of sample dates for all trees was adjusted to 27.

ant species	distribution (total = 26)	frequency (SD) (total = 27)	ant density (SD)
A. capensis	14	4.88 (3.09)	3.40 (4.02)
A. custodiens	2	5.12 (1.58)	14.5 (10.3)
C. maculatus	2	1.00 (0)	1.00 (0)
C. natalensis	2	5.20 (5.88)	2.00 (1.41)
C. nr *postoculatus*	3	4.67 (3.21)	1.21 (0.26)
Camponotus sp.1	4	1.50 (1.0)	1.25 (0.50)
C. intrudens	1	1.00 (0)	1.00 (0)
Crematogaster spp.	15	5.53 (4.35)	6.21 (5.88)
P. megacephala	19	11.4 (6.96)	29.5 (21.1)
P. fuscula	5	2.00 (1.41)	1.07 (0.15)
P. schistacea	3	10.2 (3.05)	7.89 (2.44)
small ant spp.	14	3.32 (3.07)	1.45 (0.59)
S. transversa	1	1.68 (0)	1.00 (0)
T. albipes	2	3.00 (0)	4.83 (0.71)
T. emeryi	10	1.71 (0.95)	1.17 (0.42)
T. natalensis	5	2.60 (1.82)	1.14 (0.22)

fruiting branches were considered (number of species per tree: site 1: 4.38 ± 1.69, n = 8; site 2: 6.33 ± 1.86, n = 6; site 3: 6.08 ± 2.40, n = 13) (df = 2,24; F = 2.40; p = 0.112).

The ant faunas on individual trees varied in terms of the number of species visiting the trees, the species composition and numbers of ant individuals visiting the tree over the monitoring period. The total number of ant species visiting trees without fruiting branches was significantly lower than the number visiting trees with fruiting branches (trees with fruiting branches: 5.59 ± 2.19, n = 27; trees without fruiting branches: 2.30 ± 1.34, n = 10) (1-way ANOVA: df = 1,35; F = 19.69; p = 0.0001), indicating that fruiting constitutes a significant increase in resources for the ants.

Individual trees varied greatly in the number of their ant visitors over the monitoring period. The percentage of sample dates on which a tree had ants on its fruiting branches varied from zero to 92.6% with a mean of 53.1 ± 28.1% (n = 26), and on its leafy branches from zero to 83.3% with a mean of 14.5 ± 16.7% (n = 37). Mean numbers of ants per sample date, for those dates on which ants were present, varied between trees from one to 60.4, with an overall mean of 19.9 ± 16.9 (n = 25) on the fruiting branches and from one to 5.25 with a mean of 1.94 ± 1.12 (n = 27) on leafy branches. Trees with no fruiting branches therefore had few ants, and these were mainly arboreal nesters and ants tending scale insects on leafy branches. The only species ever found on these trees were Crematogaster spp., *A. capensis*, the small ant spp. and *T. emeryi*.

If we define a species as being numerically dominant on a tree when more than 50 individuals were present over the monitoring period, then *P. megacephala* was dominant on 44.4% of the trees (Fig. 4.3) and co-dominated with *Crematogaster* spp. on 7.4%. *Crematogaster*, *P. schistacea* and *A. custodiens* also dominated a few trees but a majority of the remainder (29.6%) lacked a dominant species.

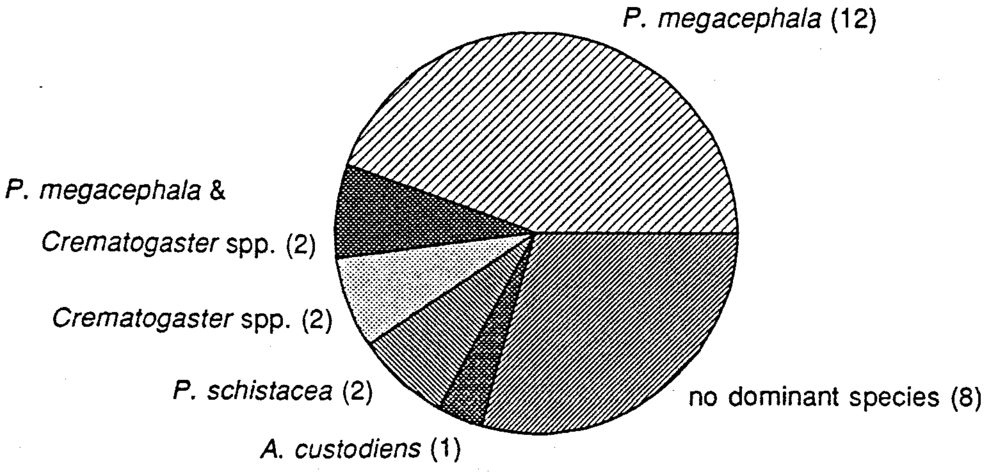


Figure 4.3. Proportion of trees on which different species or no species were numerically dominant over the monitoring period. Numbers of trees are indicated in parentheses.

4.3.3 Spatial incidences: within-tree variability

Variation in tree dimensions is reflected in the spatial patterns of fig production (Fig. 4.4; Table 4.6) - tree 1 was short and broad whereas tree 2 was tall and narrow and tree 3 intermediate. The greatest amount of fruit was borne between two and three metres on tree 1 and between three and four metres on the other two trees. *P. megacephala* accounted for the majority of ants on the trees - it was responsible for 95.6% of the figs with ants on tree 1, 93.0% on tree 2 and 100% on tree 3. On all three trees the proportion of figs on which ants were present decreased rapidly with height from ground level (Fig. 4.4; Table 4.6), so that figs higher up in the tree had few or no ants present (Spearman Rank: tree 1: $r = -0.943$, $p = 0.0350$; tree 2: $r = -0.964$, $p = 0.0182$; tree 3: $r = -1.0$, $p = 0$).

The overall percentage of figs with ants present on the tree varied from 3.46% of a total of 3290 figs on tree 2 and 3.53% of 5099 on tree 1 to 40.5% of 1086 on tree 3. The ants on tree 3 also extended into the crown in highest numbers. *P. megacephala* numbers were significantly negatively correlated with height only on tree 2 (Spearman Rank: $r = -0.883$, $p = 0.0306$). However, if the lowest height interval (0-1m) is removed from the analysis (because there were very few figs and subsequently ants here), both trees 1 and 2 display a significant negative correlation between *P. megacephala* numbers and tree height (tree 1: $r = -1.0$, $p = 0$; tree 2: $r = -0.986$, $p = 0.0275$). Other species were either too few to show a significant trend (*Crematogaster* spp., *P. fuscula*, *T. natalensis*) or appeared higher up the tree (*A. capensis* on tree 2; Spearman Rank: $r = 0.867$, $p = 0.0337$) (Table 4.6). On tree 2, *P. megacephala* and *A. capensis* were also significantly negatively correlated ($r = -0.895$, $p = 0.0284$).

Mean numbers of ants per fig and *H. patruelis* per fig varied inconsistently with height and

Table 4.6. Total numbers of figs and numbers with ants on three trees from ground level to crown. Ant species: Pm = *P. megacephala*, Ac = *A. capensis*, Cl = *C. liengmei*, Pf = *P. fuscula*, Tn = *T. natalensis*.

tree	fig phase	height interval (m)	total no. figs	no. figs with ants				
				Pm	Ac	Cl	Pf	Tn
1	small pre- to interfloral	0-1	6	3				
		1-2	1370	133		3		
		2-3	1960	20		1	1	
		3-4	1188	14	2			1
		4-5	482	5				
		5-7	93					
2	pre- to interfloral	0-1	63	15				
		1-2	395	56				
		2-3	520	22				
		3-4	665	7	1			
		4-5	530	6	4			
		5-6	450		3			
		6-9	670					
3	interfloral	0-1	0					
		1-2	53	50				
		2-3	303	190				
		3-4	535	190				
		4-6	195	10				

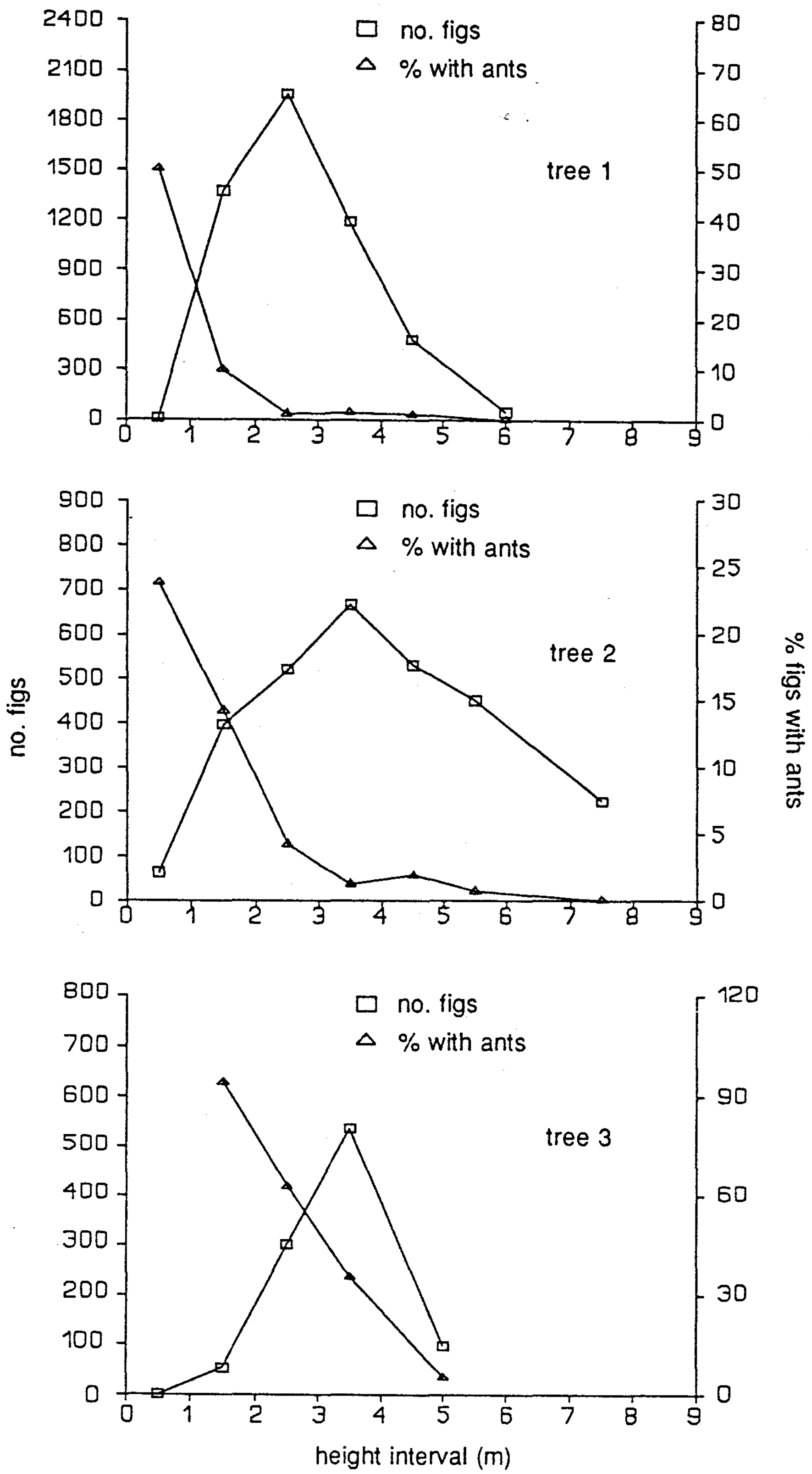


Figure 4.4. Within-tree variation in the numbers of figs with height, and the percentage of of figs on which ants were present with height, for three *F. sur* trees.

Table 4.7. Numbers of ants per fig and *H. patruelis* per fig on sampled fruiting branches at intervals from the base to the crown of three *F. sur* trees, and a comparison of changes in these values with height.

tree	fig phase	height interval	sample no.	ant no. /fig (SD)	Kruskal-Wallis		*H. patruelis* no./fig (SD)	Kruskal-Wallis	
					H	p		H	p
1	small pre- to interfloral	0-1	1	2.00 (0)	2.81	0.590	0.25 (0)	2.80	0.592
		1-2	3	1.85 (2.15)			0.89 (1.11)		
		2-3	3	1.19 (1.58)			1.25 (1.53)		
		3-4	3	1.23 (0.25)			0.47 (0.50)		
		4-5	3	0.67 (0.73)			0.17 (0.29)		
		5-7	0	-			-		
2	pre- to interfloral	0-1	3	0.58 (0.37)	1.49	0.829	0.15 (0.15)	0.19	0.996
		1-2	3	0.45 (0.76)			0.44 (0.77)		
		2-3	3	0.29 (0.28)			0.14 (0.17)		
		3-4	3	0.86 (1.28)			0.67 (1.15)		
		4-5	3	0.58 (0.79)			0.33 (0.58)		
		5-6	0	-			-		
		6-9	0	-			-		
3	interfloral	0-1	0	-	9.80	0.020	-	10.2	0.017
		1-2	3	12.9 (2.81)			2.69 (1.19)		
		2-3	3	4.07 (0.21)			0.93 (0.28)		
		3-4	3	0.83 (1.14)			0.20 (0.27)		
		4-6	3	0.11 (0.19)			0 (0)		

between trees on trees 1 and 2, probably due to low numbers of insects and multiple fig stages (Table 4.7). On tree 3, where there were high numbers of insects and only interfloral-phase figs, all three ratios decreased strongly with height (Table 4.7).

4.3.4 Temporal changes in ant numbers

Several species were present year-round (Fig. 4.5) whereas other species were recorded patchily with no clear seasonal trends (*C. intrudens*, *P. fuscula*, *T. emeryi*). A large number of species were absent during some part of the winter months (April to September) (*A. custodiens*, all *Camponotus* species, and *T. natalensis*), but *Technomyrmex albipes* (F. Smith) was the only species to be present mainly in winter. However, some of the observed patterns may be an effect of low sampling effort rather than true seasonality. The total number of ant species on the trees (Fig. 4.6) increased in spring. This was followed by a slight decrease in midsummer and another peak at the end of summer, after which there was a dramatic decrease in the number of active species.

On the fruiting branches the mean number of ants per tree was variable from date to date (Fig. 4.7a). It experienced a peak in spring followed by a sharp decrease in late spring. Another peak occurred in late summer after which it decreased into winter. The only trend in the number of trees on which ants were found was an increase in late summer.

The number of trees on which *A. capensis* was present on the fruiting branches (Fig. 4.7b) was highest in late spring and the second winter; the mean density per tree was low and inconsistent. On the whole trees no or very weak seasonal trends were evident (Fig. 4.8a). *A. custodiens* was highly seasonal, appearing only in mid-summer and on fruiting branches only, but where present it was in high numbers (Fig. 4.7c). The mean number of *Crematogaster* spp. per tree on the fruiting branches, which was fairly high, peaked in spring and again in

Figure 4.5. Seasonal distribution of individual species during the monitoring period, showing the presence or absence of each species on each sample date. Sample dates where a species was consecutively present are joined.

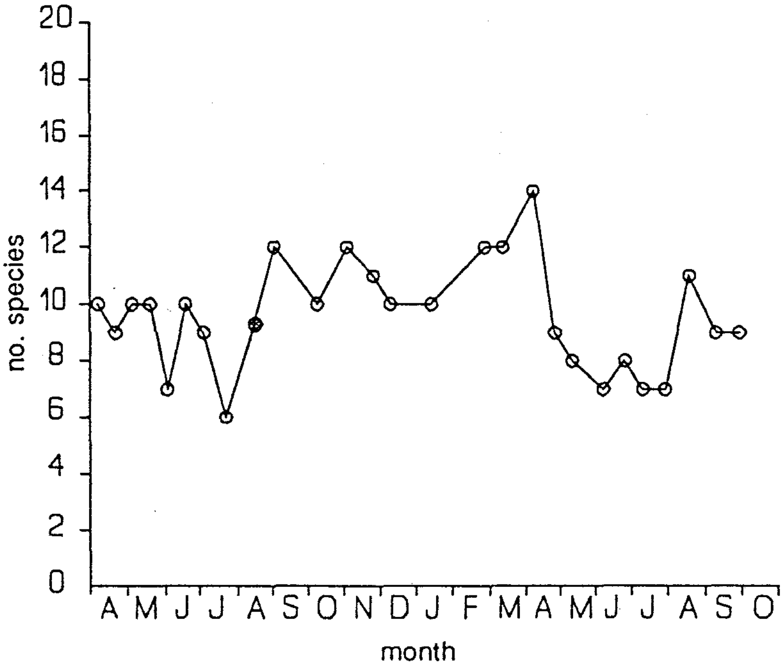


Figure 4.6. Total number of ant species active on each sample date over the monitoring period on the whole tree (fruiting branches, leafy branches and trunks).

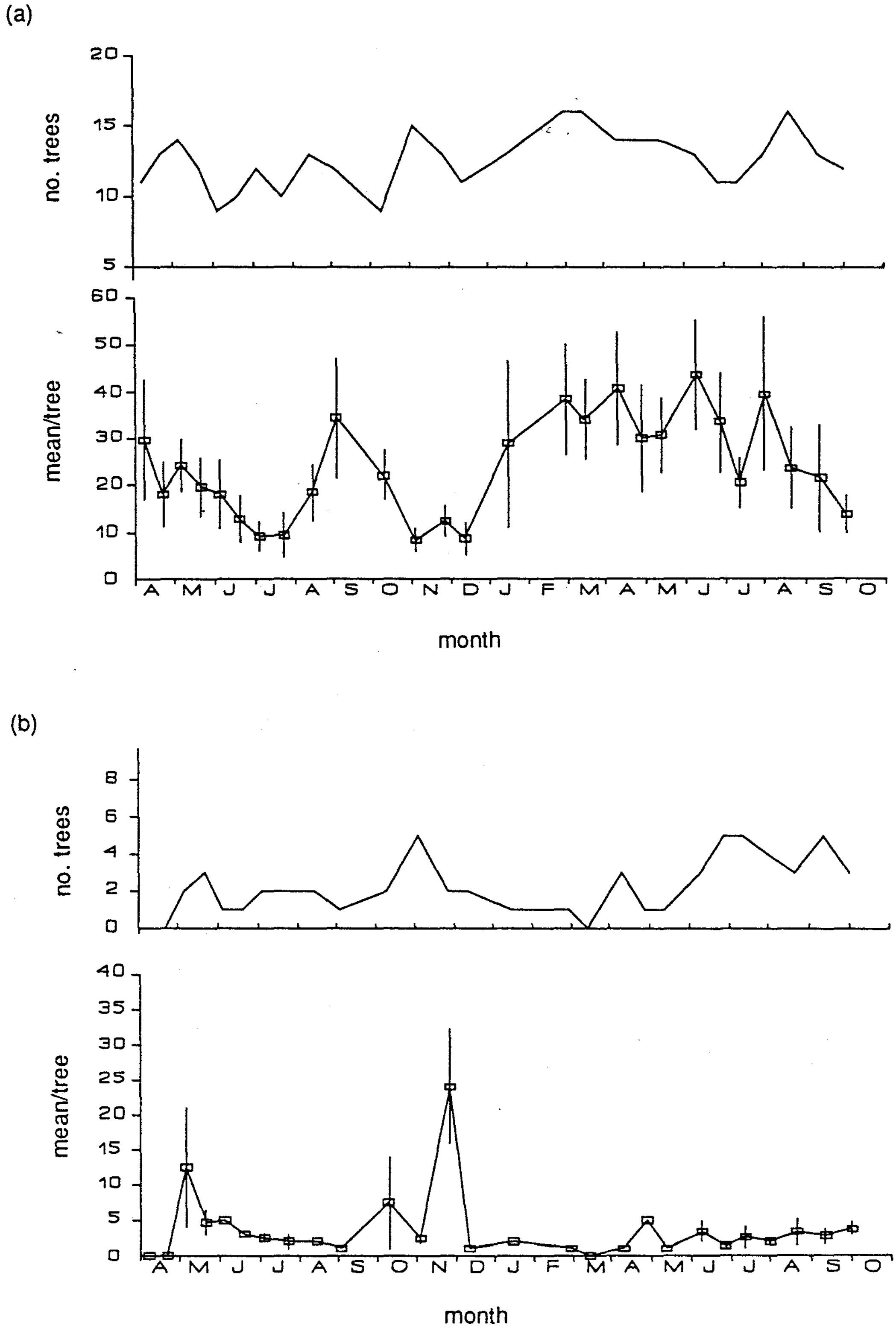


Figure 4.7. Number of trees on which ants were present on each sample date on the fruiting branches, and mean numbers of ants ± 1 SE present on the fruiting branches over the monitoring period. a) all ants. b) *A. capensis*.

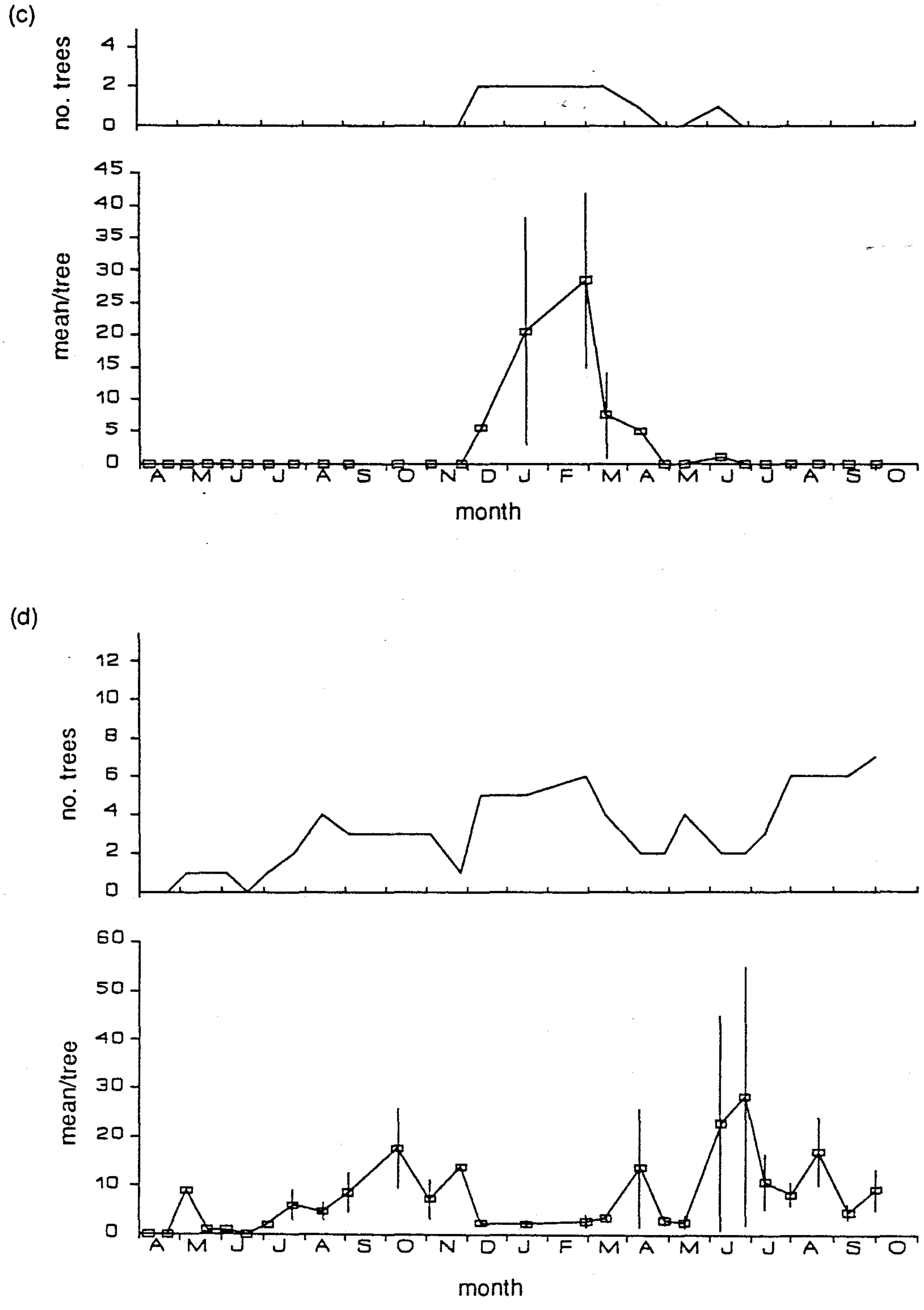


Figure 4.7. *continued.* c) *A. custodiens.* d) *Crematogaster* spp..

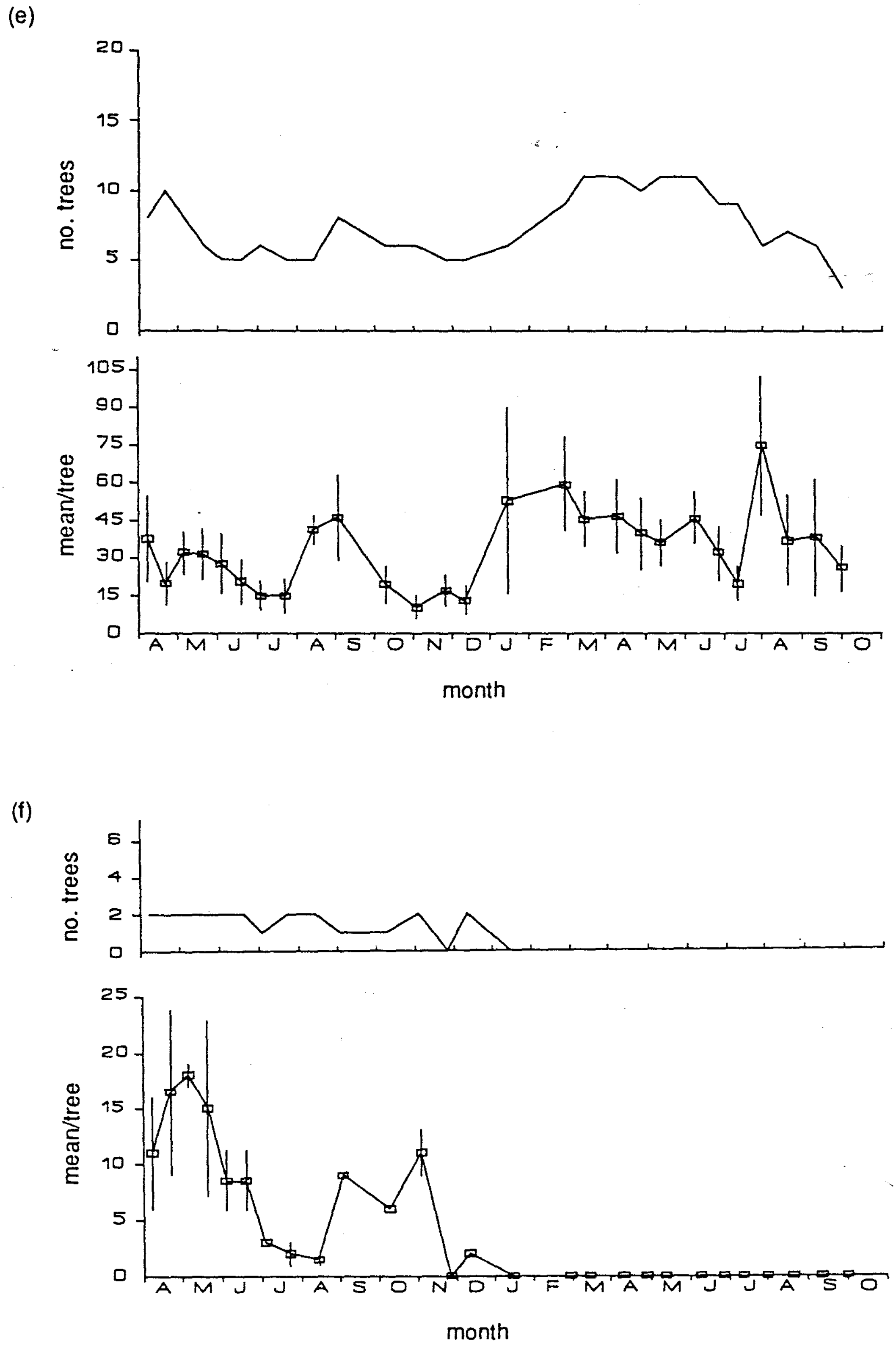


Figure 4.7. *continued.* e) *P. megacephala.* f) *P. schistacea.*

autumn (Fig. 4.7d) with a sharp trough between. The number of trees on which *Crematogaster* was present on the fruiting branches showed a different pattern: high in spring, summer and the second winter but low in autumn. The number of trees with *Crematogaster* on the whole tree follows a similar pattern (Fig. 4.8b), although mean number per trail was variable. *P. megacephala* on the fruiting branches (Fig. 4.7e) showed distinct seasonal patterns and, because it was so abundant, contributed substantially to the total seasonality in ant densities. The number of trees on which *P. megacephala* was present increased in spring and reached a peak in autumn, after which it declined; the mean number of *P. megacephala* per tree showed a similar pattern. Numbers of *P. megacephala* on the whole tree and on trails (Fig. 4.8c) followed very similar patterns - almost all *P. megacephala* on the trees were associated with fruiting branches. Finally, *P. schistacea* (Fig. 4.7f) was present in high numbers on the two trees on which it occurred. It experienced a decrease in late winter, a peak in spring and then disappeared.

On most dates *P. megacephala* was found tending *H. patruelis* on more than 50% of the trees on which the ant was present (Fig. 4.9). The percentage of trees on which the bug was tended was lowest in the early summer (November and December 1989) and highest later on in the same season. Satellite nests were built around figs mainly in summer. The highest proportion of prey items was also taken during this season. Scale tending and foraging were lowest in midsummer.

Individual trees exhibited considerable variability in their ant, *H. patruelis* and fruiting phenologies in terms of ant species, numbers of insects and crop sizes, and relative timing of appearance and peaks in numbers of the various species and the figs (Fig. 4.10a-d). On many trees with *H. patruelis* and ants the appearance of a new crop of figs was followed after a lag by a peak in *H. patruelis* and simultaneously of ants - as the figs grew they were colonised by *H. patruelis* and their associated tending ants. The ratios of ant to *H. patruelis* to fig numbers also varied dramatically from crop to crop within a tree.

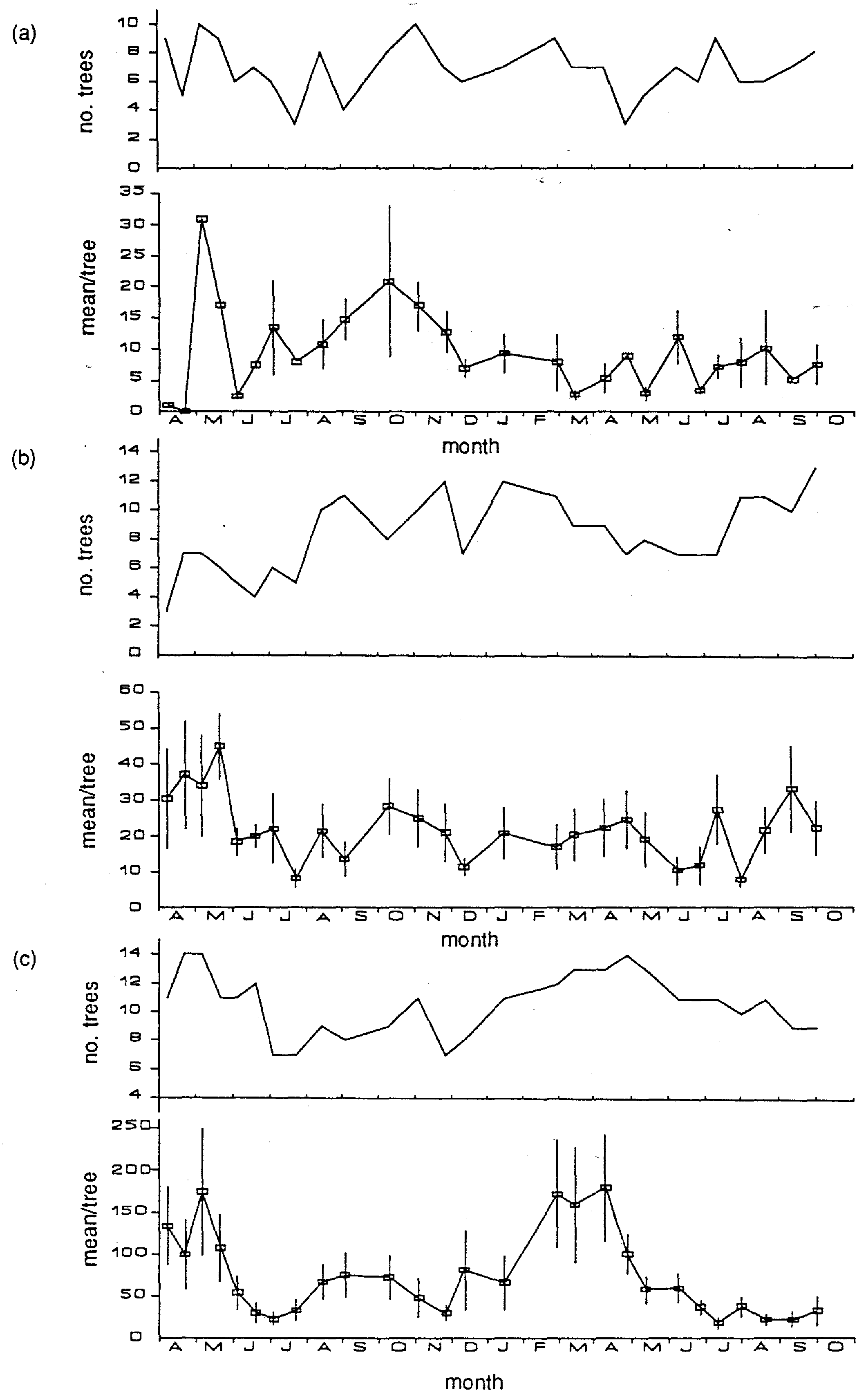


Figure 4.8. Number of trees on which ants were present on the whole tree (fruiting branches, leafy branches and trunks) and mean numbers of ants ± 1SE on trails crossing a point on the trunk over a two minute period. a) *A. capensis*. b) *Crematogaster* spp.. c) *P. megacephala*.

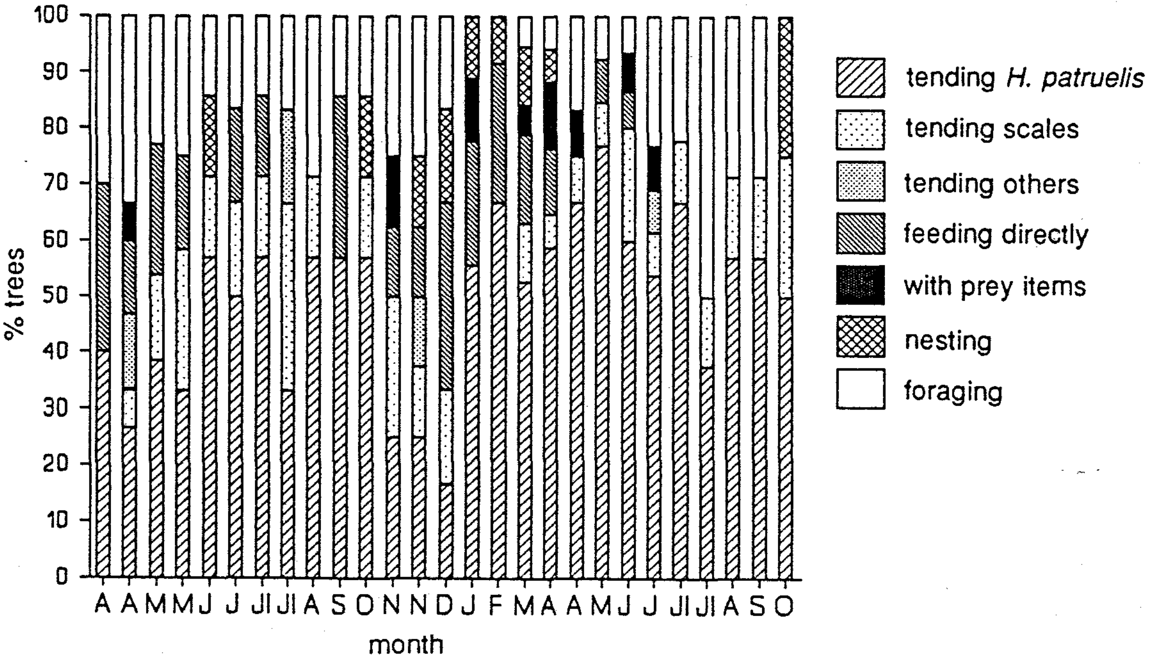


Figure 4.9. Activities of *P. megacephala* over the monitoring period. Percentages are only for those trees on which *P. megacephala* was present. The total percentage of trees was greater than 100 on some dates because ants were engaged in more than one activity on a tree. In these cases the total was adjusted to 100.

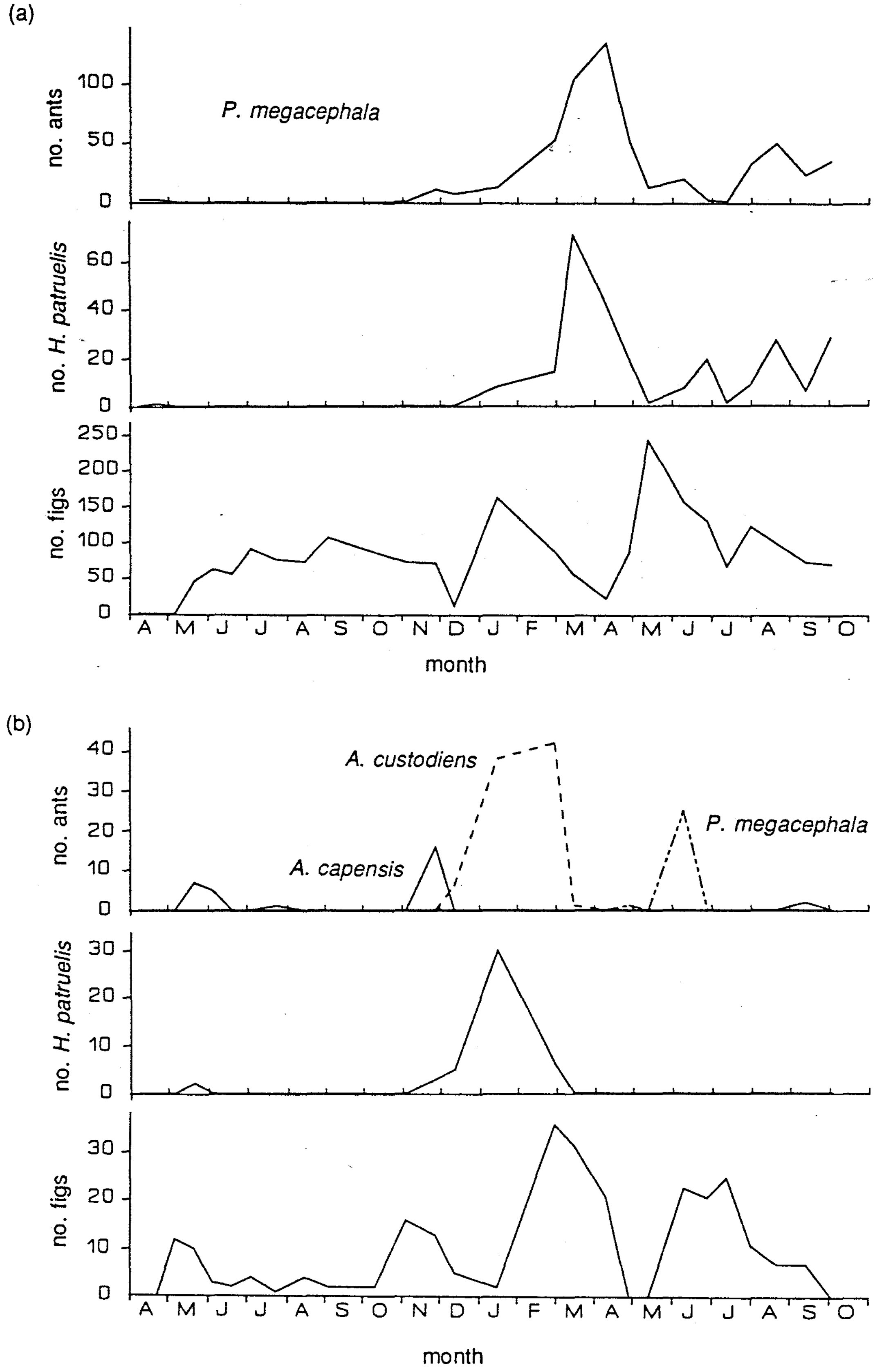


Figure 4.10. Numbers of figs, *H. patruelis* and common ants on four individual trees on each sample date over the monitoring period. Those ants which never occurred at a density of ≥ 10 per sample date are omitted. Trees a) and b) were at site 1.

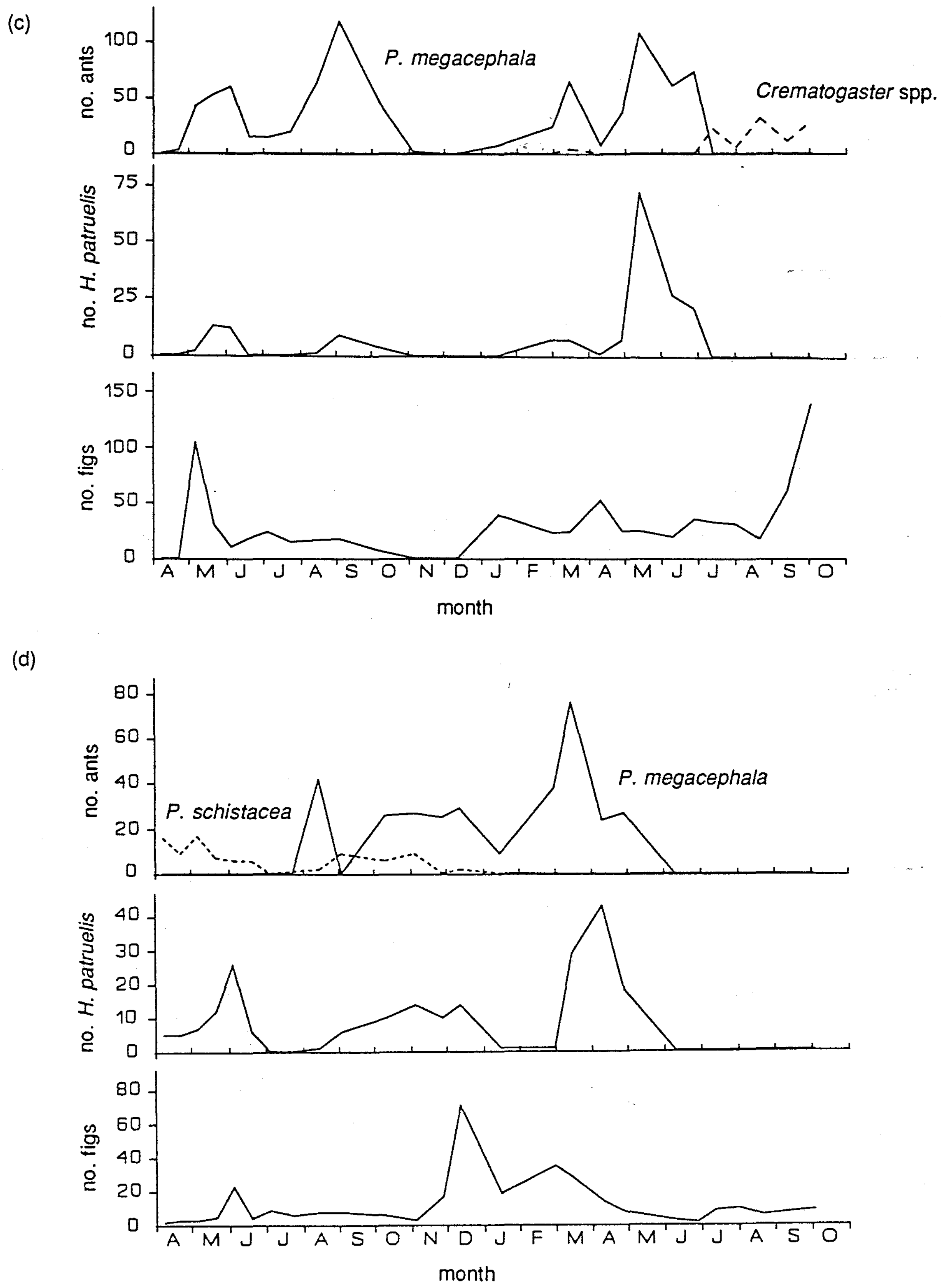


Figure 4.10. *continued.* Tree c) was at site 2 and tree d) at site 3.

4.3.5. Spatial and temporal variation in ant to fig and *H. patruelis* to fig ratios

For the whole monitoring period (April 1989 to October 1990), the mean number of ants per fig was 0.926 ± 1.881 (n = 454), with a range from zero to 19.0. This was calculated by removing all sample points on which no figs were present and determining mean ants per fig for each remaining point. Mean H. patruelis numbers per fig for the same period were 0.467 ± 1.669 (n = 454), with a range from zero to 19.0. There was therefore high variation in both per-fig ant and H. patruelis numbers over the period, to which both seasonal and between-tree effects contributed. The mean ratio is thus approximately two ants for each *H. patruelis*.

Ant numbers per fig varied between 0.29 ± 0.11 and 2.05 ± 0.81 on each sample date. A seasonal trend in ant to fig ratios was evident, despite the high variability on each date (Fig. 4.11), and numbers per fig were highest in the autumn or early winter of both years. A trough in December 1989 again reflected the decrease in the numbers of ants active diurnally during this period.

Mean ant numbers per fig varied between 0.02 ± 0.02 and 2.17 ± 0.47 on the 21 trees monitored over the whole period. There was thus higher between-tree than between-date variation in the ratio of ants to figs.

4.4 DISCUSSION

4.4.1 General biology of the ant species on *Ficus sur*

Pheidole megacephala was by far the most important species in the *F. sur* ant community around Grahamstown, in terms of the number of trees on which it occurred, the number of sample dates it was present, its numerical dominance on those trees on which it was found and its predominantly *H. patruelis*-tending behaviour. *P. megacephala* is a cosmopolitan

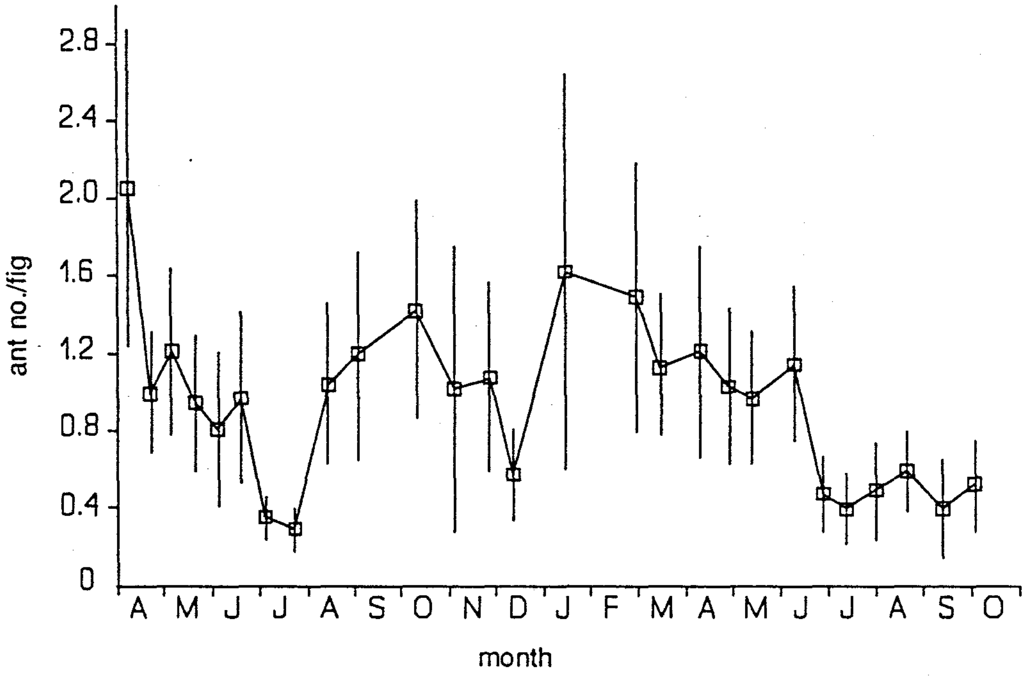


Figure 4.11. Mean number of ants per fig ± 1SE on each sample date through the monitoring period. Sample points on which no figs were present are excluded.

tramp species originating in Africa (Wheeler 1922) and is very invasive. It has been recorded invading the territories and colonies of aggressive ant species such as *Oecophylla* sp. and *Anoplolepis custodiens* (Steyn 1954; Vanderplank 1960) and acts as a dominant species, particularly in disturbed ecosystems (Greenslade 1971a; Room 1975; Taylor 1977; Majer 1985; Samways 1990; Majer & de Kock 1992). *P. megacephala* nests in the ground (Broekhuysen 1948) or in debris and soil in tree crevices (Greenslade 1972; Taylor & Adedoyin 1978), often in large polygynous and polydomous colonies. It is also recorded as taking soil up into trees to form "tents" over tended homopterans (Taylor & Adedoyin 1978). Majer (1985) and Majer & de Kock (1992) found that species diversity in ant communities decreased as they became dominated by *P. megacephala* in disturbed areas - in undisturbed ecosystems it is often present only in low numbers (Greenslade 1972; Majer 1985; Majer & de Kock 1992). This, together with the terrestrial nesting habits of *P. megacephala*, may explain its relatively low abundance at site 3, where most trees are situated along streams and are subject to periodic inundation (cf. Vanderplank 1960), thereby favouring arboreal species. *P. megacephala* is considered a generalist myrmicine (Andersen 1992), feeding on liquid nutrients as well as scavenging. As was shown by Carnegie (1960), the species was fairly seasonal, in that while it was present throughout the year, numbers were lower in winter. The mean number of *P. megacephala* per tree on trails was probably more consistent seasonally than on the fruiting branches because ants were being attracted to more than just the sampled fruiting branches on the trees. Samways (1990) considered it a eurytopic species, its numbers increasing and decreasing dramatically in response to food supply. On *F. sur* its foraging behaviour changed slightly with season, a phenomenon common in ants (Carroll & Janzen 1973; Sudd & Sudd 1985; Rico-Gray & Sternberg 1991).

Other important ant species on the *F. sur* trees near Grahamstown were *Polyrhachis schistacea* and *Anoplolepis custodiens*, although they were restricted to a few trees only. *A.*

custodiens had a narrow seasonal range on *F. sur* but when it appeared it was present in large numbers and tended *H. patruelis*. *A. custodiens* and its congener *A. longipes* have been recorded as dominant aggressive species, particularly on crop trees (Steyn 1954; Vanderplank 1960; Greenslade 1971a). It is also known to be highly seasonal, restricted by a low temperature regime in winter (Steyn 1954; Louw 1968). Louw (1968) found that in the Orange Free State, South Africa, it displayed a spring and autumn activity peak, and was restricted directly or indirectly by low humidity. It is also ground nesting and requires high nest insolation (Steyn 1954; Greenslade 1971a). The genus *Polyrhachis*, many of whose species are also ground nesting, has not often been classed as dominant in the literature, rather it is regarded as non-dominant and retiring (Majer 1972; Andersen 1992) and is recorded as an *Oecophylla* sp. prey item (Vanderplank 1960). On the three trees on which it was present in this study, however, *P. schistacea* appeared to be dominant and almost exclusively tended *H. patruelis*. Its low numbers are deceptive as it is a large ant, and no more than five can be accommodated on a mature fig. It was not highly seasonal, but disappeared from the trees shortly after a period of high rainfall and flooding.

Three other species were qualitatively important in the *F. sur* ant community: *Acantholepis capensis*, *Crematogaster liengmei* and *Crematogaster* nr *delagoensis*. Of the two *Crematogaster* species the former was the more common, while the second species was probably restricted to large colonies on two trees. Both genera were widespread but appeared sporadically and often in low numbers, engaging in activities other than *H. patruelis* tending - mainly tending scales and feeding on exudates. The *Crematogaster* spp. were arboreal, nesting in dead branches or twigs. Although *C. liengmei* was widespread its nests were usually small. The scarcity of *Crematogaster* spp. at site 1 may be due to the systematic removal of dead wood from the trees by man. *A. capensis* is recorded variously as nesting in soil and under stones (Arnold 1915; Wheeler 1922) but also in dry dead wood, both on the ground and in trees (Taylor & Adedoyin 1978). However, *A. capensis* is regarded as a species group, and the *A. capensis* in this study was probably ground nesting (H. Robertson pers. comm.). *Crematogaster* spp. probably use the trunks of fig trees in which they are nesting as access routes to other foraging areas - this is reflected in the consistently high numbers of ants on trails even when none were found on the fruiting branches. *Crematogaster africana* Mayr and *C. depressa* (Latrielle) use trunks of cocoa trees in Nigeria for this purpose when they cannot move through the canopy (Taylor & Adedoyin 1978). In West African cocoa plantations a number of *Crematogaster* species formed the major dominant species, together with *Oecophylla longinoda* (Latrielle) (Room 1971; Majer 1972; Taylor 1977; Jackson 1984). *Crematogaster* was dominant on two of the *F. sur* trees over the monitoring period and co-dominant, together with *P. megacephala*, on a further two. *A. capensis* was not dominant on any trees in this study although it was found to be dominant on a large number of cocoa trees in Nigeria (Taylor 1977) - the West African *Acantholepis* was possibly a different species though (H. Robertson pers. comm.). Neither *A. capensis* nor *Crematogaster* spp. displayed dramatic seasonal trends on F. sur in Grahamstown.

Most other species occurred in comparatively low numbers. *Camponotus natalensis* (F. Smith), a very retiring species, was quite common on the only two trees where it was recorded, and tended *H. patruelis* almost exclusively; it is probably ground nesting. *Camponotus* nr *postoculatus* Forel nested arboreally in dead branches and was a fairly common and important *H. patruelis* tender. The other *Camponotus* species were rare, appearing as occasional foragers. *Camponotus maculatus* Fabricius is nocturnal (Arnold 1915; H. Robertson pers. comm.) and numbers were underestimated, while *Camponotus* sp.1 was relatively common on leafy branches and may be an arboreal nester. The Camponotini, which include *Polyrhachis*, are usually considered subordinate ants (Majer 1972; Hespenheide 1985; Andersen 1992) which coexist through their submissive behaviour and large size (Andersen

1986). *Cataulacus* species nest arboreally, usually in small nests (Wheeler 1922); *C. intrudens* was very rare on fruiting branches and fruiting branches in comparison to its appearance on trunks. In Nigeria *C. guineensis* F. Smith succeeded in coexisting with dominants through its passive behaviour (Taylor & Adedoyin 1978).

The small ant species *Monomorium boerorum*-complex, *Plagiolepis* sp.1, *Technomyrmex* sp.1 as well as *Plagiolepis fuscula* were quite common but inconspicious. Most or all of these ants nested arboreally in dead twigs or branches and did little or no *H. patruelis* tending, but rather scavenged on small prey items and fed on exudates. In West Africa, *Plagiolepis brunni* Mayr is a small, discreet, common species which is probably nocturnal and lives in dead twigs on the tree (Taylor & Adedoyin 1978). *Technomyrmex albipes* nests in dead logs in Papua New Guinea (Room 1975), where it is a dominant species in cocoa plantations and thought to be an invasive tramp species. It was only ever recorded on two trees in this study and was the only species more active in winter than summer. *Smithistruma transversa* (Santchi) was only recorded once, on a geocarpic fig - the genus *Smithistruma* is a specialist predator on collembolans and other soil arthropods (Carroll & Janzen 1973; Hölldobler & Wilson 1990) and is therefore incidental to the fig tree. The two *Tetraponera* species were also fairly common. All known *Tetraponera* species nest arboreally (Wheeler 1922); they are fast-moving solitary predators, and on *F. sur* they also commonly fed on exudates.

The ant species differed in their predatory tendencies. The most predatory ants were *T.emeryi* and *T. natalensis*, although *P. megacephala*, due to their high numbers, took a greater total number of items. *A. capensis*, *Crematogaster* spp. and the small ant species were also occasionally recorded with prey.

4.4.2 Richness of the *Ficus sur* ant fauna

In comparison to many other tree species in the same ecosystem, *F. sur* might be expected to support a larger number of ants, by virtue of the diversity of the food resources it offers. However, it is difficult to compare faunal richness with other studies in the same region (e.g. Moran & Southwood 1982; Southwood *et al.* 1982) due to differences in the sampling methodologies employed.

In terms of numbers of individuals, the 19 ant species together comprised 30.3% of the total arthropods recorded on *F. sur*. This figure is inflated because no parasitoids or tourists were recorded, yet is low in comparison to data from tropical areas. For example, ants comprise 87% of the insects on cocoa in West Africa (Taylor 1977). *F. sur* may nonetheless support a richer and larger ant fauna in the tropical regions of its distribution, as ants are usually present in larger numbers and form a greater proportion of the insect fauna in tropical and arid than in temperate arboreal ecosystems (Room 1975; Majer 1976b; Taylor 1977; Whitford 1978; Andersen 1983, 1986; Basset *et al.* 1992). Similarly, Southwood *et al.* (1982) found more ants on certain tree species in warm temperate South Africa than in the cool temperate United Kingdom. Stork (1987) showed that temperate trees had a lower proportion of ants (3.7%) than Bornean rainforest trees (18.9%). Australian subtropical forests are exceptional in the low ant fauna they support (Basset 1990; Majer 1990). This may be due partly to the presence of a cool dry season, resulting in a period with low food resources (Majer 1990).

4.4.3 Temporal and spatial heterogeneity

Temporal variation in the ant species on *F. sur* occurred at several levels. A change in ant species and/or numbers often occurred from one crop to the next on the same tree, and within a single crop from one period to another (cf. Greenslade 1971a; Kansky 1988). These shifts probably reflect changes in foraging patterns due to competition, the availability of other food-sources and short-term environmental effects such as rainfall. The outcome of competition for a food-source depends partly a priority effect: the species which finds a food-source first has a greater probability of monopolising it (Greenslade & Greenslade 1977; Torres 1984). Subordinate species are often more efficient at finding and utilising food (Fellers 1989). The short-term effects of rainfall on ant activity are different in tropical and arid areas - in the former activity is depressed (Basset 1991b), while in the latter it is stimulated (Whitford 1978; Briese & Macauley 1980). Ant activity on *F.sur* in Grahamstown may have been depressed by persistent rainfall in the early summer of 1989.

Changes in the foraging activity of individual ant species with season is due to interactions between weather, food supply and the reproductive cycle of the colony (Greenslade 1971b; Briese & Macauley 1980). Seasonal patterns and the factors influencing them differ also between species (Greenslade 1971b; Briese & Macauley 1980; Andersen 1983, 1986; Fellers 1989). Seasonal variation in *P. megacephala* activity may reflect both changing weather and *H. patruelis* population sizes. Ant communities as a whole also display seasonal variation. In regions experiencing noticeable changes in seasonal temperatures, ant communities are characterised by a summer peak and a winter trough (Briese & Macauley 1980; Andersen 1983, 1986; Samways 1990; Basset 1991b) whereas in the wet tropics, where temperature fluctuates very little, rainfall is the most important weather parameter affecting ant activity (Greenslade 1971b; Basset 1991b). That there was no seasonal pattern in the number of trees on which any ants were present in this study may be partly explained by differences in seasonal patterns between the individual common ant species. The decrease in early summer of mean ant numbers on the fruiting branches, which is largely due to fluctuations in *P. megacephala* numbers, could be due to the high rainfall during this period, resulting in depression of activity or flooding of nests. It could also be due to a shift in the diel foraging pattern of *P. megacephala*, which often becomes nocturnal under conditions of high temperature (Steyn 1954; Carnegie 1960; Greenslade 1971a, 1972; Chapter 7), and of other ant species. However, the trough in ant numbers preceded peak summer temperatures by two months, so this last explanation is less likely.

Patterns of ant activity also change over longer than annual periods. At a local level ant colonies have a finite lifespan and one species may be superceded by another once a colony has died. Expansion and contraction of the territorial and foraging areas of individual species occurs with vegetation and weather changes and invasion by new ant species (Vanderplank 1960; Greenslade 1971a; Brian *et al.* 1976; Whitford 1978; Samways 1990). For example, *A. longipes* thrives in drier periods (Greenslade 1971a) whereas *P. megacephala* prefers vegetated conditions with higher humidity and therefore thrives in disturbed areas only in later successional stages (Greenslade 1971a; Majer 1985).

The mean numbers of ants and *H. patruelis* per fig varied seasonally, although this variation was low in comparison to that between trees. Because only diurnal ant numbers were recorded, seasonal changes in the ant to fig ratio may have been underestimated. However, in terms of the interaction of ants with fig wasps (Chapters 7 and 8) the recorded figures were probably representative, as the wasps are diurnally active (Ware & Compton 1994). The numbers of *H. patruelis* and ants displayed clear seasonal trends despite the lack of clear seasonal differences in the percentage of trees on which figs were present. However, the total numbers of figs on trees were not recorded and fruiting branches were not selected randomly for monitoring - only those possessing figs were used. No absolute measure of changes in the numbers of figs on a tree with season were therefore obtained. Although this does not affect estimates of the mean numbers of ants per fig, assuming that the fruiting branches chosen give a good measure of per-fig ant densities for the entire tree over the year, if most figs are borne in summer the effect of low ant numbers on figs in winter may receive unwarranted bias.

Ant species composition and species numbers also varied from site to site. This may be due to habitat differences as well as the distance of sites from one another (Greenslade & Greenslade 1977). The richness of an ant community has often been related to the structural complexity of its habitat (Greenslade & Greenslade 1977; Andersen 1983, 1986; Majer 1985; Majer & de Kock 1992), with ant species richness usually richer in woodland, forest and undisturbed areas. Disturbance results in a decrease in habitat complexity and a corresponding loss of rare or specialised ant species and the proliferation of common and pioneer species (Greenslade 1971a; Greenslade & Greenslade 1977; Majer 1985; Majer & de Kock 1992). The proliferation of species such as *P. megacephala* may itself result in reduced species richness through competition (Majer 1985; Majer & de Kock 1992). Judging which factors affect species richness most is not easy. In this study, site 1 appears to approach site 3 in structural complexity, but has the poorest ant fauna, whereas site 2 appears superficially to have the lowest structural complexity. However, site 1 is dominated by *P. megacephala* and is more distinct in climate, greater distance from the other sites and possibly in soil type from the other sites than site 2 is from 3.

Within sites, the numbers of ants and *H. patruelis* as well as ratios of ant to fig numbers and *H. patruelis* to fig numbers varied considerably from tree to tree over the monitoring period. This may be partly related to tree heterogeneity: trees varied considerably in size and in the number of fruiting branches present, and consequently their crop sizes varied considerably. The number of crops borne over the monitoring period varied too: some trees produced a small number of discrete crops while others produced young figs continually (Chapter 3). The predictability and availability of resources therefore varied from tree to tree.

Within-site differences in ant species and numbers on trees may also be related to other aspects of microhabitat heterogeneity, the positions of ant nests and competition. In plantations in West Africa, Papua New Guinea and the Solomon Islands where ant mosaics were studied, dominant genera most commonly included *Crematogaster*, *Oecophylla*, *Pheidole* and *Anoplolepis*, among others (Greenslade 1971a; Room 1975; Taylor 1977; Jackson 1984). This study does not lend itself to the analysis of mosaic patterns because trees were often widely separated, with other tree species or no trees between them. However there was usually only one and sometimes two species numerically dominant on a tree at any one time, although a high percentage of trees lacked numerically dominant species. An absence of dominant species on some trees has also been recorded in cocoa and coconut plantations (Greenslade 1971a; Majer 1976b; Taylor & Adedoyin 1978).

Within-tree spatial heterogeneity in ant numbers and species was evident in this study and others (Greenslade 1971a; Majer 1972, 1976b; Taylor 1977; Basset *et al.* 1992). This has been attributed to nest position, food distribution and competition within individual trees. Dominant ant species sometimes exist as co-dominants on the same tree through spatial or temporal separation or through mutual tolerance (Majer 1972, 1976b). *P. megacephala* in this study was present mainly in the lower tree whereas the numbers of other species such as *A. capensis* were sometimes greater higher in the canopy. The extention of *P. megacephala* into the crown on tree 3 may be related to the distribution and number of *H. patruelis* in the tree or saturation of ant numbers at lower levels. Vertical stratification of ant species has also been recorded in Nigerian cocoa plantations (Taylor 1977). Basset *et al.* (1992) found that the total number of ants in the canopy of Cameroonian rainforest was much greater than in the shrub layer, despite the presence of myrmecophilic plant species in the latter - they attributed this partly to high numbers of Coccoidea in the canopy ecotone.

Overall, high heterogeneity in the ant community on *Ficus sur* is evident - both spatially and temporally - at several levels, in the ant species present, ant numbers and activities. This heterogeneity has important implications for the interaction between figs and their wasps and ants, and is investigated further in Chapters 8 and 9.

5 THE EFFECTS OF FEEDING BY *HILDA PATRUELIS* ON THE REPRODUCTION OF *FICUS SUR*

5.1 INTRODUCTION

Herbivores play a significant role in the growth, reproduction and evolution of the plants on which they feed, and plants and herbivores interact in a complex manner. The effects of herbivory depend on the type of plant attacked (Inouye 1982), the plant part attacked (Maschinski & Whitham 1989), the type of herbivory and therefore herbivore species (Inouye 1982; Meyer 1993; Meyer & Whitlow 1993) and the herbivore load (Newbery 1980b; Marquis 1984; Sacchi *et al.* 1988; Meyer 1993).

Herbivory can result in changes in both growth and reproductive output in plants. Changes in plant fitness can be best assessed by measuring reproductive output, as a change in the growth rate of one plant part does not necessarily imply an increase of fitness to the plant - plants can channel resources from one part to another (Belsky 1986). A large decrease in plant growth or reproductive output has been found in many studies of the effects of herbivory (Rockwood 1973; Newbery 1980a, b; Inouye 1982; Marquis 1984; Sacchi *et al.* 1988; Meyer 1993). A high herbivore load can result in negative plant growth (Meyer 1993) and even mortality (Newbery 1980a, b), and a herbivory or defoliation threshold, beyond which productivity is affected, can be defined (Rockwood 1973). Although high defoliation or herbivory levels have been used in most studies, Crawley (1985) showed that low defoliation levels (5-15%) could still result in substantial reproductive loss.

Although some herbivores decrease reproductive output by feeding directly on seeds, herbivory on the fruit pericarp (Stephenson 1981; Andersen 1988) or other plant parts

(Rockwood 1973; Bentley *et al.* 1980; Stephenson 1980, 1981; Inouye 1982; Marquis 1984; Crawley 1983, 1985; Tedders & Wood 1985; Sacchi *et al.* 1988; Maschinski & Whitham 1989; Meyer & Root 1993) also results in a decrease in reproductive output by acting as a nutrient sink, or by reducing photosynthetic rates and nutrient uptake. Although some plant species use stored energy sources for reproduction, for many species, including *Ficus* (Herre 1989), the vegetation on the plant surrounding the flowers and fruits is the source of all fixed carbon used in reproduction (Stephenson 1980).

The timing of herbivory in relation to the flowering and fruiting phenology of a plant is also important in determining the effects it has on fruiting. Herbivory during flowering has been shown to be capable of causing a decrease in the number of inflorescences produced, while early in fruiting it may result in a decrease in numbers of fruit and seeds. Later during fruit development, once the number of seeds has been fixed, herbivory is more likely to result in a decrease in seed size or viability (Stephenson 1980; Andersen 1988; Sacchi *et al.* 1988).

Insects are very important as plant herbivores: there are an estimated 361000 described species of phytophagous insects worldwide (Strong *et al.* 1984). All homopterans are phytophages and remove plant sap through sucking mouthparts, but the details of their feeding habits are diverse. Some feed on cell contents while others feed on xylem or phloem sap (Strong *et al.* 1984). They can seriously harm and even kill plants by reducing growth and reproductive output (Newbery 1980a, b; Weaving 1980; Tedders & Wood 1985; Behle & Michels 1993; Meyer 1993) and by introducing pathogens (and in particular viruses), and phytotoxins (Meyer 1993). The growth of mould subsequent to honeydew buildup also causes increased shading of leaves and therefore decreased photosynthesis (Newbery 1980b; Tedders & Wood 1985). Many homopterans are of great economic importance as major crop pests (Carver *et al.* 1991).

Most Fulgoroidea are phloem sap feeders on angiosperms (Fletcher & Carver 1991). *Hilda patruelis* (Tettigometridae: Fulgoroidea) has been shown to stunt and kill groundnut plants in Zimbabwe and South Africa (Weaving 1980; H. du Plessis pers. comm.) as well as to reduce yields. *H. patruelis* was observed to cause greater harm to young groundnut plants than to larger, more well established ones (Weaving 1980). It can also cause dieback on *Hibiscus rosa-sinensis* shoots (pers. obs.). However, it does not visibly affect many other plants on which it feeds (Weaving 1980). Weaving (1980) was not able to isolate pathogens, and therefore found no evidence that it was a disease vector.

H. patruelis, together with a large number of other homopterans, is frequently tended by ants which remove excreted honeydew. Ants often increase homopteran numbers and sometimes honeydew excretion rates, thereby increasing damage to their host plants (Beattie 1985; Buckley 1987a, b; Bach 1991). The ants attracted by *H. patruelis* on groundnuts also inflicted damage on the plants by forming tunnels around the roots that resulted in dessication (Weaving 1980).

On *Ficus sur* and other fig species, *H. patruelis* feeds mainly on the developing figs, possibly due to the presence of a strong sap flow there. Because it is a phloem feeder it does not directly feed on or damage fig ovules and seeds, but may still affect reproduction indirectly. Prior to pollination figs contain flowers (i.e. figs are inflorescences) which later become fruits (i.e. figs become infructescences). *H. patruelis* usually arrives on a *F. sur* tree before pollination, but achieves its greatest numbers later on (Chapters 3 and 7). Both the numbers and biomasses of seeds and fig wasps are therefore potentially affected by *H. patruelis* feeding, and differences in the sizes of pollinator females and the seeds that are produced may affect their fecundity (Herre 1989; Nefdt 1989). The body sizes of wasp progeny are apparently affected both by genetic (maternal) and environmental (seed size) factors (Herre 1989).

The pollination of *F. sur* is very similar to that of *F. sycomorus* (Galil & Eisikowitch 1968, 1974; Bronstein 1992). Female pollinating fig wasps, *Ceratosolen capensis*, enter figs through the ostiole at the receptive (female) phase. On entering a fig they attempt to oviposit into a large number of the thousand or more florets lining the lumen, but if the styles are too long they withdraw the ovipositor without laying an egg. They also pollinate all or most of the florets in which they have made oviposition attempts by removing pollen grains from their sternal corbiculae (Ramirez 1969) and placing them on the floret stigmas.

When ovipositing, the egg is laid between the nucellus and inner integument (Galil & Eisikowitch 1968; Verkerke 1989) so that the ovule is not damaged and pollination and formation of the endosperm occurs normally. The presence of endosperm is necessary for larval nutrition (Kjellberg *et al.* 1987; Nefdt 1989). After ovipositing, the wasp secretes a drop of fluid which results in the swelling of the ovule wall (Galil 1977) to form a gall, which can reach its final size in as little as eight days (Verkerke 1989; pers. obs.). Empty galls, or "bladders", are suggested to be the result of oviposition without pollination or of double oviposition (Verkerke 1989), leading to egg or larval mortality (Gardiner 1986; Bronstein 1992), but could also be due to other factors, including resource limitation (Bronstein 1992) and parasitoid probing (Compton & Robertson 1988).

The aim of the work described in this chapter was to examine the effects of *H. patruelis* feeding on aspects of the reproductive output of *F. sur*. These included fig abortion and growth rates, the numbers of seeds formed, seed viability, the numbers of wasp larvae reaching adulthood, and the numbers of empty galls (a measure of wasp egg or larval mortality). The results are discussed within the context of other factors that affect wasp and seed numbers.

5.2 MATERIALS AND METHODS

To assess the effects of *H. patruelis* on several fig tree growth and reproductive parameters, five pairs of fruiting branches bearing young prefloral figs on four trees were selected. Initial fig numbers were recorded and all branches were banded with Formex Insect Barrier (Ciba-Geigy Pty. (Ltd.)). *H. patruelis* nymphs or egg batches were then placed on one branch of each pair (the experimental branch) and a section of drinking straw transversing the Formex was tied to the branch. This enabled *Pheidole megacephala* workers to access the branch in order to tend *H. patruelis*, but to a large extent prevented *H. patruelis* from leaving. It proved necessary to provide ant attendants because in preliminary experiments it was found that if ants were absent, honeydew and mould buildup resulted in the abortion of prefloral figs. All *H. patruelis* were removed from control branches. Gauze bags were then placed over the branches in order to prevent predation of *H. patruelis* on experimental branches, sap removal by hemipterans on control branches, and oviposition by non-pollinating wasp species. *H. patruelis* and fig numbers were recorded at approximately weekly intervals, when the diameters of five randomly chosen figs on each branch were also measured. When figs reached the female stage their pollinators (*C. capensis*) were released into each bag in sufficient numbers to ensure adequate pollination. Just before wasp progeny were due to emerge from maturing, male-phase figs, the figs from four of the branch pairs (three trees) were picked and placed in emergence bottles with gauze lids. Figs from the fifth branch pair were not collected, but growth and abortion data from this pair were still used. After wasp emergence the following measurements were made on five figs from each branch:

(i) the numbers of wasp progeny, bladders and seeds in each of the figs.

(ii) germination rates of 60 seeds per fig to the cotyledon stage. Twenty seeds in each of three petri dishes were placed on filter paper in a Controlled Environment Room at Relative Humidity = 70, T = 26-27°C and with a diel cycle of 14 hours light: 10 hours dark. The filter paper was kept damp with distilled water and the numbers of seeds reaching the cotyledon stage were recorded.

5.3 RESULTS

5.3.1 *H. patruelis* densities on fruiting branches

Mean numbers of *H. patruelis* adults and nymphs per fig over the sample period on the experimental fruiting branches ranged from 1.81 to 3.12 (Table 5.1). These were 3.85 to 6.64 times higher than the mean of 0.47 recorded for the whole fig tree monitoring period (Chapter 4). Very few *H. patruelis* were present on the control branches.

5.3.2 Changes in fig numbers and diameters

On most branch pairs the decline in fig numbers per branch was greatest at the prefloral stage (up to about day 10) (Fig. 5.1a - e); interfloral figs did not usually abort. Fig numbers decreased again at maturation (after day 40). No consistent trend in abortion rates occurred between treatments (Fig. 5.1a - e; Table 5.2).

Fig diameters increased linearly until after pollination, after which growth rates decreased (Fig. 5.1a-e). No difference in growth rate between treatments was evident (Fig. 5.1a-e). Branch pair 3 (Fig. 5.1c) showed the greatest variation between growth rates, but this was also not significant (Table 5.2).

Table 5.1. Numbers of *H. patruelis* per fig over the fig development period. The mean number of bugs per fig on each sample date was calculated and a mean value for all the sample dates was taken.

tree	branch	no. sample dates	mean no. *H. patruelis*/fig (SD)	
			experimental	control
1	1	7	2.92 (1.77)	0.10 (0.16)
1	2	7	2.70 (1.71)	0.03 (0.08)
2	3	6	1.81 (1.30)	0.14 (0.14)
3	4	7	2.50 (1.85)	0.06 (0.08)
4	5	8	3.12 (2.50)	0.00 (0)
total		35	2.65 (1.85)	0.06 (0.11)

Table 5.2. 2-way ANOVA of fig number per fruiting branch (sample dates 1-4) and fig diameter for branch pair 3.

source of variation	no. figs			fig diameter (branch 3)		
	d.f.	F	p	d.f.	F	p
treatment	1	0.293	0.598	1	1.378	0.246
date	3	3.973	0.017	5	50.46	$<5\times10^{-5}$
interaction	3	0.163	0.920	5	0.126	0.986

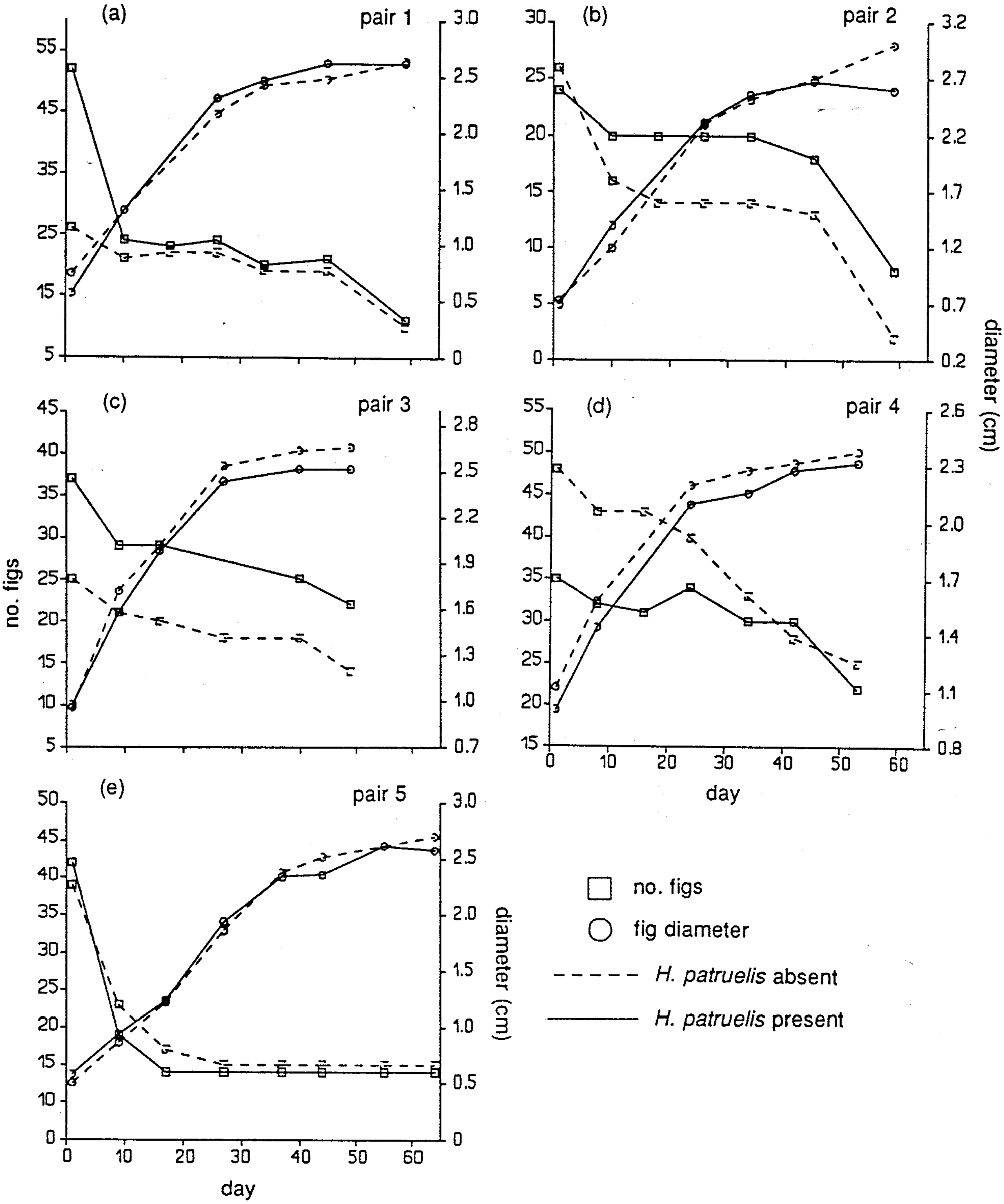


Figure 5.1. a) to e). Changes in fig numbers and mean diameters over time on five pairs of branches with and without *H. patruelis*. Branch pairs 1 and 2 were on the same tree.

5.3.3 Germination rates

Seed germination rates were extremely high both for figs with and without *H. patruelis* (Table 5.3). Within branch pairs, differences between germination rates for control versus experimental branches were non-significant (Table 5.3).

5.3.4 Wasp progeny numbers, seed numbers and bladders

Per-fig wasp numbers varied considerably between treatment branches and between branch pairs (Table 5.3). Only for branch pair 4 was the number of wasps almost significantly higher on the control than experimental branch. For pairs 1 and 2 fewer wasps were present in control than experimental figs, but the difference was not significant. The presence of *Apocryptophagus* spp. at a mean of 17.6 ± 10.5 per fig in figs of the control branch of pair 2 indicates that the figs should preferably have been bagged at an earlier developmental stage; *Apocryptophagus* spp. may have depressed numbers of florets pollinated or oviposited in by *C. capensis* (unpubl. data), and thus reduced seed or progeny numbers. The presence of 11 *Apocrypta guineensis* females in one fig of pair 4 should not have affected seed or total progeny numbers more than marginally.

Seed numbers also varied considerably between some branch pairs and treatment groups (Table 5.3). Seed number may again be depressed in the control branch (without *H. patruelis*) of pair 2 due to *Apocryptophagus* spp. presence. Seed numbers were significantly higher only for the control branch of pair 3 - for the three other branch pairs seed numbers were lower on control than experimental branch, but not significantly.

The proportions of the galls occupied by wasps (as opposed to being empty bladders) varied

Table 5.3. Mean values and Mann-Whitney U statistics for five parameters for each of 5 figs on control branches (without *H. patruelis*) and 5 figs on experimental branches (with *H. patruelis*).

parameter	tree	branch	mean (SD)		Mann-Whitney U	
			with *H. patruelis* (n = 5 figs)	without *H. patruelis* (n = 5 figs)	Z	p
no. seeds germinating of 60 seeds from each fig	1	1	59.6 (0.55)	60.0 (0.0)	1.350	0.177
	1	2	59.6 (0.55)	59.6 (0.55)	0	1.0
	2	3	57.8 (2.28)	58.2 (1.30)	0.109	0.913
	3	4	56.4 (1.82)	56.8 (1.30)	0.319	0.750
	total		58.4 (1.95)	58.7 (1.57)		
no. pollinator progeny produced per fig	1	1	246.6 (84.9)	192.4 (49.8)	-0.836	0.403
	1	2	229.2 (135.2)	125.6 (22.3)	-0.419	0.675
	2	3	164.0 (67.9)	212.2 (68.2)	0.105	0.917
	3	4	658.2 (323.5)	1306.8 (397.7)	1.880	0.060
	total		356.5 (268.0)	459.3 (536.7)		
no. seeds produced per fig	1	1	1214.8 (252.6)	1209.6 (99.6)	0.418	0.676
	1	2	1359.6 (396.7)	1041.8 (146.2)	-1.253	0.210
	2	3	1044.8 (543.8)	1857.0 (509.7)	2.089	0.037
	3	4	984.8 (90.2)	684.6 (444.4)	-1.462	0.144
	total		1151.0 (365.1)	1198.3 (541.3)		

Table 5.3. *continued*

parameter	tree	branch	mean (SD)		Mann-Whitney U	
			with *H. patruelis* (n = 5 figs)	without *H. patruelis* (n = 5 figs)	Z	p
proportion of galls occupied per fig	1	1	0.903 (0.095)	0.804 (0.147)	-1.253	0.210
	1	2	0.836 (0.057)	0.812 (0.117)	-0.418	0.676
	2	3	0.724 (0.172)	0.718 (0.090)	0	1.0
	3	4	0.883 (0.105)	0.936 (0.052)	0.418	0.676
	total		0.837 (0.127)	0.818 (0.127)		
no. seeds+galls produced per fig	1	1	1488.6 (298.0)	1463.4 (182.8)	0	1.0
	1	2	1629.0 (504.7)	1196.8 (154.8)	-1.253	0.210
	2	3	1265.2 (537.1)	2150.8 (542.3)	2.089	0.037
	3	4	1766.2 (491.2)	2086.8 (187.6)	0.836	0.403
	total		1537.3 (469.0)	1725.5 (505.0)		

between branch pairs to some extent but little between treatment groups (Table 5.3). This indicates that there was no difference between experimental and control groups in terms of wasp larval mortality.

There was considerable variation between treatment groups and branch pairs in the numbers of wasps and seeds. However, the numbers were not consistently lower on branches with *H. patruelis* than on those without. To ensure that this lack of consistency was not an artifact of differential pollination versus oviposition by foundress pollinators, the sum of seeds and bladders per fig was compared between treatments (Table 5.3). This sum is a reflection only of the numbers of fig florets pollinated or oviposited in by *C. capensis* and not directly of total floret numbers - it is therefore more a measure of pollinator foundress numbers and success.

Seed + bladder number was significantly greater for the control branch only for pair 3, where seed numbers contributed most to this difference (Table 5.3). No other branch pairs had differences between treatment groups approaching significance.

A 2-way ANOVA was performed on seed + bladder number, testing for variability between branch pairs and between treatments. Seed + bladder numbers varied significantly between branch pairs 2 and 4 (Tukey's Multiple Range Test), but not between treatments (Table 5.3, 5.4). If pairs 1 and 2, which were on the same tree, are combined, both between-tree (branch pair 1 + 2 versus branch pair 4 - Tukey's Multiple Range Test) and between-treatment variation is significant (Table 5.4). This is because combining the first two pairs reduces their weighting; both have lower seed + bladder counts on control branches than experimental branches. A highly significant interaction term indicates, however, that treatment is highly dependent on the branch pair on which it was performed, i.e. the direction in which seed + bladder numbers vary with or without *H. patruelis* is not consistent between trees.

Table 5.4. 2-way ANOVA of seed + bladder number per fig.

source of variation	d.f.	F	p
branch pair	3	3.489	0.0269
treatment[1]	1	2.225	0.1460
interaction	3	4.943	0.0062
tree	2	5.256	0.0103
treatment[1]	1	6.168	0.0181
interaction	2	6.871	0.0031

1: variances non-homogeneous

5.4 DISCUSSION

Feeding by *H. patruelis* was not shown to have any clear-cut negative effects on any of the parameters of fig development and reproductive success that were measured in this study. *H. patruelis* did not appear to affect fig abortion or growth rates, although there is evidence that mould growth caused by the accumulation of honeydew caused the abortion of young figs. The accumulation of significant amounts of honeydew is probably rare in this system, however (Chapter 6).

Feeding by the homopteran did not affect seed germination rates. Wasp progeny numbersand seed numbers varied between treatments, but not in any fixed direction. The sizes of wasp progeny and their consequent viabilities were not measured, but gall occupancy rates, an important indicator of wasp mortality, did not vary between treatments. In addition, the *H. patruelis* densities used in this study were four to 6.5 times higher than the mean for the whole population studied (Chapter 4). Therefore any effects of *H. patruelis* on the *F. sur* population as a whole can be expected to be even lower than in this study.

The removal of sap from *F. sur* figs by *H. patruelis* has the potential to act as a resource sink, diverting nutrients away from developing seeds and pollinator larvae and thus resulting in decreased reproductive output. The lack of detectable damage or a decrease in the reproductive output of *F. sur* due to *H. patruelis* feeding in this study is attributable to a number of possible factors. The bugs did not transmit any detectable disease, and in the presence of ant attendants they did not cause a substantial buildup of honeydew or mould (see also Chapter 6). The inherent variability of both the herbivore-plant relationship and the fig-fig wasp relationship, as well as possible methodological artifacts in the latter case (see below), may nonetheless have led to variability between treatment branches and branch pairs, or may have hidden differences in reproductive output caused by *H. patruelis* feeding.

The impact of herbivory for a given plant-herbivore pair is modulated by environmental variables such as competition with other plants (Belsky 1986; Maschinski & Whitham 1989), water and nutrient availability to the plant (Newbery 1980b; Sacchi *et al* 1988; Maschinski & Whitham 1989; Meyer & Root 1993), the timing of herbivory in relation to season and plant phenology (Stephenson 1980; Inouye 1982; Andersen 1988; Sacchi *et al.* 1988; Maschinski & Whitham 1989), simultaneous herbivory by other animals (Meyer & Root 1993) as well as plant age (Rausher & Feeny 1980; Marquis 1984; Sacchi *et al.* 1988) and genotype (Marquis 1984; Crawley 1985; Sacchi *et al.* 1988). For any particular plant, there is variation in environmental conditions and herbivory levels from year to year (Newbery 1980b; Maschinski & Whitham 1989). The effects and consequences of herbivory are therefore complex and strongly reliant on the context of the herbivory (Crawley 1983), and cannot necessarily be extrapolated from one year to the next.

Within a species of fig tree, many factors affect the number of pollinators and seeds produced per fig, their relative proportions and the proportions of florets that produce wasps or seeds. High intraspecific variation in fig size and floret number has been recorded for several species, including *F. sur* (Galil & Eisikowitch 1968; Berg 1990; Bronstein 1992; pers. obs.), and may be genetically or environmentally induced. The number of foundress pollinators entering a fig affects the numbers of progeny and seeds produced, as well as their relative proportions, in a complex manner (Janzen 1979; Herre 1989; Nefdt 1989). Nefdt (1989) estimated that, in *F. sur*, a maximum of four pollinators was able to lay a full complement of eggs in accessible ovules. Under natural conditions the number of pollinators reaching fig crops is often variable (Kjellberg *et al.* 1987; Bronstein 1989) and pollinator availability may generally be limited (Berg 1990; Bronstein 1992). Nutrient limitation may also be important in restricting the percentage of florets in which seeds or wasps develop (Herre 1989; Bronstein 1992) and a high percentage of non-developed florets has been found in several studies (Nefdt 1989; Compton & Nefdt 1990; Bronstein 1992). Although they were excluded from this study, under natural situations other non-pollinating fig wasps may compete with pollinators for nutrients or oviposition sites, or act as parasitoids, depending on their life histories (Bronstein 1991). The numbers of empty galls, which did not vary much in this study, may reflect oviposition without pollination, double oviposition (Verkerke 1989) or resource limitation - the latter may be due to competition between wasp larvae, or possibly a lack of available nutrients (Bronstein 1992) - and in the presence of *A. guineensis*, through parasitoid probing (Compton & Robertson 1988).

A number of artifacts of the experimental design may have affected seed and progeny numbers in this study. The number of foundress pollinators entering each fig may have varied, depending on the numbers placed in the gauze bags, the number of figs receptive within the bags when wasps were introduced, and wasp mortality due to prevailing weather conditions and predation by *P. megacephala.* Some of the pollinators were obtained from the lumens of male-phase figs before their emergence. However, in the closely related species *F. sycomorus*, females collect pollen as soon as they emerge from their galls (Galil & Eisikowitch 1974) so this is unlikely to have resulted in pollen-poor wasps.

Although the amount of sap which the tree lost to *H. patruelis* was not measured directly in this study, it could be low. *P. megacephala* carried down an estimated 210-420g wet weight of honeydew and sap from *F. sur* over an entire fruiting period (Chapter 7). As homopterans excrete most of the sap they ingest (Slansky & Scriber 1985; Lei & Xu 1993) this is a good estimate of sap loss from a tree. Taking into account that *F. sur* is a large, generally riverine tree, and can thus be expected to have a high phloem flow and rate of carbohydrate production, the quantity of sugar removed by *H. patruelis* may not be very important to the plant. The impact of the nutrient drain on a tree caused by phloem-feeding homopterans cannot be fully evaluated without quantification, however, as it varies with species and conditions. For example, Mittler (1958) estimated that a single *Tuberolachnus salignus* (Gmelin) aphid on a *Salix* species resulted in a 1-4mg sucrose drain per day on the plant, which is the amount of carbohydrate produced by 5-20cm^2 of leaf area per day. In contrast, van Hook *et al.* (1980) showed that the populations of the aphid *Macrosiphum liriodendri* Monell on the tree *Liriodendron tulipifera* L. removed less than 1% of the carbohydrate produced by the tree annually, without taking into account compensatory primary production. The aphid may have removed a significant amount (17%) of foliar nitrogen, however.

Although no short-term changes in *F. sur* fecundity were detected in this study, the possibility of a long-term effect of resource removal by *H. patruelis* cannot be ruled out. A years' time lag occurs in the effects on nut production in pecans due to aphid feeding (Tedders & Wood 1985) and in acorn production due to herbivory (Crawley 1985), for example.

Other herbivores are probably more important than *H. patruelis* in their effects on reproductive output. The lygaeid *Dinomachus marshalli* and other species cause direct damage to seeds by feeding on them. Areas of dead pericarp and seeds are often present in figs (pers. obs.) and appear to be attributable to these species, which are often present in large numbers on figs (Slater 1971, 1972; Chapter 3). The lepidopterans *Botyodes hirsutalis* and *Cirrhochrista convoluta* and the weevil *Omophorus* sp. also cause large losses of whole figs, at both the pre- and interfloral stages.

Thus, if *H. patruelis* does cause a reduction in fig reproductive success, it is probably small in comparison to that caused by other phytophagous species, and its effects are masked by the intrinsic variability of the system. Larger sample sizes and more rigorous experimental conditions would be necessary to detect these effects, if they are present at all.

6 THE EFFECTS OF ANTS ON *HILDA PATRUELIS*

6.1 INTRODUCTION

Many ants are attracted to a variety of insects which produce nutritious or attractive substances. These include honeydew-secreting Homoptera (Way 1963; Carroll & Janzen 1973; Buckley 1987a, b), Lepidoptera such as lycaenids (Pierce & Mead 1981; Maschwitz *et al.* 1984) and riodinids (Cottrell 1984), the exudates of galls produced by cynipid wasps (Washburn 1984; Abe 1988) and the eggs of stick insects (Compton & Ware 1991). The high frequency of such ant-insect interactions are a consequence of the temporal and spatial stability of the tended insects as a source of nutrition (Washburn 1984) and of the evolution of eusociality in ants (Cushman & Beattie 1991). Many tended insects show behavioural or morphological adaptations which favour myrmecophily (Sudd 1987).

In the case of homopterans, ants derive nutritional benefits, mainly in the form of carbohydrates (honeydew), but sometimes also proteins if they prey on the homopterans they tend. Some of the lycaenids, however, produce chemical attractants from specialised glands or from the epidermis which are of little or no nutritional value and serve only to attract protective ants (Pierce & Mead 1981; Cottrell 1984).

In many cases ants have been shown to provide benefits to the insects which they attend, in the form of protection against predators or parasitoids (Wood 1977; Pierce & Mead 1981; Washburn 1984; Hanks & Sadof 1990; Bach 1991), removal of sap and honeydew which otherwise accumulates and interferes with development (Buckley 1987b; Bach 1991), provision of shelters against the weather (Way 1963; Weaving 1980), transport to more favourable feeding sites (Maschwitz & Hänel 1985) and decreased development times (Pierce *et al.* 1991) or increased reproductive rates (Bach 1991). This last benefit usually accrues through the protection of eggs and nymphs (Buckley 1987b), although Bristow (1983) found that the membracid *Publilia reticulata* van Duzee laid more eggs in the presence of tending ants.

Great variability exists in the characteristics of ant-insect mutualisms, depending on the species involved. The intensity of the interaction varies from facultative and occasional to obligatory on either or both sides (Maschwitz & Hänel 1985; Buckley 1987a; Sudd 1987; Bristow 1991). The degree of protection conferred on a given species of herbivore by attendant ants depends on both the ant and enemy species (Bristow 1984; Takada & Hashimoto 1985; Völkl 1992). Some parasitoids and predators, for example, are immune to ants due to chemical or behavioural characters and can oviposit or prey on the homopterans without interference (Takada & Hashimoto 1985; Völkl 1992). Parasitoids may even benefit from ant presence through protection from hyperparasitoids (Washburn 1984; Völkl 1992). Under some circumstances, ants may switch to preying on the homopterans they are tending (Way 1963; Sudd 1987).

For a given group of interacting species the magnitude and sign of the effect of ant presence on homopterans has also been shown to vary with factors such as ant numbers, the life history stage and numbers of the homopteran, predator or parasitoid densities, and competition by homopterans for ant mutualists (Bristow 1984; Compton & Robertson 1988; Cushman & Addicott 1989; Cushman & Whitham 1989, 1991). Such conditionality due to local biotic conditions and other factors is being increasingly recognised as an overridingly important factor in mutualisms (Cushman & Addicott 1991).

Compton & Robertson (1988, 1991) suggested that *Hilda patruelis* on *Ficus sur* is likely to benefit from the presence of tending ants through protection from predators and parasitoids.

The only recorded parasitoid on *H. patruelis* throughout its range is *Psyllechthrus oophagus* (Hymenoptera: Encyrtidae) (Ghesquière 1968; Weaving 1980). A closely related species (genus near *Arrhenophagus*) was recorded from *H. undata* Walk. in Nigeria (Jerath 1967).

The aim of this chapter was to assess the importance of several factors to the biology and survival of *H. patruelis*, and to consider the effects of ant presence on these parameters, which included parasitoids, invertebrate predators and the accumulation of honeydew. Changes in *H. patruelis* numbers in the presence and absence of tending ants were also assessed.

6.2 MATERIALS AND METHODS

6.2.1 Honeydew and sap removal by ants

Qualitative observations on mould growth and honeydew or sap accumulation, as well as the state of health and numbers of *H. patruelis*, were compared on three control fruiting branches (with ants) and three experimental fruiting branches (without ants) on two trees at site 1. On both trees the experimental branches were banded with Formex - on the first tree gauze bags were also placed around both control and experimental bags.

6.2.2 Parasitism of *H. patruelis* eggs by *Psyllechthrus oophagus*, and interactions between the parasitoid and ants

P. oophagus was the only species recorded parasitising *H. patruelis* during this study. Observations were made on aspects of the general biology of *P. oophagus* and on interactions between it and the ant *Pheidole megacephala*. *H. patruelis* egg batches were collected at random in the field in order to determine the levels of parasitism and ant numbers in their vicinity. Ants were also excluded from *H. patruelis* egg batches and parasitism levels recorded.

P. oophagus adults were obtained by rearing them from *H. patruelis* eggs for observations of interactions between them and *P. megacephala.* In most cases wasps were used within 24 hours of eclosion. The first 20 wasps were kept in a container with saturated sugar solution or dilute honey solution as food. In order to negate the possibility that the food affected the wasps' odour, making them more vulnerable to ant predation, food was not provided for a further five wasps.

Individual wasps were observed on the fruiting branches of three fig trees. Each wasp was placed on a fig on which *P. megacephala* workers were present, using a paintbrush. The number of ants on the fig was counted, and the behaviour of the wasp, as well as wasp-ant interactions, was recorded using a dictaphone. Observations were terminated once the wasp disappeared or was captured by *P. megacephala.* Additional data were also obtained from incidental observations on *P. oophagus* interactions with ants.

Random samples of egg batches were collected over two periods. The first was between January and April 1991 (late summer), when a total of 18 egg batches was collected from 10 trees at the three sites, and the second was between October 1991 and January 1992 (early summer), when a total of 21 egg batches was collected from 10 trees at the three sites. In most instances egg batches were located on fig trees and monitored for several days until most of the eggs had hatched, whereupon they were collected, together with the section of the fruiting branch to which they were attached. The numbers and identity of tending ants, as well as the numbers of *H. patruelis*, within a 10cm radius of the egg batch were also recorded on each visit. Batches were collected after most of the eggs had hatched so as not to affect hatching conditions by removal to the laboratory, to disturb the population structures of *H. patruelis* and *P. oophagus* as little as possible, and to maximise the likelihood of parasitism. Eggs were counted under a dissecting microscope and, if they had not all hatched prior to being collected, they were placed in glass gauze-topped vials. Counts were made of the total number of eggs present, the numbers of eggs from which parasitoids and nymphs had emerged, the number of dead eggs, and the number of egg scars, where eggs had been removed or fallen off.

To record parasitism rates following the exclusion of ants from *H. patruelis* egg batches, pairs of batches of young *H. patruelis* eggs were chosen on fruiting branches near one another on the same tree. One batch was used as a control while the fruiting branch to which the other was attached was banded with Formex and any ants present were removed. The number of ants and *H. patruelis* nymphs and adults on the fruiting branch were recorded at the start of the experiment and at weekly intervals thereafter, until the eggs were collected. The eggs were removed once most had hatched, and they were placed into gauze-topped vials. The parameters recorded were the same as for the randomly collected egg batches.

6.2.3 Predation of *H. patruelis* by *Lachnocnema bibilus* (Lepidoptera: Lycaenidae) larvae, and interactions between the larvae and ants

Larvae of the lycaenid *L. bibilus* were chosen for study because they were the most commonly encountered invertebrate predator of *H. patruelis* and were found exclusively in the presence of these homopterans on *F. sur* (Chapter 3). In order to assess the importance of *L. bibilus* as an *H. patruelis* predator, the abundance of the insect in relation to *H. patruelis* was determined by recording numbers of eggs and larvae near groups of the homopteran or its eggs.

The predation rates and characteristics of two larvae were also recorded. A 2mm (first instar) *L. bibilus* larva was collected and placed on a fruiting branch with a known number of *H. patruelis* nymphs and eggs. Observations on larval behaviour and interactions with ants and *H. patruelis* nymphs were made. The fruiting branch was then banded with Formex, in order to prevent the larva escaping, and a gauze bag placed around it to prevent predation. At approximately six day intervals the numbers of live nymphs remaining were counted. Frass, exuviae and dead nymphs were also collected. After pupation the larva was collected and allowed to eclose. Frass and dead nymphs were examined using a dissecting microscope. A second, 10mm long (probably third instar) larva was placed on a banded fruiting branch with unhatched eggs and nymphs, and monitored for 20 days. Additional observations were recorded on the biology of a number of other *L. bibilus* larvae, and their interactions with ants. The presence of a relationship between ant densities and the presence or absence of *L. bibilus* was also tested for.

6.2.4 Changes in *H. patruelis* numbers on fruiting branches following the exclusion of ants

Data from an ant exclusion experiment (Chapter 8) were used to assess changes in *H. patruelis* numbers in the presence or absence of tending ants. One to six pairs of fruiting branches were chosen on each of seven crops from six trees, and ants were excluded from one branch of each pair by the application of Formex to its base. No attempt was made to choose branch pairs with similar initial *H. patruelis* numbers. The numbers of *H. patruelis* adults and nymphs, together with the numbers and identities of tending ants, were recorded at approximately fortnightly intervals for the duration of the developmental period of the figs.

6.3 RESULTS

6.3.1 Removal of honeydew and sap by ants

The isolation of large *H. patruelis* groups on banded fruiting branches resulted in the buildup of large amounts of sap and honeydew on the figs, and the consequent growth of sooty mould. Nymphs were frequently observed struggling through honeydew droplets. Nevertheless, on bagged, isolated fruiting branches, a substantial number of nymphs developed successfully into adults, although growth and survival rates on isolated versus control fruiting branches were not determined.

6.3.2 Parasitism of *H. patruelis* eggs by *Psyllechthrus oophagus*, and its interactions with ants

Newly laid *H. patruelis* eggs were light green in colour. Later, it was possible to distinguish parasitised *H. patruelis* eggs from unparasitised eggs, as the former turned grey as they matured, whereas the latter turned yellow, with red eye spots eventually distinguishable. Furthermore, eggs from which a parasitoid had eclosed remained grey, whereas those from which a nymph had hatched were white. In addition, the parasitoid chewed a circular serrated exit hole through the upper surface of the egg whereas the nymph appeared to burst out of the capitular end.

Wasps were observed to walk along fruiting branches or on figs, antennating the surface, possibly searching for eggs in which to oviposit. One wasp was observed under a dissecting microscope ovipositing into a *H. patruelis* egg at the opposite end to the capitulum.

Some of the egg batches collected during the random monitoring and exclusion experiments were used to examine the relative timing of the emergence of *H. patruelis* nymphs and

Table 6.1. Relative emergence times of *H. patruelis* nymphs and *P. oophagus* adults. Numbers of each were counted when the eggs were collected (time 1), and additional emergence events were counted at the end of the recording period (time 2).

batch	no. eggs emerged				X^2	P
	H. patruelis time 1	*H. patruelis* time 2	*P. oophagus* time 1	*P. oophagus* time 2		
1	348	22	0	11	119.4	***
2	460	115	8	0	1.99	NS
3	18	4	0	422	359.9	***
4	106	2	0	96	196.1	***
5	271	0	5	45	283.7	***
6	395	90	38	77	108.4	***
total	1598	233	51	651	1429.8	***

p: NS ≥ 0.05, ** < 0.01, *** < 0.001

Table 6.2. Behavioural interactions between the parasitoid *P. oophagus* and the ant *P. megacephala*, after *P. oophagus* had been palced amongst the ants. The number of encounters in which wasps were antennated includes those after which *P. oophagus* wasps were taken by ants.

observation set	no. wasps observed	no. encounters			no. wasps taken
		total	antennate	ignore	
I	6	63	13	50	1
II	3	18	12	6	2
III	8	24	10	14	6
IV	5	65	47	18	2
total	22	170	82	88	11

P. oophagus adults. *P. oophagus* adults emerged significantly later than *H. patruelis* nymphs in five of the six egg batches which were parasitised and suitable for this analysis (Table 6.1). When summed, wasp emergence from the batches was also significantly later. A high proportion of the nymphs therefore emerged before any parasitoids. That *P. oophagus* ecloses later than the nymphs is not surprising as it has to undergo both larval and pupal development in the egg.

Observations on interactions between *P. oophagus* and *P. megacephala* indicated that the wasp was not fully immune to predation by *P. megacephala*, as 50% of the introduced wasps were taken by the ant (Table 6.2). They were therefore clearly not toxic, as damaged wasps were not discarded. Wasps were taken in 13.4% of the encounters in which they were antennated and in 6.5% of the total encounters (Table 6.2). This predation rate may have been abnormally high, however, as the wasps were introduced directly into areas of high ant density. The wasps may also have exhibited atypical behaviour or odour due to laboratory rearing, although the feeding regime did not affect the likelihood of ant predation. Nine of the 17 (sets I-III) wasps which had received food were captured, compared with two of the five (set IV) which had not received food ($X^2 = 0.259$, $p = 0.611$). On several occasions *P. oophagus* was observed walking through or along a trail of *P. megacephala* without being antennated or perturbed. *P. megacephala* often walks over the wasps due to their small size. During one observation a single wasp was watched for 8min, during which time seven interactions occurred in which the wasp was antennated for less than 5s, and two in which it was ignored. The wasp appeared unperturbed by these interactions. Interactions only occurred when *P. oophagus* and *P. megacephala* crossed paths.

If antennation occurs, it usually lasts for less than 5s, but during one behavioural observation a single *P. megacephala* worker attended a wasp for 550s, either antennating it or standing motionless with mandibles open. The *P. oophagus* appeared to flatten itself against the fig while being antennated. During another observation a wasp walking down a fruiting branch was followed and antennated by a *P. megacephala* worker for 15s; again the wasp appeared unperturbed.

Wasps which were attacked by ants were often antennated for a few seconds before being seized in the mandibles. Often several other ants antennated the wasp once it had been seized, and sometimes appeared to become agitated, rapidly twitching their gasters. During two observations a wasp was held for 460s and 370s respectively in the mandibles of a single ant before being taken away.

Ants were attracted to fruiting branches by both *H. patruelis* adults and nymphs. There was a wide range of ant densities near *H. patruelis* egg batches during both sampling periods, many of which were high (Table 6.3). The majority of the ants were *P. megacephala* (Period I: 90.8% of 488 ants; Period II: 99.9% of 1235 ants). The other species present were *Camponotus natalensis*, *Tetraponera emeryi*, *Crematogaster liengmei* and *Polyrhachis schistacea*. During period II, ant and *H. patruelis* numbers were recorded several times for each fruiting branch (Table 6.3).

Period I egg batches suffered very low parasitism rates: only one out of 18 egg batches produced any parasites (Table 6.4). Of the 4495 eggs which produced insects only 13 (0.3%) produced wasps. This parasitised batch had 45 *P. megacephala* within 10cm of it at the time of collection, compared with the average of 30.5 ants per batch for period I. During period II, batches experienced higher parasitism rates. Seven of the 21 egg batches were parasitised, and of the 5300 eggs from which insects emerged, 706 (or 13.3%) were parasitised. Unexplained egg mortalities during period I were 3.35% (as opposed to 0.3% parasitism), while for period II other mortality was 16.6% (as compared to 11.1% parasitism). During both periods other mortality factors therefore appeared more important than parasitism.

The relationship between ant numbers and *H. patruelis* numbers, the numbers of eggs in a

Table 6.3. Ant and *H. patruelis* densities on fruiting branches over two periods of random sampling. n = total number of samples, taking into account repeat samples over time.

sampling period	no. ants			no. *H. patruelis*			no. eggs per batch		
	no. samples (n)	mean (SD)	range	no. samples (n)	mean (SD)	range	no. samples	mean (SD)	range
I	16	30.5 (24.4)	2.5-100	16	22.9 (14.2)	2-45	18	258.4 (149.0)	47-520
II	21 (48)	24.2 (17.4)[1]	0-60	21 (48)	20.2 (13.8)[1]	0-46.7	21	302.5 (211.9)	72-824

1: means of temporal means

Table 6.4. Composition of *H. patruelis* egg batches collected during two periods of random sampling.

period	total no. trees	total no. egg batches	no. parasitised egg batches	total no. eggs	no. hatched (%)		no. dead eggs (%)	no. egg scars
					P. oophagus	*H. patruelis*		
I	10	18	1	4651	13 (0.28)	4482 (96.4)	156 (3.35)	630
II	10	21	7	6353	706 (11.1)	4594 (72.3)	1053 (16.6)	463

batch, the proportions of nymphs hatching and of dead eggs, and the numbers of egg scars were examined for each of the two periods using Spearman Rank Correlations. No significant correlations were obtained except during period II, when ant numbers were significantly correlated with *H. patruelis* numbers (r = 0.454, p = 0.0423, n = 21).

Due to the low parasitism rates during period I (Table 6.4), only period II data were used for analysis of parasitism by *P. oophagus*. Parasitism often tended to be clumped, with a few egg batches displaying fairly high parasitism and the rest none. The data were therefore divided into two sets (batches with and without parasites), and numbers of ants and *H. patruelis*, and egg batch sizes, were compared for the two sets using a Mann-Whitney U test (Table 6.5). No significant differences were detected for any of the variables, i.e. parasitism rates were independent of ant and *H. patruelis* numbers as well as of batch size. If anything, ant numbers were slightly higher near parasitised egg batches.

Low parasitism frequencies were experienced by *H. patruelis* egg batches following the exclusion of ants, with only one egg batch producing parasitoids (Table 6.6). This high parasitism level (21.8% of emerged eggs) occurred in the presence of large numbers of *P. megacephala* (Table 6.7). Clearly, creating ant free *H. patruelis* egg batches does not result in increased parasitism rates and, conversely, low parasitism rates are not necessarily due to the absence of ants. There were also no differences in the proportions of dead eggs on banded and unbanded branches (Table 6.6) (Mann-Whitney U: Z = 0, p = 1.0).

6.3.3 Predation of *H. patruelis* by *Lachnocnema bibilus* larvae, and interactions between the larvae and ants

Of the 48 egg batches collected for parasitism studies, 13 had *L. bibilus* eggs nearby (Table 6.8). There, the mean number of *L. bibilus* eggs per *H. patruelis* egg batch was 1.84. The

Table 6.5. Characteristics of parasitised and unparasitised *H. patruelis* egg batches during Period II: means and Mann-Whitney U statistics.

factor	mean for unparasitised batches (SD) (n = 14)	mean for parasitised batches (SD) (n = 7)	Mann-Whitney U	
			Z	p
ants within 10cm	20.1 (15.7)	32.2 (18.8)	1.082	0.279
H. patruelis	21.8 (13.2)	16.9 (15.5)	-0.672	0.501
no. eggs/batch	270.6 (175.1)	366.1 (276.0)	0.709	0.479

Table 6.6. Effects of ant exclusion on *H. patruelis* egg batches.

tree	ants	no. eggs	no. eggs hatched (%)		no. dead eggs (%)	no. egg scars
			H. patruelis	*P. oophagus*		
1	absent	215	207 (96.3)	0 (0)	8 (3.7)	0
	present	598	580 (97.0)	0 (0)	18 (3.0)	57
2	absent	175	161 (92.0)	0 (0)	14 (8.0)	0
	present	650	485 (74.6)	135 (20.8)	30 (4.6)	2
3	absent	145	128 (88.3)	0 (0)	17 (11.7)	110
	present	92	65 (70.7)	0 (0)	27 (29.3)	125
total	absent	535	496 (92.7)	0 (0)	39 (7.3)	110
	present	1340	1130 (84.3)	135 (10.1)	75 (5.6)	184

Table 6.7. Ant exclusions: numbers of ants and *H. patruelis* on banded (ants absent) and control (ants present) fruiting branches.

tree	ants	no. sampling dates	no. *P. megacephala* (SD)	no. *H. patruelis* (SD)
1	absent	3	0 (0)	6.67 (8.96)
	present	3	24.0 (19.1)	12.4 (15.5)
2	absent	4	0 (0)	8.25 (11.6)
	present	4	71.8 (38.0)	33.8 (27.9)
3	absent	2	0 (0)	8.50 (6.36)
	present	2	36.5 (9.19)	8.0 (11.3)

mean number of *H. patruelis* eggs in batches at which *L. bibilus* had oviposited was 294.8 ± 239.0 (n = 12). Six of the 48 egg batches contained partially eaten *H. patruelis* eggs. *L. bibilus* eggs or larvae were present on four of the six batches. One batch had been entirely eaten, while in the others the percentage of eggs partially eaten ranged from 3-60%, although it was not always possible to determine whether they had been eaten before or after hatching. *H. patruelis* egg batch sizes with and without lycaenid eggs or larvae did not differ significantly during either period (Period I: *L. bibilus* present: 320.0 ± 207.9 eggs, n = 2; absent: 250.8 ± 147.4 eggs, n = 16; Mann-Whitney U: Z = 0.211, p = 0.833. Period II: *L. bibilus* present: 345.3 ± 288.6 eggs, n = 7; absent: 281.1 ± 170.7 eggs, n = 14; Mann-Whitney U: Z = -0.261, p = 0.794). Therefore the caterpillar did not preferentially lay its eggs near larger *H. patruelis* egg batches.

Over a period of 20 days prior to pupation the first *L. bibilus* larva devoured a maximum of 47 *H. patruelis*, comprising either all nymphs or 27 nymphs and 20 unhatched eggs (Table 6.9). Nineteen of these dead nymphs were collected, of which 12 showed visible signs of damage. The caterpillar produced a total of 51 pieces of frass, of which 39 consisted mainly of nymphal exoskeleton and 12 were more compact and contained little or no exoskeleton. Possibly the latter consisted of honeydew, sap, or soft body contents, as no damage to the figs on which the larva was confined was observed. As the larva matured its mode of attack and eating of nymphs changed, as did the size of the nymphs on which it fed. The young larva grasped small *H. patruelis* nymphs dorsally on the thorax, chewed them and then released them. The nymphs were injured or dead when released. When it was older, the caterpillar held larger nymphs beneath itself using its mid and hind legs, and consumed the entire animal. The change in the size of nymphs eaten may have been a reflection of preference and/or availability.

The second *L. bibilus* larva devoured at least 32 nymphs. In addition it ate 520 (74.3%) of

Table 6.8. Frequency of *L. bibilus* oviposition near *H. patruelis* egg batches. *H. patruelis* egg batches were from random sampling periods I and II and the ant exclusion experiment (egg source 1-3 respectively). Numbers of both *L. bibilus* larvae and eggs were recorded.

egg source	no. trees	no. *H. patruelis* egg batches	*L. bibilus* present		no. *L. bibilus*/ batch (range)
			no. trees	no. batches	
1	10	18	2	2	1.50 (1-2)
2	10	21	4	7	1.14 (1-2)
3	4	9	3	4	3.25 (1-5)

Table 6.9. *L. bibilus* development on banded fruiting branch with *H. patruelis*. U denotes the numbers of unhatched eggs, N the number of nymphs and A the number of adults. *L. bibilus* passes through four larval instars (Clark & Dickson 1971).

day	larval length (mm) (probable instar)	no. live *H. patruelis*			no.dead *H. patruelis*		no. pieces of frass	
		U	N	A	N	A	with exoskeleton	without exoskeleton
1	2-2.5 (I)	20	66	0	0	0	0	0
6	3-4 (II)	0	62	0	8	0	1	0
12	8 (III)	0	52	0	9	0	9	2
20	pupa	0	30	9	2	0	30	9

the 700 available eggs - 97.2% of the remaining eggs hatched. Feeding on the eggs was not observed, but only 26 nymphs were present at the second inspection, suggesting that whole rather than hatched eggs were being eaten.

On another tree a first instar larva was observed biting and nibbling at nymphs with its mandibles without causing them to move away. Five days later the same larva had chewed holes in a number of hatched eggs but had also eaten the contents of 12 unhatched eggs.

The first larva was placed on a fruiting branch with 78 ants within a 10cm radius and observed for 2130s. During this time approximately 41 encounters with *P. megacephala* occurred in which the larva was antennated. In some cases several encounters with the same ant were recorded in quick succession. Lengths of encounters ranged from 12-142s with a mean of 41.7 ± 36.8 (n = 19). In all encounters the larva appeared unperturbed and the ants did not become agitated.

A second instar larva was placed on a fruiting branch on which *Anoplolepis custodiens* workers and *H. patruelis* nymphs were present, and observed for 30s. During this time it was antennated by two ants but otherwise ignored. On another fruiting branch, 12 *P. megacephala* were observed tending a small *H. patruelis* nymph and a 2mm *L. bibilus* larva.

The mean numbers of ants on/in the vicinity of egg batches with (25.4 ± 17.7 ants, n = 7 batches) and without (23.6 ± 17.9, n = 14 batches) lycaenid larvae were not significantly different (Mann-Whitney U: Z = -0.299, p = 0.765).

6.3.4 Changes in *H. patruelis* numbers on fruiting branches following the exclusion of ants

For the purpose of analysis, the numbers of *H. patruelis* adults and nymphs, and ant numbers, were summed within each crop. The mean numbers of *H. patruelis* adults and nymphs per crop for the seven crops was calculated for each of the first five sampling dates after ant exclusion, as were mean ant numbers (Fig. 6.1a-c). Mean ant numbers on unbanded fruiting branches peaked at 95.7 per crop during week 2-3 and decreased to 37.6 on week 8-9 (Fig. 6.1a). The number of ants on unbanded branches through the whole period varied greatly between crops, from 5.0 to 200.2 (a mean of 65.3 ± 68.7 ants per crop on unbanded branches). Again, most ants were *P. megacephala* (99.6% of the 2452 ants recorded in total).

Mean numbers of adult *H. patruelis* were initially similar on banded and unbanded fruiting branches (Fig. 6.1b). With time the numbers on banded branches decreased while those on unbanded branches increased. However, none of these differences were significant (Fig. 6.1b), although weeks 4-5 and 6-7 approached significance. The mean number of nymphs was initially significantly lower on banded than unbanded branches (Fig. 6.1c). However, nymphs increased in number at a much higher rate on banded than unbanded branches, so that by weeks 4-5 and 6-7 there were more nymphs on banded than unbanded branches, although differences were not significant.

Before performing a two-way analysis of variance, the data were transformed by $\sqrt{(x+1)}$, in order to shift them from a Poisson to a Normal distribution (Snedecor & Cochran 1980). The only comparison to approach significance was the difference in adult numbers on banded and unbanded branches (Table 6.10). The absence of a significant interaction term between time and treatment indicates that the length of time after exclusion did not affect differences in numbers between treatment, even when the ANOVA was repeated using only four sample dates (weeks 1-7) (encompassing only one generation).

6.4 DISCUSSION

The presence of tending ants did not benefit *H. patruelis* in any obvious way, but did not harm the homopterans either. Ants were only once recorded as predators of *H. patruelis*, when two small yellow ants were observed removing unhatched eggs from a fruiting branch. However, this group of species occurred at low densities, and were rarely observed tending

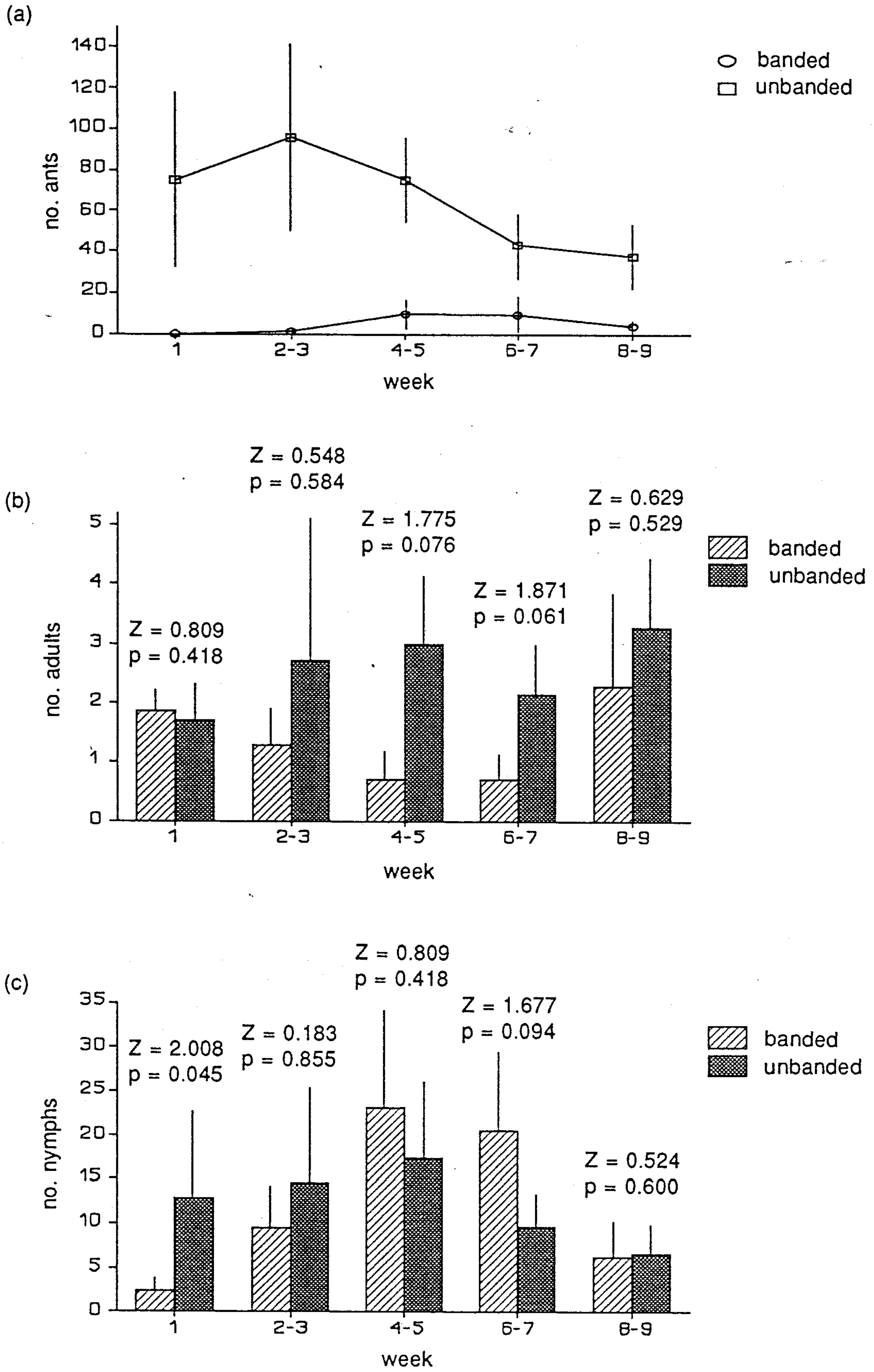


Figure 6.1. Mean number ±/+ 1SE of a) ants, b) *H.patruelis* adults, c) *H. patruelis* nymphs present on banded and unbanded fruiting branches on seven crops over time. Branches were banded on week 1. Wilcoxon Signed-Ranks Z and p values are indicated for each *H. patruelis* sample occasion.

Table 6.10. 2-way ANOVA of *H. patruelis* numbers ($\sqrt{(x+1)}$ transformed), using treatment (banded or unbanded) and time.

H. patruelis stage	source of variation	F	d.f.	p
adult	treatment	3.302	1	0.074
	week	0.446	4	0.775
	interaction	0.580	4	0.678
nymph	treatment	0.0	1	0.991
	week	1.229	4	0.308
	interaction	0.450	4	0.772

H. patruelis (Chapter 4).

H. patruelis nymphs are mobile within a tree, readily dispersing from their natal fruiting branch to others by walking (pers. obs.), and can therefore probably escape any buildup of honeydew and mould. The removal of honeydew by ants may be important to the homopteran when nymphs are occasionally forced to stay in one area, as they might be if they occur on small trees or on trees with small crops. Similarly, although Bach (1991) showed that ant exclusion from scale insects on *Pluchea indica* resulted in increased honeydew accumulation, mould growth and leaf abscision, she believed that these effects were exaggerated because, in natural situations, scale insects occurring without ants were present at lower densities.

Jerath (1967) recorded *Camponotus acvapimensis* Mayr as carrying *H. undata* nymphs from one branch to another on *Acacia farnesiana*, but no such mutualistic behaviour was ever recorded in this study or by Weaving (1980).

The egg parasitoid *Psyllechthrus oophagus* is relatively, but not entirely, immune to predation by *P. megacephala*. Weaving (1980) did not observe any aggression between the two species. Immunity is probably chemically and/or behaviourally based. The random sampling indicated that *P. oophagus* oviposits successfully in the presence of ants and there was no indication of deterrence. Even for parasitoid species which are not ant-immune, high parasitism levels have been recorded in the presence of ants (Washburn 1984; Abe 1992). Furthermore, as the total percentage of eggs parasitised in this study was low, the overall benefit received from ants would be correspondingly small. Weaving (1980) reported much higher parasitism rates by *P. oophagus* in Zimbabwe, where the benefits of ant protection might be detectable. He also reported large fluctuations in parasitism levels between egg batches and sampling dates, as were found in this study.

Two potential methodological problems were evident in the experiment in which ants were excluded from *H. patruelis* egg batches. Ants may have been excluded from the egg batches insufficiently soon after they had been laid, thus reducing or eliminating the potential for parasitism. Secondly, if *P. oophagus* locates egg batches by walking from fruiting branch to fruiting branch, banding would create a bias towards parasitism of unbanded egg batches.

It appears that the entire subfamily Miletinae, to which *Lachnocnema bibilus* belongs, is aphytophagous. *L. bibilus* is an obligate homopteran predator which may supplement its diet with honeydew (Cottrell 1984) and has been recorded as feeding on membracids, cicadellids and psyllids (Clark & Dickson 1971; Cottrell 1984; Migdoll 1987). No negative interactions were observed between ants and *L. bibilus* larvae, implying complete larval immunity, and perhaps a mutualism, as ants might protect the caterpillars from their parasitoids. The caterpillars have previously been recorded in association with ants without being molested by them (Clark & Dickson 1971; Cottrell 1987; Migdoll 1987). Cottrell (1984) recorded that small ant species such as *Pheidole* ignore the larvae, but that larger ant species have been observed tending, carrying and exchanging honeydew with larvae (Cottrell 1984). The adult butterflies also appear largely immune - they have furry legs, adopt a "stilt-legged" posture while feeding on honeydew, and frequently roost in ant colonies at night, presumably for protection (Cottrell 1984). It has been suggested that such predatory lycaenids use homopterans and ants as oviposition cues (Pierce & Elgar 1985).

Initial changes in numbers of adult *H. patruelis* on banded and unbanded fruiting branches are probably a reflection of immigration and emigration, while increases in the numbers of nymphs probably reflects hatching. The increase in adult numbers (and concomitant decrease in the numbers of nymphs) during weeks 8-9 may have been due to adult eclosion. Weaving (1980) and Broad (1966) gave a generation time of about six weeks in Zimbabwe in summer. There are a number of problems interpreting patterns of change in *H. patruelis* numbers on banded and unbanded fruiting branches following the exclusion of ants. Numbers of adults may have increased on unbanded branches due to immigration from other parts of the tree, which is less likely on banded branches due to the strong walking tendency of adults. Adults are probably more likely to fly off a small banded area in search of food or mates than on to it. In addition, the movement of adults might not be in response to ants but to other factors, such as the presence of other adults (*H. patruelis* is gregarious). Nymphs may have increased more rapidly on banded than unbanded branches because they were unable to disperse, and/or because invertebrate predators were unable or less likely to access banded branches to prey on them. The lack of consistency in initial numbers of *H. patruelis*, and particularly nymphs, as well as in the stage of the *H. patruelis* lifecycle at which the exclusion was initiated, pose additional problems. The data from ant-exclusion experiments were therefore not entirely suitable for predicting effects of ant presence on changes in *H. patruelis* densities over a period of time. Ant-exclusion through banding is probably more suitable for sedentary species. Even ant exclusion by other means may not be entirely satisfactory: Cushman & Addicott (1989) and Cushman & Whitham (1991) advocate the general use of ant reduction rather than exclusion experiments as a closer reflection of natural situations.

In addition to *L. bibilus*, a number of invertebrate predators were occasionally recorded preying on *H. patruelis* in this study. A single larva of *Celama* sp. (Lepidoptera: Noctuidae) was recorded preying on *H. patruelis* nymphs. Facultative, opportunistic predation is widespread among phytophagous lepidopteran larvae (Cottrell 1984). Weaving (1980) recorded adult *H. patruelis* captured in spider webs and predicted that salticids and preying mantids might be important predators. He also recorded egg predation by adult coccinellids. Feeding by coccinellids was not recorded in this study but a salticid spider was observed removing an adult *H. patruelis* on one occasion. A neuropteran larva was also recorded feeding on *H. patruelis* eggs on one occasion. No interactions between these species and ants were observed.

The effects of vertebrate predators on *H. patruelis* were not examined but may be considerable. For example, flocks of the Cape white-eye, *Zosterops pallidus*, commonly glean in *F. sur* trees (pers. obs.) and have been observed taking *H. patruelis* on *Hibiscus* (S. Compton pers. comm.). *Zosterops* species are avid consumers of insects (Skead & Ranger 1958; Wearing & McCarthy 1992). Thomas (1988) found that the presence of *Oecophylla longinoda* on *F. sur* in West Africa deterred the removal of fruit by birds and bats. However, *P. megacephala* is much less aggressive and therefore may be less effective in deterring vertebrate predators of *H. patruelis*.

Although no specific benefits to *H. patruelis* of ant presence were detected, this interaction is nonetheless a close one. *H. patruelis* is almost always found in the presence of ants (Weaving 1980; pers. obs.), as are other tettigometrid species (Jerath 1967; pers. obs.). Very rarely a solitary *H. patruelis* adult with a few eggs, or a small batch of eggs on its own, was discovered away from ants (pers. obs.). Obligately tended homopterans often move off if abandoned by ants (Bristow 1984). *H. patruelis* may use ant presence as an oviposition cue, as does the lycaenid *Jalmenus evagoras* (Pierce & Elgar 1985). In addition, it may use the presence of conspecifics or it may arrive at a tree, lay a few eggs, and await discovery by scout ants, which in some systems occurs within a few hours (Buckley 1987b).

H. patruelis is therefore highly dependent on ants in the sense that it is only found in association with them. One explanation for this dependency is that the adult homopterans respond to ant presence not for protection but because ants act as an indicator of good oviposition sites, if the ants have been attracted to the site by previous *H. patruelis* groups (M. Villet pers. comm.). Alternatively, the selective pressures that led to the association may be no longer be evident in the present predator and parasitoid guild, as the enemy species that remain are only able to do so because they are specialists which have overcome the homopterans' ant defense. *H. patruelis* is not subject to generalist predation because of its biology. In the presence of ants the homopteran is protected from generalist invertebrate predators and in their absence, it leaves to look for sites where it will be protected. Elucidating the benefits of ant presence to *H. patruelis* experimentally is therefore difficult because such benefits are intrinsic to the biology of the homopteran. One approach would be to artificially expose the nymphs to generalist predators in the presence or absence of ants, although the ecological significance of such predators at this time is minimal. The homopteran may have originally evolved its dependency on ants for honeydew removal, in order to encourage them and thus to provide protection against predators and parasitoids, including the ants themselves (Cushman 1991; Cushman & Addicott 1991; M. Villet pers. comm.). An ant-tended leafhopper, *Dalbulus quinquenotatus* DeLong and Nault, has a higher honeydew output than its non-tended congeners (Larsen *et al.* 1992), as do some ant-tended aphids (Klingauf 1987). Therefore, even if ant presence had been shown experimentally to benefit *H. patruelis* in terms of honeydew and sap removal in this study, no conclusion can be drawn as to whether this last benefit is original or derived.

7 BENEFITS GAINED BY A *PHEIDOLE MEGACEPHALA* COLONY TENDING *HILDA PATRUELIS* ON A FRUITING *FICUS SUR* TREE

7.1 INTRODUCTION

In associations involving ants, plants and homopterans, the ants are invariably assumed to gain nutritionally in some way (Beattie 1985; Buckley 1987a), even if benefits to the other two parties are conditional or non-existent. However, very few studies have quantitatively demonstrated benefits to ants or other visitors in mutualisms (Cushman & Beattie 1991). Food gains to ants from homopterans are usually in the form of honeydew, but sometimes also through direct predation on the tended homopteran (Buckley 1987a, b). In addition to obtaining nutrients from homopterans, ants may also gain from the plants on which the homopterans are feeding by imbibing sap from wounds (pers. obs.) or nectaries, preying on insects on the plant or on seeds or elaiosomes (Beattie 1985). Ant species differ in their reliance on honeydew; it forms a large and essential part in the diet of many species (Hölldobler & Wilson 1990), but the amount of honeydew entering a colony, both absolute and in proportion to other foodstuffs, often varies with seasonal availability and colony needs (Skinner 1980; Beattie 1985).

Because honeydew-producing homopterans represent one of the most stable and persistent food sources for ants (Carroll & Janzen 1973), continuous usage of the plant by ants over the entire period during which the homopterans are producing honeydew is common (Carroll & Janzen 1973; Hölldobler & Wilson 1990). On a diel scale, ant foraging patterns and rates in general may be related to temperature and humidity, patterns of food production and availability, and interspecific competition (Whitford 1978; Andersen 1983; Hölldobler & Wilson 1990). In the longer term, changes in seasonal weather parameters such as temperature, humidity and daylength become important, and interact with food availability and quality as well as the reproductive state and nutritional needs of the ant colony (Beattie 1985; Andersen 1983; Hölldobler & Wilson 1990). Distance to the food source, as well as its size and quality, and colony size can all affect the number of ants foraging at any particular site (Cushman 1991).

The fitness gain by a colony from a food source, in terms of worker production and reproductive output, is a complex function of the type of food brought in and its use by the colony, in combination with colony parameters such as size, age, reproductive and nutritional state, and "cost" allocation to defense and foraging (Beattie 1985; Traniello 1989; Hölldobler & Wilson 1990). Independent of its quantity and quality, the relative contribution of one foraging site to the colony economy can therefore be expected to depend on the number, size and quality of other food sources, as well as on colony size.

Pheidole megacephala, a cosmopolitan tramp species of African origin (Wheeler 1922), is considered a generalist myrmicine (Andersen 1992) acting as a scavenger, predator and exudate collector. It forms large polygynous and polydomous colonies and is an aggressive, dominant species (Steyn 1954; Greenslade 1971). Two worker castes are present - the "megacephalic" soldier caste remains largely in the nest while the small minor workers often forage in large numbers and display mass recruitment using trail pheromones (Attygale & Morgan 1985).

P. megacephala is the most important ant species (Chapter 4) found on the Cape fig, *Ficus sur*, in the Grahamstown region of South Africa. It tends the polyphagous tettigometrid *Hilda patruelis*, which feeds on the figs and fruiting branches of *F. sur*. *P. megacephala* also feeds on sap from wounds inflicted by various insects and preys on insects visiting figs, including fig wasps. The ant preys on wasps at various stages of the fig cycle: those entering female-phase figs, those ovipositing through the fig wall, and those emerging from male-phase figs. It also enters postfloral-phase figs to remove male wasps and possibly anthers and other plant material. As *P. megacephala* largely restricts its foraging to the fruiting branches and access trunks of *F. sur* (Chapter 4), it does not come into much contact with foliar-feeding insects. Finally, it is possible that *P. megacephala* removes fig seeds and material from below the tree.

The aim of the research described in this chapter was to assess the foraging patterns of a *P. megacephala* colony on a fruiting *F. sur* tree through one fruiting cycle, and to examine the benefits accruing to the ants. This was achieved through the monitoring of ant numbers and the amounts of food brought from the tree throughout the period. No assessment was made of colony size, other gains, such as those from fallen figs and seeds, or of alternative food sources elsewhere.

7.2 MATERIALS AND METHODS

7.2.1 Activity levels of *P. megacephala* on a fruiting tree

A tree at site 2 with very immature figs and detectable *P. megacephala* activity was selected and monitored through its entire fruiting period. The tree was also selected because it was only accessible to ants via a single trunk and had a synchronous crop of figs. To assess foraging parameters, the number of *P. megacephala* passing a line on the trunk over a five minute period was counted at midday twice a week for the duration of the fruiting period of

98 days. Ants moving up the trunk were counted separately from those moving down. On each occasion, approximately 20 ants moving each way were collected using an aspirator. These were killed using ethyl acetate and their wet weight was recorded using a Cahn C-31 microbalance. Any items which these ants were carrying, such as fig wasps, were recorded and, where possible, identified. On a different occasion a number of fig wasps was collected, dried at 64°C for four days, and weighed, to obtain an estimate of the fig wasp biomass taken from the tree by the ants.

On two days during the monitoring period (days 48 and 73), the numbers of *P. megacephala* moving up and down the trunk were recorded in the same way as above, but at regular (3-4hr) intervals for a period of about 18hrs (6am - midnight). On each occasion three counts were made, one after the other, of ant numbers in each direction in order to assess the variability of within-sample counts. For night-time counts, a torch covered in red cellophane was used, so as not to disturb the ants. Ambient temperatures were recorded on each counting occasion.

To compare the relationship between the numbers of ants moving on the trunk with the numbers per fig on the tree, the numbers of *P. megacephala* and *H. patruelis,* and the numbers and stages of figs on three fruiting branches at less than 2m from the ground on the tree were recorded at weekly intervals. This also allowed an assessment of changes in *H. patruelis* numbers over the fruiting period. The total number of figs on the tree was estimated and their developmental stages recorded once a week. Data collection was terminated after 98 days, when the figs had ripened and had fallen to the ground or been eaten, and ant numbers on the trunk had fallen to a low level.

Weekly rainfall and mean temperatures were plotted for the duration of the experiment, using data from the Rhodes University Weather Station.

7.2.2 Chemical analyses of *P. megacephala* workers

To obtain material for the analysis of carbohydrates and protein collected by *P. megacephala* tending *H. patruelis*, ants were collected at regular intervals from the trunks of two trees at site 1 over a period of three weeks, using an aspirator. Ants were collected over an extended time period because their removal disturbs other ants on the trail, after which they scatter and become difficult to collect. In addition, a several-week timespan should have encompassed any variability in honeydew or sap concentration/composition. Two sets of ants were collected from each tree: those with swollen and those with non-swollen gasters. This maximised the volume of gaster contents collected in order to facilitate chemical analysis. However, it also excluded the possibility to determining the mean mass of gaster contents being brought down the tree to the nest, as a few ants with swollen gasters were moving away from the nest and many returning to the nest had non-swollen gasters. Ants were killed, and frozen, and later weighed.

The samples from these two trees were oven-dried to constant mass at 58°C for 67 hours and their dry masses recorded on a Cahn C-31 microbalance. 1.0ml distilled water was added to the samples. They were then ground using a pestle and mortar, homogenised with a sonicator and centrifuged. 0.1ml of supernatant was diluted to 1.0ml with distilled water. For the analysis of protein concentration the Folin-Ciocalteu assay (Clark & Switzer 1977) was used. The absorbance was read on a spectrophotometer at 500nm and the concentration determined by comparison to a standard curve. For carbohydrate analysis, Nelson's test for equivalents of reducing sugar (Clark & Switzer 1977) was used. The absorbance was read at 540nm and concentration determined by comparison to a standard curve. For both tests the ant extract was diluted again by a factor of 10 and the tests were performed on two replicates.

The mean protein and carbohydrate content per ant was calculated for each sample and swollen versus non-swollen gaster samples were compared.

7.3 RESULTS

7.3.1 Activity levels of *P. megacephala* on a fruiting tree

The study was conducted from mid-February to the end of May, a period of 98 days covering late summer to early winter. Temperatures were therefore initially fairly high, but showed a slow steady decline over the monitoring period (Fig. 7.1). The highest rainfall (15.1mm) was recorded during the third week of monitoring.

Female-phase figs appeared on the tree between days 1 and 9 (Fig. 7.2). All figs had reached the interfloral phase by day 34, and male-/postfloral-phase figs began to appear on day 67. The last figs disappeared from the tree on day 90.

Numbers of *P. megacephala* moving up the trunk were very similar to those moving down over the whole fruiting period (Fig. 7.3). Ant numbers increased fairly rapidly both on the trunks and on the three fruiting branches (Fig. 7.3, 7.4a). Numbers on the fruiting branches and trunks agreed reasonably closely and corresponded to the changes in *H. patruelis* numbers (Fig. 7.4b). Low *P. megacephala* numbers on the trunk on day 21 (Fig. 7.3) corresponded to a peak in rainfall (Fig. 7.1), but ant numbers on the fruiting branches that day were not affected. Turnover, but not relative densities, therefore declined here. A simultaneous sharp drop in *P. megacephala* numbers on the fruiting branches and trunk on day 34, as well as of *H. patruelis* and figs, was due to the destruction of about 100 heavily infested figs by livestock.

Both ant and *H. patruelis* numbers peaked during the relatively long interfloral phase (Fig.

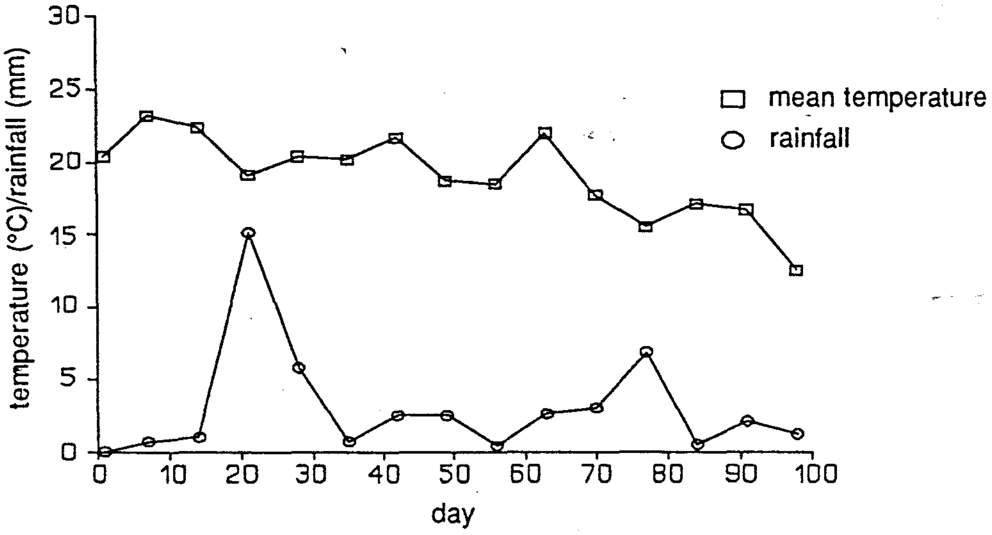


Figure 7.1. Mean weekly temperatures and weekly rainfall over the monitored *F. sur* tree fruiting cycle, from mid-February to the end of May.

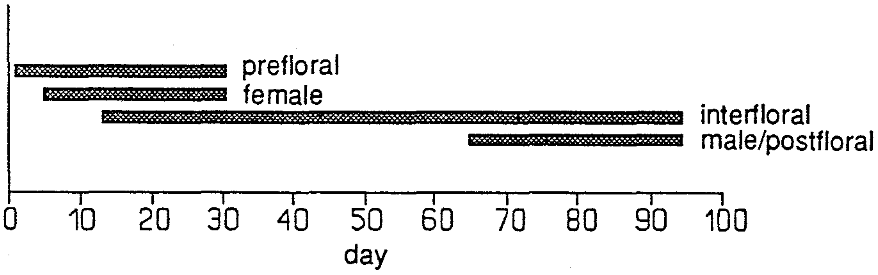


Figure 7.2. Developmental stages of figs present on the *F. sur* tree on each sampling date through the monitoring period.

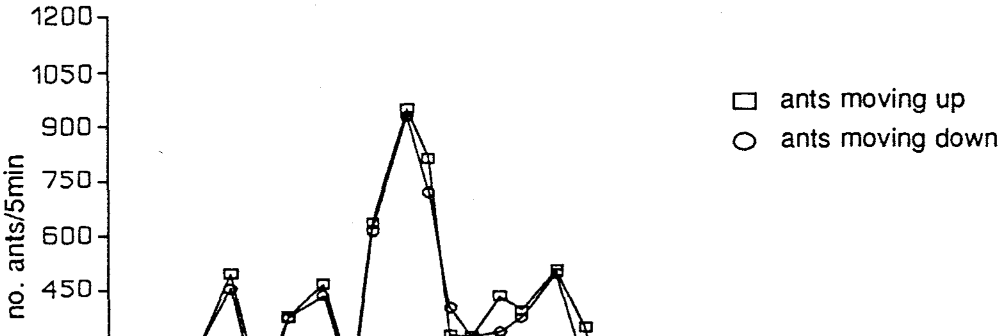


Figure 7.3. Numbers of *P. megacephala* workers crossing a line on the *F. sur* tree trunk in 5min at midday on each sampling date.

7.3, 7.4a, b) and then declined to virtually zero after the crop had ripened and disappeared. *P. megacephala* numbers on the fruiting branches decreased earlier than those on the trunk. The ants on the trunk were presumably moving higher up the tree and may reflect the movement of *H. patruelis* from lower to higher parts of the tree, or the earlier maturation and emigration of *H. patruelis* on the lower part of the tree.

The recorded fig numbers (Fig. 7.4c) are only for the three fruiting branches. Fig stages were the same for the whole tree (Fig. 7.2) but figs disappeared from these three branches after day 73. The presence of figs on other parts of the tree after these have disappeared is indicated by the presence of ants carrying wasps on the trunk. In addition, figs were in the male phase on other parts of the tree earlier than those on the three fruiting branches, although this was not recorded (Fig. 7.2), as ants were recorded with male fig wasps on the trunk at this time (Fig. 7.5).

Ant numbers were high at the figs' female phase but only a low percentage of the ants were carrying captured females of the internally ovipositing wasp species (Fig. 7.5). These captures recorded on days 42 and 45 were probably from late-stage figs. The captured females of externally ovipositing wasp species may have been ovipositing on interfloral-phase figs, or individuals of the next generation emerging from male-phase figs. The majority of the 27.5 (each part considered half a wasp) wasps (61.8%) brought down over the whole period were male wasps that had emerged from male-phase figs (Fig. 7.5; Table 7.1). Ants were recorded carrying pieces of females on several occasions but only whole males.

The dry masses of females of both species of fig wasps weighed more than their male counterparts (Table 7.2). No *Sycophaga cyclostigma* or *Apocryptophagus* wasps were obtained for weighing. *S. cyclostigma* can be expected to be of similar mass to *C. capensis*, while *Apocryptophagus* spp. have the highest masses of the species found in *F. sur* around

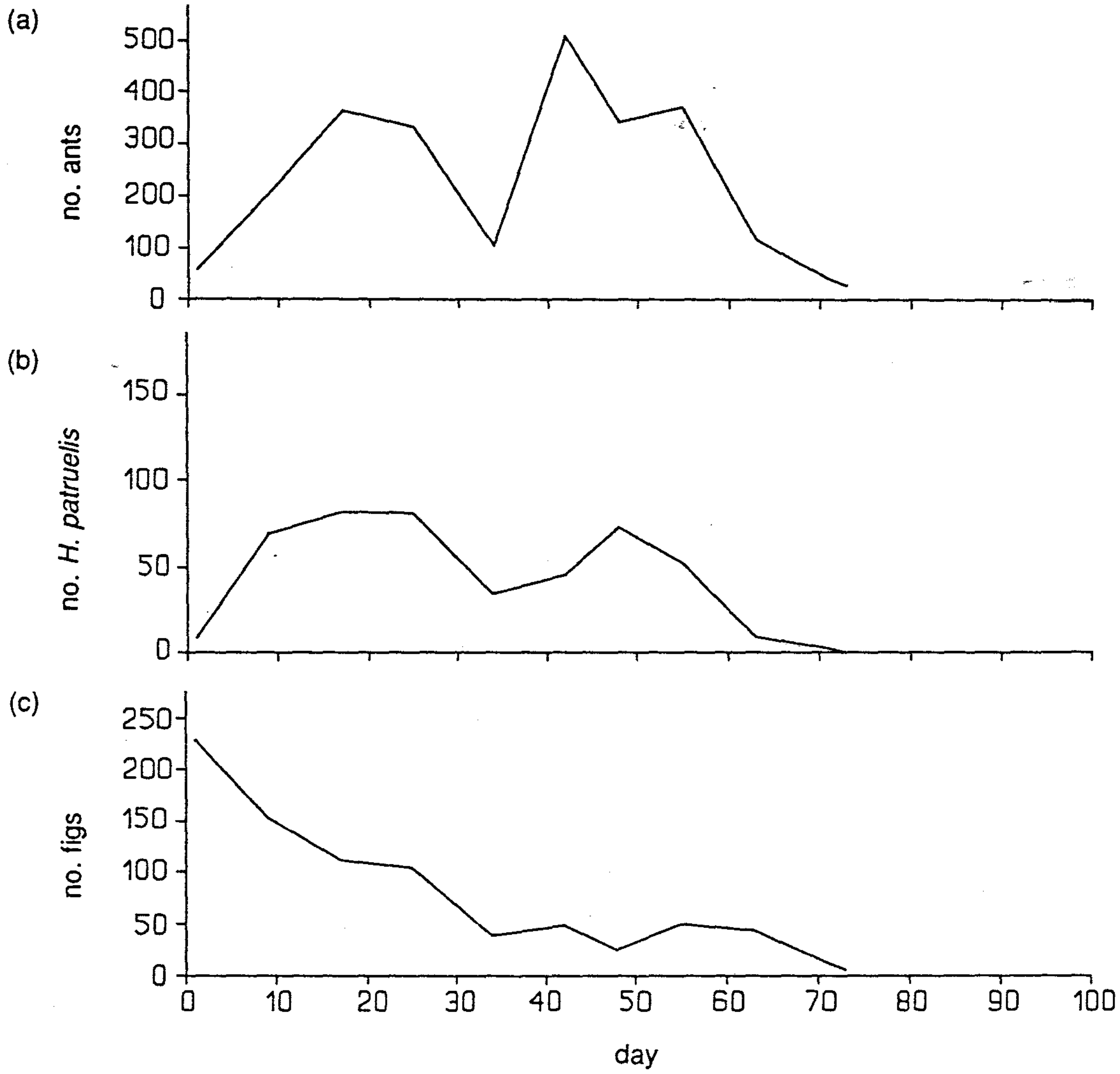


Figure 7.4. Numbers of a) *P. megacephala*, b) *H. patruelis* and c) figs on three fruiting branches of the *F. sur* tree on each sampling date.

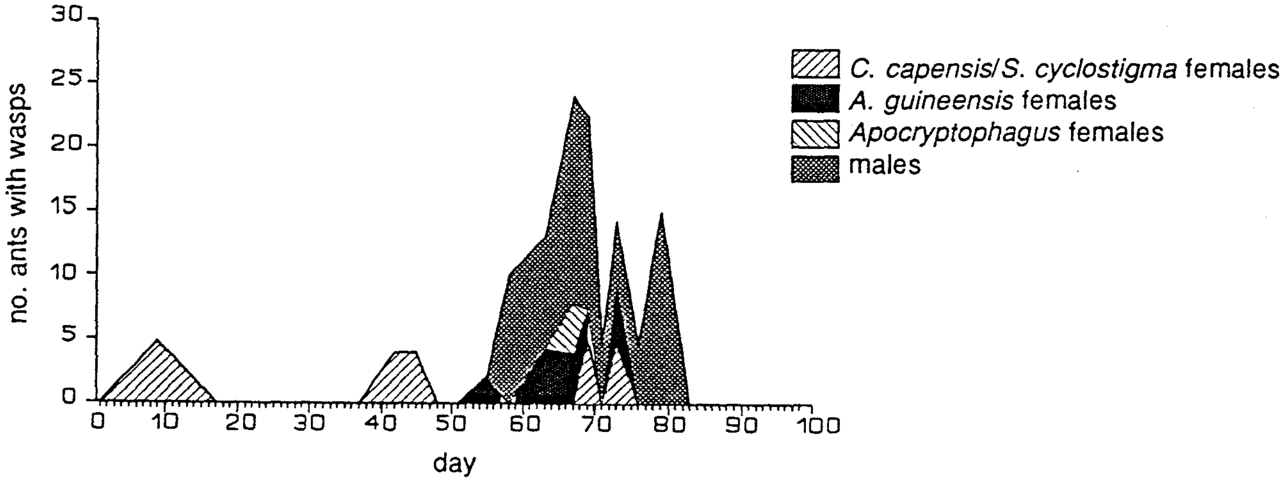


Figure 7.5. The percentage of *P. megacephala* leaving the *F. sur* tree carrying particular fig wasps on each sampling date.

Table 7.1. Numbers of fig wasps collected from 506 *P. megacephala* workers walking down the trunk on 24 sample dates (mean no. ants per date = 21.1 ± 5.2).

wasp species	sex	no. removed		no. sample days present (%)
		whole	part	
C. capensis/ S. cyclostigma	female	5	1	5 (20.8)
A. guineensis	female	3	2	5 (20.8)
Apocryptophagus spp.	female	1	0	1 (4.2)
all	male	17	0	8 (33.3)
no species				11 (45.8)

Table 7.2. Dry masses of fig wasps.

wasp species	sex	no. weighed	total mass (mg)	mass per wasp (mg)
C. capensis	female	21	2.905	0.1383
	male	8	0.872	0.1090
A. guineensis	female	21	2.653	0.1263
	male	21	1.167	0.0556

Grahamstown.

Diel activity patterns of *P. megacephala* on the trunk varied between the two monitoring days mainly in terms of the number of ants active (Fig. 7.6a). Day 1 fell on day 48 of the long-term monitoring period and at the peak of *P. megacephala* activity, while day 2 fell on day 73, when most of the crop had disappeared and overall *P. megacephala* activity was low. Changes in numbers moving along the trunk within each day corresponded closely to temperature changes (Fig. 7.6b). On day 1 *P. megacephala* activity was initially very low but increased rapidly until 4pm (T_{max} was at 1-2pm) and then declined slightly. Large numbers of ants were still active at midnight, however. This corresponded to a high temperature of about 20°C at that time. On day 2 both ant numbers and temperature were lower but more constant. Again ant numbers peaked in the late afternoon following a T_{max} at 1-2pm. *P. megacephala* numbers moving up the trunk were similar to those moving down at each sample point on both days. There was no evidence of a consistent time lag between numbers going up and down the tree. A difference in the temperature curve between the two days, in combination with a difference in the total number of ants visiting the tree on the two days due to the different (fig) developmental stages on which they fell, therefore appears to account for the observed between-day variation.

In order to assess the amount of honeydew and sap brought back to the nest by the *P. megacephala* colony foraging on the monitored tree, it is necessary to take both diel and longer-term patterns of *P. megacephala* activities into account. The ratio of mean ant numbers per 5min period down the trunk over the whole day to the number at midday varied from 0.8 to 1.5 (Table 7.3). If it is assumed that these ratios are representative, the mean number of ants moving down the trunk per 5min for the whole of each long-term monitoring day can be estimated, and thus

$$T_{down} = \sum_{i=1}^{n} [k(x_i y_a / x_a)(d_{i+1} - d_i)]$$

where T_{down} = total no. *P. megacephala* moving down trunk over fruiting period,

a = diel-pattern monitoring days

i = long-term monitoring days (n = 24),

x_i = no. *P. megacephala*/5min moving down trunk at midday on day i,

y_a = mean no. *P. megacephala*/5min moving down trunk over whole day on day a (a=1, 2),

x_a = mean no. *P. megacephala*/5min moving down trunk at midday on day a (a=1, 2),

k = 288, conversion factor from 5min to 24hr,

$d_{i+1}-d_i$ = interval in days between monitoring day i and i+1

From diel-pattern day 1 (a = 1) $T_{down} = 5.87 \times 10^6$ while from day 2 (a = 2) $T_{down} = 10.827 \times 10^6$. A more conservative ratio of 0.667 (which assumes that the number of ants descending from the tree in 5 minutes over midday is 1.5 times that for the mean per 5 minutes over a 24-hour period), takes into account the possibility of low *P. megacephala* numbers from 12am-6am, when monitoring was not carried out, and yields a $T_{down} = 4.92 \times 10^6$. Thus between five and ten million ants moved down the trunk back to the nest over the entire fruiting period.

The mean mass of 20 ascending *P. megacephala* (n = 31 groups) was 5.36 ± 0.82mg, for 20 descending *P. megacephala* (n = 31 groups) 6.22 ± 0.92mg and the difference in mass was therefore 0.84 ± 0.47mg. Thus individual ascending ants weighed an average of 0.268 ± 0.041mg each, descending ants weighed 0.311 ± 0.046mg each and the difference was 0.042 ± 0.024mg. Five million ants would therefore carry down 210 ± 118g of liquid gaster contents and 10 million would carry down 420 ± 235g. If the whole fruiting period was divided into four (Table 7.4), there was no significant difference in the mass of honeydew brought down per 20 ants between these periods (1-way ANOVA F = 2.438; d.f. = 3,16; p = 0.102).

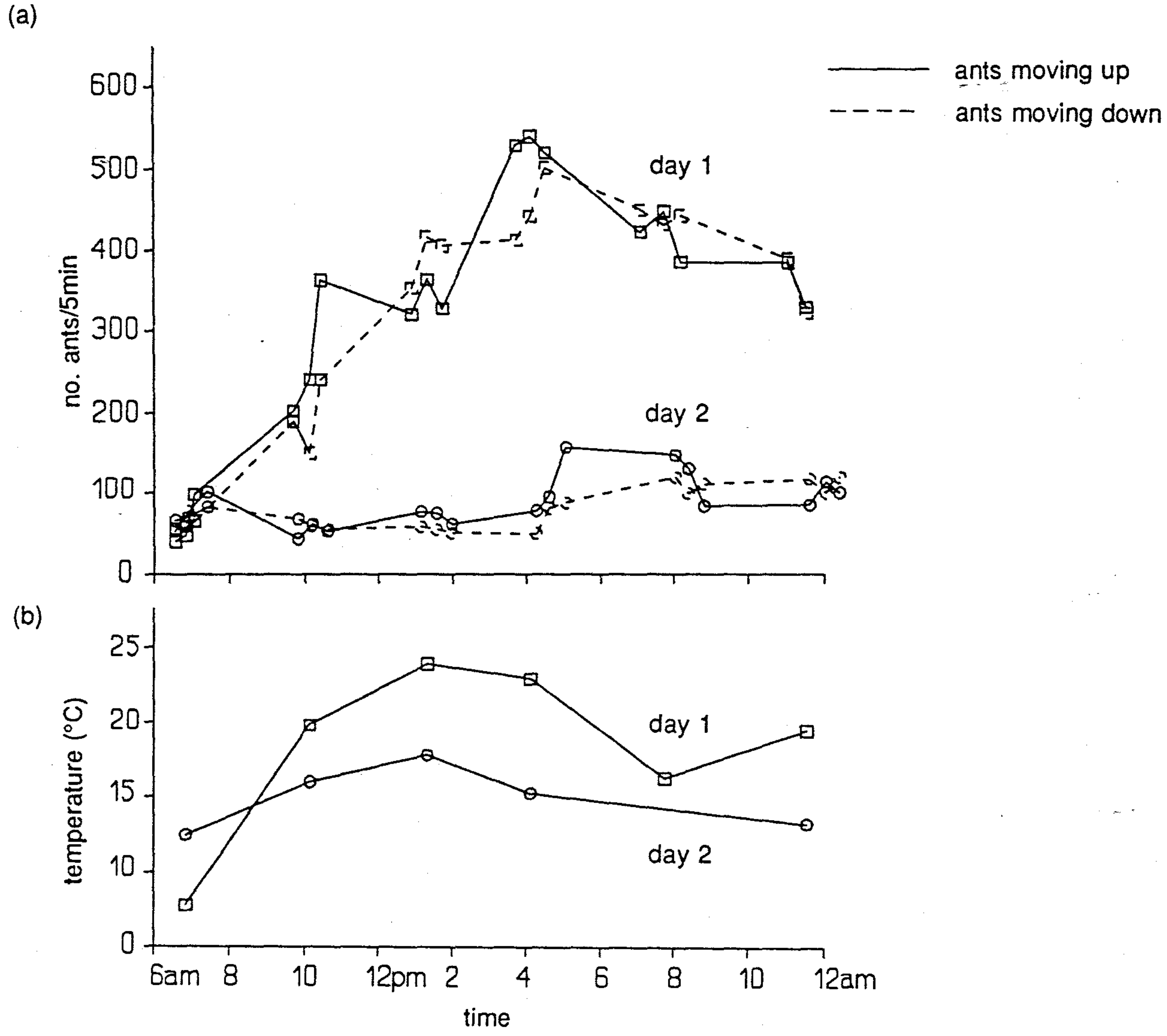


Figure 7.6. Diel patterns of *P. megacephala* activity on a fruiting *F. sur* tree on two different days. a) Numbers of ants crossing a line on the trunk in 5min over the 18hr period on each day. b) temperatures over the monitoring periods.

Table 7.3. Ratio of mean number of *P. megacephala* descending the tree in 5 minutes at midday to the number descending the tree in 5 minutes for the whole day on days 1 and 2.

	mean no. ants down/5min (whole day)	mean no. ants down/5min (midday)	ratio whole day:midday
day 1	313.4 (n = 17)	392.0 (n = 3)	0.799
day 2	80.5 (n = 18)	54.7 (n = 3)	1.473

Table 7.4. Mean masses of honeydew brought down from the tree by 20 *P. megacephala* workers over four periods within the fruiting cycle.

days	no. samples	mass (SD)
1-25	5	1.0 (0.580)
30-45	5	1.274 (0.387)
48-63	5	0.868 (0.452)
69-79	5	0.462 (0.497)

Table 7.5. Sizes, wet and dry weights and dry:wet ratios of ant samples.

tree	gaster state	no. ants	per-ant wet weight (mg)	per-ant dry weight (mg)	dry/wet weight
1	swollen	456	0.255	0.102	0.399
	non-swollen	578	0.194	0.084	0.431
2	swollen	491.3	0.271	0.108	0.398
	non-swollen	631	0.215	0.090	0.419

7.3.2 Analysis of *P. megacephala* gasters for soluble protein and carbohydrate contents of collected sap and honeydew

The two samples were dried to 40-43% of their wet weight (Table 7.5). Ants with swollen gasters lost a higher percentage of their weight than non-swollen ants (indicating a higher water content), but still weighed more after drying.

Both ant samples lost approximately 70% of their gaster weight on drying (Table 7.6), implying that gaster contents consisted of 70% water by weight. An individual ant with a swollen gaster therefore contained 18µg of dry weight substances.

Between 14.9 and 16.5µg of protein per ant was detected using the Folin-Ciocalteu assay (Table 7.7); there appeared to be no difference in protein content of ants with swollen and non-swollen gasters, although this could not be statistically tested.

The levels of reducing sugars were much higher in swollen than non-swollen ants for both samples (Table 7.8). Swollen ants contained at least four to five times as much reducing sugar as non-swollen ants.

Comparing masses obtained from chemical analysis with those from weighing indicates that at least 10.4µg (57.7%) of the 18µg dry gaster weight comprised reducing sugars for both samples.

7.4 DISCUSSION

The *P. megacephala* colony in this study foraged on the fruiting branches of a *F. sur* tree throughout the tree's fruiting cycle, collecting honeydew from the *H. patruelis* feeding on the figs and probably sap from their feeding tubes, and preying on the fig wasps visiting the tree. Ant activity changed on a diel as well as a longer term scale.

Table 7.6. Per-ant weight changes of gaster contents (= per-ant swollen - non-swollen weight) with drying.

tree	state	per-ant gaster weight (mg)	per-ant gaster weight loss with drying (mg) (%)
1	wet	0.061	0.043 (70.5)
	dry	0.018	
2	wet	0.056	0.038 (67.9)
	dry	0.018	

Table 7.7. Folin-Ciocalteu assay of protein concentration: sample absorbances, concentrations and differences for swollen vs non-swollen ants.

tree	state	absorbance (500nm) (n = 2)	concentration (μg/ml)	per-ant protein mass (μg)	mass difference (μg)
1	swollen	0.109	80	16.3	-0.2
	non-swollen	0.142	104	16.5	
2	swollen	0.106	77	14.9	-0.2
	non-swollen	0.137	102	15.1	

Table 7.8. Nelson's test for equivalents of reducing sugar: sample absorbances, concentrations and differences for swollen vs non-swollen ants.

tree	state	absorbance (540nm) (n = 2)	concentration (μg/ml)[1]	per-ant CHO mass (μg)	mass difference (μg)
1	swollen	0.721	67.9	13.8	10.5
	non-swollen	0.219	20.7	3.28	
2	swollen	0.706	66.2	12.8	10.4
	non-swollen	0.173	16.2	2.39	

1: this assumes that a reducing equivalent of glucose has the same molecular weight which is only true for monosaccharides; di- and trisaccharides have a higher mass per reducing equivalent.

7.4.1 Diel activity patterns

The diel patterns of ant activity depend on the physiological tolerances of the species in combination with the ambient temperature-humidity envelope (Hölldobler & Wilson 1990). In mesic temperate environments, such as the Grahamstown sites used in this study, foraging peaks are often during the middle of the day. Many species are capable of shifting the peak foraging time from day to day depending on the vagaries of the environment (Whitford 1978; Hölldobler & Wilson 1990) and seasonally (Whitford 1978; Briese & Macauley 1980; Andersen 1983). Differences in physiological tolerances between sympatric species may have evolved in order to decrease competition by temporal partitioning (Andersen 1983), although differences in diel foraging time may also relate to the food type eaten (Whitford 1978).

Diel patterns of *P. megacephala* activity were temperature related (humidity was not measured). Direct competition with other ant species was not likely to influence these patterns because no other ant species was exploiting the tree in significant numbers. It is possible that *H. patruelis* excretion rates varied over the diel period (e.g. Lei & Xu 1993; but see Mittler 1958) and thus indirectly affected *P. megacephala* foraging rates. However, the mass of honeydew carried by *P. megacephala* did not vary in a consistent way through the day. *P. megacephala* is considered a cold- and high humidity-tolerant species (Greenslade 1971a, 1972) and is mainly a nocturnal forager in hotter areas (Steyn 1954; Carnegie 1960; Greenslade 1971a, 1972). Carnegie (1960) studied diel patterns of *P. megacephala* activity on trunks of trees on which the species was tending scale insects. Ant activity in relation to temperature was found to be very similar to that described in this study - during the summer activity continued through the night. A slight time lag in the number of ants moving up and down the trunk led Carnegie to believe that a large number spent the night in the tree when the temperature dropped below activity level, but this was not investigated in the present study.

7.4.2 Longer term foraging patterns and levels

The level of recruitment to a particular food source exhibited by ants depends on the nutritional needs of the colony, the availability of alternative food sources, the distance from the colony and the quantity and quality of the food source (Buckley 1987b; Sudd 1987; Hölldobler & Wilson 1990; Cushman 1991), as well as the prevailing weather conditions. Recruitment levels will therefore change with time if these parameters change.

The numbers of *P. megacephala* on the trunk and in the tree over the fruiting period appeared to correlate primarily with changes in *H. patruelis* numbers and only secondarily to changes in temperature and rainfall. The numbers and sizes of *H. patruelis* individuals increased during the first few weeks of crop development. While the presence or direction of change in honeydew production rates between first instar and adult is unknown for *H. patruelis* (see below), the increased number of individuals present should have resulted in increased honeydew and sap availability with time and therefore increased potential ant recruitment. It is possible that ants were also responding to some other factor such as changes in nutritional needs in the nest or a change in phloem sap quality via honeydew quality (Auclair 1963; Maurizio 1975). The presence of large numbers of emerging fig wasps may also have resulted in increased recruitment at that time and may explain the last peak in Fig. 7.1b. In this tree and several others, *P. megacephala* nests, or part of them, were situated directly below the trees, probably resulting in low travel costs and possibly indicating the importance of the tree to the colony. Nevertheless, each colony must utilise other food sources, particularly when the tree is not in fruit, either through scavenging for protein, predation or exploiting other sap or honeydew sources.

7.4.3 Honeydew composition

Although ants in this study may have imbibed sap from *H. patruelis* feeding tubes, their major food was certainly honeydew. Therefore only honeydew composition is considered here. Honeydew typically contains large amounts of reducing sugars in the form of fructose and glucose, as well as non-reducing sugars and oligosaccharides in the form of sucrose, melezitose and trehalose (Auclair 1963; Tsuiki *et al.* 1963; Klingauf 1987). Various amino acids are present, often in substantial concentrations (Auclair 1963; Maurizio 1975). Strong (1965) found 0.60% lipids (dry weight) in the honeydew of the aphid *Myzus persicae* (Sulzer). The composition and complexity of honeydew varies from species to species - sometimes sugars are replaced or accompanied by sugar alcohols (Maurizio 1975).

The dry weight of honeydew ranges from 5-27% of its wet weight (Auclair 1963; van Hook *et al.* 1980; Klingauf 1987). Carbohydrates form the bulk of the dry weight (88-95% Auclair 1963; Maurizio 1975), with the proportions of different sugar types varying greatly, and reducing sugars forming up to 51.5% (Auclair 1963). Amino acids form from 0.2-16.1% dry weight (Auclair 1963; Maurizio 1975; Lei & Xu 1993) while vitamins, minerals and other substances contribute a smaller fraction. A dry weight of 30% for the gaster contents of *P. megacephala* is therefore not exceptionally high. At least 58% of this comprised reducing sugars, and probably mainly fructose and glucose. Amino acid levels were low and the chemical assay used did not show any differences in amino acid levels in swollen and non-swollen ants. Non-reducing sucrose and oligosaccharides probably constitute the bulk of the remaining 42% dry weight of gaster contents.

7.4.4 Honeydew excretion rates

Rates of honeydew excretion by various homopterans - mainly aphids but also coccids, pseudococcids and aleyrodids - have been investigated. Feeding and excretion rates are dependent on the species and developmental stage of insect, the host plant species part, and phloem composition, the time of day and year, the weather conditions or the presence of ants (Auclair 1963; van Hook *et al.* 1980; Klingauf 1987; Lei & Xu 1993). Most aphid species excrete 0.04-1.42µl/10hr/individual (Auclair 1963) or 1.65-8.20 mg dry honeydew/day/mg dry aphid (van Hook *et al.* 1980). The aphid *Tuberolachnus salignus* (Gmelin) on *Salix* had an exceptionally high rate of 4.5-17.1µl/10hr/individual (Auclair 1963) or 30.8-122.7mg/day/mg (van Hook *et al.* 1980). Excretion rate data quoted by other authors (Maurizio 1975; Klingauf 1987; Lei & Xu 1993) generally fall within the same range. Two aphid species were found to produce 5mg and 10mg (= 50 and 100µl) dry weight honeydew respectively during their development from first instar to adult (Klingauf 1987).

Assuming a specific gravity of 1.03 (van Hook *et al.* 1980; Klingauf 1987) for *H. patruelis* honeydew and sap, the mean volume brought down by each ant for trees 1 to 3 is 0.0408µl, 0.0592µl and 0.0544µl respectively, the second and third trees having higher values due to the selection of ants with distended gasters only. Over a period of 100 days 210-420g of honeydew and sap is removed from the tree, and therefore a mean per day of 2.10-4.20g or 2.04-4.08ml. Using data from vertical stratification studies (Chapter 4) and assuming this was constant through the fruiting period, a mean of 316 *H. patruelis* on the tree each day was calculated. Thus each *H. patruelis* was estimated to produce 6.5-12.9µl of honeydew per day, a fairly high excretion rate in relation to values for other homopterans. However, because ants also remove some sap from *H. patruelis* feeding tubes, the use of gaster contents to calculate excretion rates will result in a slight overestimate of honeydew production rates.

7.4.5 Energy and fitness gains

Ant species vary in the proportion of their food intake that is made up of honeydew (Way 1963), but in a number of species it constitutes a large part of the diet (Way 1963; Carroll & Janzen 1973; Skinner 1980; Hölldobler & Wilson 1990). Cushman & Beattie (1991) have pointed out, however, that very few studies have quantitatively demonstrated that visitors in mutualistic associations benefit from the association in terms of increased fitness. In the context of ant-homopteran associations, benefits to the ants of tending homopterans need to be quantified in terms of the changes in reproductive fitness which a colony experiences in the presence and absence of a honeydew source (Carroll & Janzen 1973; Cushman & Beattie 1991).

Controversy exists as to whether honeydew can form a "complete diet" for an ant species. Sugars are thought to have their primary importance in providing foragers with energy (Carroll & Janzen 1973) and are either fed preferentially to foragers or retained by foragers depending on the species and colony state (Markin 1970; Beattie 1985), whereas protein is fed preferentially to larvae and queens (Markin 1970; Beattie 1985). Degen *et al.* (1986) showed that a *Polyrhachis simplex* worker feeding on honeydew gained between 4.4 and 9.4 times the energy which it expended in collecting the honeydew. Lipids are also essential for normal metabolism (Beattie 1985). While ant colonies may be able to survive on the protein content of honeydew while other protein sources are scarce (Way 1963; Hölldobler & Wilson 1990), protein is essential to growth. A protein deficiency affects species in different ways, resulting in the production only of workers or alates, or of small pale workers (Way 1963; Beattie 1985). Almost all ant species exploit a protein source when it is available (Buckley 1987a).

Ants sometimes not only collect honeydew from homopterans they attend; they also prey on them and therefore obtain a source of protein. The decision to prey rather than tend depends on the amount or quality of honeydew produced, the distance to the nest, and colony nutritional requirements, i.e. an optimisation of the cost to benefit ratio (Buckley 1987a, b; Cushman 1991). However, there is no indication either from this study or others (Weaving 1980; Compton & Robertson 1988, 1991) that *P. megacephala* ever preys on *H. patruelis*.

The *F. sur* tree studied here provided a *P. megacephala* colony with 210-420g honeydew and therefore 65-130g dry honeydew (at 31% dry weight) over the period of a single fig crop. The carbohydrate content translates to 39-79g (at 60% dry weight carbohydrate) or 59-117g (at 90%). Skinner (1980) quotes an energy content of about 16kJ/g for mono- and disaccharides. The energy provided by the honeydew and sap therefore was in the range of 624-1872kJ. Captured wasps and other prey items provided the bulk of protein obtained from the tree. If we assume that the proportion of the ants collected with wasps is representative, an estimated 537-1073 wasps were brought down in total and therefore 59.1-118.0mg, if a mean mass per wasp of 0.11mg is used (the mean of *C. capensis* and *A. guineensis* male and female masses). Using Skinner's (1980) figure of 23.9kJ/g for insect material, this equates to 1.41-2.82kJ of energy. This is likely to be an underestimate of the protein removed from the tree because large, infrequent items such as caterpillars may have been missed, or small pieces of insects may have been brought down in the crop. Small pieces of food carried in the mandibles may also have been overlooked.

Few studies have quantified the amounts of honeydew brought into a nest over extended periods, and their findings vary widely - between 10kg and 230kg per season for *Formica rufa* L. (Skinner 1980) and 2.4kg per season for *F. pratensis* Retz., which has smaller colonies (Jensen 1978b). However, *F. rufa* individuals are much larger than those of *P. megacephala* and each ant brings down 150 times the weight of honeydew carried by individual *P. megacephala* (Skinner 1980). In addition, *F. rufa* colonies contain up to 100000 individuals (Hölldobler & Wilson 1990) in comparison to 8250-20000 ants (n = 2) and a mass of 1.16-4.25g for a *P. megacephala* colony (W. Coetzer unpubl. data).

During a given season an ant colony has an ergonomic phase, during which worker numbers are built up, followed by conversion to reproductives during the breeding season. Hölldobler & Wilson (1990) consider energy to be a reasonable measure of colony fitness during the ergonomic phase, as all colony processes can be converted into energy equivalents. Foraging success, brood care and other such activities can be translated into energy gained; protective activities resulting in decreased mortality, into energy saved; and metabolism and mortality into energy lost. The biomass accumulation rate and total can be converted into net energy assimilation. If the energy required for the total *per annum* production of workers and reproductives and for respiration is known, an estimate can then be made of the contribution of a particular food source to the energetics of the colony. Few studies have so far addressed aspects of colony energetics (e.g. Rogers *et al.* 1972; Jensen 1978a; Lighton *et al.* 1987). Rogers *et al.* (1972) quantified energy flow in *Pogonomyrmex occidentalis* (Cresson) colonies by measuring colony respiration and secondary production rates and calculated that a colony used 195.9kJ per year for the production of individuals and 1751kJ per year in respiration. The average colony contained 4123 individuals (including alates, larvae and pupae) and produced 2032 workers and 315 alates per year. The dry weight for a *P. occidentalis* worker is 3.0mg and for all workers in the colony 8.06g. A high *per annum* rate of turnover of individuals has also been reported in a number of other studies and appears to be typical (Jensen 1978a). Therefore we can expect that an energy gain of 624-1872kJ from honeydew and 1.41-2.82kJ from wasps into a *P. megacephala* colony with 20000 ants and a mass of 4.25g might provide the colony with a high percentage of its energy needs, although without quantification of respiration and production rates and other necessary parameters, no conclusive predictions can be made.

8 VARIABILITY IN THE EFFECTS OF ANTS ON THE SURVIVORSHIP OF WASP PROGENY IN *FICUS SUR* FIGS

8.1 INTRODUCTION

Indirect interactions between ants and plants mediated by ant attraction to honeydew-producing homopterans or lepidopterans have received considerable attention recently (Laine & Niemelä 1980; Messina 1981; Fritz 1983; Bach 1991; Ito & Higashi 1991; see also Beattie 1985; Buckley 1987a, b). Ants frequently protect and increase the growth rates and sizes of homopteran populations on plants, resulting in increased nutrient loss and greater likelihood of pathogen transmission (Beattie 1985; Buckley 1987b). However, ants are generally opportunist foragers, and also utilise other food sources while on the plant. In particular, they may prey on other plant herbivores, and thereby reduce herbivory (Laine & Niemelä 1980; Bach 1991; Ito & Higashi 1991). To complicate matters, ants may prey on predators of these herbivores as well as on the herbivores themselves (Fritz 1983), with uncertain consequences for herbivory levels. A few studies have shown that the benefits accruing to plants in this way outweigh nutrient loss and damage to the plant caused by the tended homopterans (e.g. Messina 1981) - i.e. that an indirect ant-plant mutualism is operating. The outcome of the interactions is dependent on the ecological conditions or settings in which they occur (Cushman & Addicott 1991). Mutualisms may vary both in magnitude with a change in the "strength" of the mutualism and in their sign (+/-/0), such that under some conditions the interaction is mutualistic while under others it is commensal or harmful (Cushman & Addicott 1991). Within the context of indirect ant-plant interactions via homopterans, the sign or magnitude of the interaction from the plant's perspective would be a function of the harm ants caused plants by promoting homopterans versus the benefits or otherwise accruing to the plants through the ants' interactions with other species on the plant.

In the eastern Cape region at least six species of fig wasps are associated with the Cape fig, *Ficus sur*. More species are present in other parts of its range (Compton & Robertson 1991). Of the species found in the eastern Cape, only *Ceratosolen capensis* is beneficial to *F. sur*, as it pollinates the florets in addition to ovipositing in some of them. Both it and *Sycophaga cyclostigma*, which oviposits in the florets but does not pollinate them, enter the lumens of the figs through their ostioles. They oviposit during the short female phase of fig development (Galil 1977). In contrast, three species of *Apocryptophagus* oviposit into the florets through the outer walls of the figs, using their long ovipositors. Taken together, these species oviposit over a long period in the figs' development, from the prefloral through to the interfloral phase. Larvae of the non-pollinating species potentially act as indirect competitors for nutrients with *C. capensis* within the figs, and also directly compete for oviposition sites. The final member of the fig wasp community is *Apocrypta guineensis*, which acts as a parasitoid or inquiline of the other species. As the effects of a parasitoid and inquiline on their host are essentially the same, it will be referred to as a parasitoid in this chapter. *A. guineensis* also oviposits through the fig wall from the outside, mainly during the interfloral phase, but possibly also the prefloral phase when parasitising *Apocryptophagus*.

As has been shown, ants are attracted to *F. sur* by honeydew produced by the homopteran *Hilda patruelis*. As *H. patruelis* feeds mainly on phloem sap from the fruiting branches of *F. sur* while the trees are in fruit (Chapter 4), most ants on the tree are attracted to these branches. Here they not only tend *H. patruelis*, but opportunistically prey on other insects present on the figs. Ants have been recorded as predators of fig wasps both when they are ovipositing or entering the ostiole to oviposit and when the progeny emerge from the male-phase figs (Frank 1984; Bronstein 1988, 1991; Compton & Robertson 1988, 1991; pers. obs.). Bronstein (1988) noted that externally ovipositing species were more vulnerable to ant predation as they spent a longer period on the fig surface. Compton & Robertson (1988, 1991) showed that when present in sufficient numbers on figs, ants modified the proportions of fig wasp progeny produced, by disturbing and preying more on external than internal ovipositors. At high ant densities *C. capensis* progeny numbers increased and those of *A. guineensis* and *Apocryptophagus* spp. decreased. At lower densities trends were weaker. The numbers of externally ovipositing females recorded probing or ovipositing into the figs were also lower at high ant densities.

A. guineensis sex ratios were also less male-biased in the presence of ants (S. Compton & H. Robertson, unpubl. data). Cutting down on an excessive number of male *A. guineensis* progeny in this situation could minimise the effects of ants on the wasps' reproductive success. However, this change in sex ratios is a result of ants reducing *A. guineensis* oviposition rates, and thereby superparasitism, which may favour the survival of male progeny, and is therefore not adaptive as such.

The aim of the research described in this chapter was to investigate the effects of ants on all the species of fig wasps arriving at the figs to oviposit. The effects of ant predation on internally ovipositing females was investigated at and just after the interfloral phase, while the effects of ant disturbance and predation on externally ovipositing wasps was investigated mainly at the male phase, by counting the numbers of progeny of both sexes of each wasp species that emerged from the figs. This chapter aimed particularly to determine variability in the effects of different ant species and densities in relation to variation in the numbers and proportions of wasp species. Estimates of how widespread the effects of ants on wasp production and tree fitness were therefore produced. Chapter 9 is complementary, and describes the patterns and effects of ant predation on wasp progeny as they are emerging.

8.2 MATERIALS AND METHODS

8.2.1 Effects of ants on the numbers of internally ovipositing foundress wasps entering figs

Twelve branch pairs on five crops (four trees) with pre-receptive figs, and on which *P. megacephala* was present, were selected at the three sites, and one branch of each pair banded with Formex to exclude ants. The numbers of ants and figs on the branches were counted at regular intervals and the timing of fig receptivity was noted. If ants managed to gain access to banded branches they were removed and the branch was re-isolated. Figs were picked about one week after the receptive period was judged to have ended, in order to allow a full complement of wasps to enter the figs. The figs were dissected and the numbers of *C. capensis* and *S. cyclostigma* foundresses counted. For the purpose of analysis, data from branch pairs within each crop were combined to increase the sample sizes. Observations on the interactions of ants with wasps at receptive figs provided supplementary information.

8.2.2 Wasp progeny production in relation to ant numbers

Between one and thirteen branch pairs with young, prefloral figs present were selected on each of 39 crops on 23 of the 26 fruit-bearing trees monitored at the three sites, mostly within a two year period. One branch of each pair was banded with Formex to exclude ants. Trees were not selected randomly, but rather to encompass a wide range of ant densities and species. Numbers and species of ants on the figs, numbers of *H. patruelis*, and fig numbers were counted, as well as the densities of externally ovipositing fig wasps and other insects. Counts continued, usually at fortnightly intervals, until shortly before the figs entered their male phase. If ants gained access to banded branches they were removed and the branch was re-isolated. Figs were picked before exit holes had been formed, placed in emergence bottles with gauze lids and the wasps were allowed to emerge. Figs and wasps were then frozen and the numbers of each sex and species of wasp were counted. Due to a methodological problem, females of the three *Apocryptophagus* species were separated only for some trees. Males of the *Apocryptophagus* species could not be distinguished from those of *S. cyclostigma* and were therefore assigned in the same proportions as females of those species present.

Fourteen crops were successfully harvested, and a total of 19 branch pairs from 8 crops (8 trees) were used for analysis (77 figs on banded and 70 on unbanded branches). Of these, five were from site 1, two from site 2 and one was from site 3. Within each crop, data from all the banded branches were combined for analysis, as were those from all unbanded branches, in order to increase sample sizes. In addition, the eight branch pairs with the highest numbers of ants were combined as a high ant density branch (HDB) sample, in an attempt to assess the effects of the higher ant densities on the production of wasp progeny in a larger sample of figs. Finally, the data were combined for all figs from banded and all those from unbanded branches.

Individual species, as well as total wasp numbers and combined internal (*C. capensis* + *S. cyclostigma*) and external (*A. guineensis* + *Apocryptophagus* spp.) ovipositors were used. Grouping wasps into internal and external ovipositor categories only takes into account the direct effect that ants have on them, rather than their general biology. Indirectly, ants affect *Apocryptophagus* positively through predation on its parasitoid, but directly affect

Apocryptophagus negatively. However, this grouping is useful as it combines the two internal ovipositors, which are competitors and act as a complementary unit, thereby simplifying the picture. Wasp proportions were analysed in addition to numbers because they are useful in eliminating the variable of fig size, which is correlated with wasp abundance. Also, without knowing the way in which *A. guineensis* parasitism rates change with host number or density, we cannot predict whether changes in proportions or absolute numbers are more important indicators of ant effects.

8.3 RESULTS

8.3.1 Effects of *Pheidole megacephala* on the numbers of internally ovipositing wasps gaining access to figs

On several non-experimental fig trees with crops of receptive female-phase figs, warm, non-windy conditions resulted in the occasional presence of a large number of female wasps of the two internally ovipositing species (*C. capensis* and *S. cyclostigma*) swarming around and landing on the figs. If some ants were present, recruitment often occurred, resulting in large-scale predation of these wasps.

All ants on the five experimental crops were *P. megacephala*, apart from two *Camponotus* nr *postoculatus* recorded on crop 4. Mean ant densities per fig on unbanded branches over the sampling period ranged from 12.41 on crop 1 to 0.213 on crop 5 (Table 8.1), with a mean of 5.55 ± 5.18 for the five trees. However, the mean number of ants per dissected fig was 3.24 ± 3.77 on banded branches and 0.10 ± 0.13 on unbanded branches. This discrepancy is due to differences in the numbers of figs dissected per crop.

High variability in both the proportions of the two internally ovipositing fig wasp species and total numbers of foundress females was evident between branches and crops (Table 8.2, 8.3). Between-crop differences in foundress numbers must be ascribed to temporal and spatial variation in fig receptivity in relation to wasp availability and weather conditions. Over the five crops, pollinator foundress numbers ranged from zero to 20 per fig, with a mean of 3.44 ± 3.61 (n = 290 figs). *S. cyclostigma* foundress numbers ranged from zero to 44 per fig, with a mean of 5.86 ± 6.78 (n = 290 figs). Total numbers of foundresses of both species per fig ranged from zero to 45 with a mean of 9.31 ± 6.44. Only on crop 5 were *C. capensis* numbers higher than those of *S. cyclostigma* (Table 8.2). *C. capensis* foundresses apparently often attempted to exit from a fig in which they had oviposited, as wasps were frequently found trapped in the ostiolar bracts, facing outwards. The occasionally successful exiting of foundresses may explain the lack of any detectable foundress wasps in certain figs which had been oviposited in. *S. cyclostigma* was rarely found in this position.

Foundress numbers were significantly lower (Table 8.2) on unbanded branches (with ants) only for *C. capensis* on crop 3. On three of the five crops, and for the total, there were significantly more *S. cyclostigma* foundresses and total foundress numbers on unbanded than banded branches (Table 8.2). Furthermore, crops 1 and 2, on which the highest number of ants were present on unbanded branches, had significantly higher numbers of *S. cyclostigma* and the combined wasp species in figs on unbanded than banded branches.

On two crops, as well as for the total sample, the proportion of foundress wasps to which *C. capensis* contributed was significantly lower in figs on unbanded than banded branches (Table 8.3). On these same crops, and for the total, the proportion of *S. cyclostigma* was significantly higher on unbanded branches.

On unbanded branches for the whole sample, there was a significant negative correlation between the number of *C. capensis* and *S. cyclostigma* foundresses per fig (Spearman Rank Correlation: $r = -0.370$, $p < 5\times10^{-5}$, $n = 136$). The mean number of ants on unbanded branches

Table 8.1. Ant numbers per fig on banded and unbanded branches.

crop no.	no. sample dates	mean ant no. (SD)	
		banded	unbanded
1	2	0.45 (0.64)	12.41 (2.79)
2	2	0.13 (0.18)	8.41 (0.87)
3	3	0.02 (0.04)	5.99 (5.96)
4	4	0.14 (0.17)	0.71 (0.40)
5	3	0 (0)	0.21 (0.22)

Table 8.2. Numbers of figs with wasps and numbers of internally ovipositing wasp foundresses per fig on banded and unbanded branches.

species	crop no.	total no. figs		% figs with wasps		mean no. wasps (SD)[1]		Mann-Whitney U	
		B	U	B	U	B	U	Z	p
C. capensis	1	15	5	53.3	80.0	1.07 (1.79)	1.40 (1.14)	1.063	0.287
	2	24	25	62.5	56.0	1.17 (1.58)	1.52 (2.12)	0.252	0.801
	3	18	22	100	45.5	3.50 (1.95)	0.68 (1.0)	-4.657	<0.0001
	4	37	37	73.0	94.6	2.0 (2.04)	2.65 (2.31)	1.528	0.126
	5	60	47	96.7	85.1	6.27 (3.80)	6.04 (4.40)	-0.186	0.852
	total	154	136	81.8	75.7	3.62 (3.55)	3.25 (3.69)	-1.417	0.156
S. cyclostigma	1	15	5	86.7	100	2.60 (2.41)	6.20 (3.77)	2.485	0.013
	2	24	25	100	96.0	6.71 (4.32)	15.08 (12.05)	2.845	0.004
	3	18	22	100	90.9	8.50 (5.23)	11.27 (7.40)	1.322	0.186
	4	37	37	100	97.3	7.62 (3.80)	8.35 (4.10)	0.760	0.447
	5	60	47	25.0	44.7	0.33 (0.63)	1.70 (2.96)	2.745	0.006
	total	154	136	69.5	77.9	4.25 (4.69)	7.68 (8.19)	3.683	0.0002
total wasps	1	15	5	86.7	100	3.67 (3.54)	7.60 (4.83)	2.024	0.043
	2	24	25	100	100	7.88 (4.32)	16.60 (12.04)	2.796	0.005
	3	18	22	100	90.9	12.0 (5.02)	11.95 (7.94)	-0.164	0.870
	4	37	37	100	100	9.62 (4.34)	11.0 (4.42)	1.437	0.151
	5	60	47	96.7	89.4	6.60 (4.02)	7.74 (4.47)	2.047	0.041
	total	154	136	97.4	94.9	7.87 (4.75)	10.93 (7.64)	3.790	0.006

1: figs with zero wasps included.

Table 8.3. The proportions of *C. capensis* and *S. cyclostigma* on banded and unbanded branches.

species	crop no.	mean proportion (SD)		Mann-Whitney U	
		banded	unbanded	Z	p
C. capensis	1	0.182 (0.202)	0.170 (0.097)	-0.091	0.928
	2	0.188 (0.198)	0.130 (0.230)	-1.306	0.192
	3	0.346 (0.235)	0.056 (0.084)	-4.672	<0.0001
	4	0.207 (0.201)	0.256 (0.219)	1.171	0.242
	5	0.920 (0.202)	0.699 (0.385)	-3.294	0.001
	total	0.496 (0.399)	0.351 (0.378)	-3.160	0.002
S. cyclostigma	1	0.685 (0.336)	0.830 (0.097)	0.888	0.374
	2	0.812 (0.198)	0.870 (0.230)	1.306	0.192
	3	0.654 (0.235)	0.853 (0.288)	3.659	0.0003
	4	0.793 (0.201)	0.744 (0.219)	-1.171	0.242
	5	0.046 (0.106)	0.194 (0.305)	2.563	0.010
	total	0.478 (0.398)	0.598 (0.394)	2.60	0.009

was negatively correlated with *C. capensis* numbers ($r = -0.531$, $p < 5\times10^{-5}$) and positively correlated with both *S. cyclostigma* ($r = 0.621$, $p < 5\times10^{-5}$) and total ($r = 0.278$, $p = 0.0012$) numbers. However, crop 5 was very large (34.6% of unbanded figs) and had very low ant and *S. cyclostigma* numbers. When it was removed from the analysis, the only relationship that remained significant was that between ant and *C. capensis* numbers ($r = -0.320$, $p = 0.0026$, $n = 89$).

Data from the whole sample for unbanded branches were transformed using $\sqrt{(x+1)}$ in order to conduct a Partial Correlation analysis. When crop 5 was included, the numbers of *C. capensis* and *S. cyclostigma* were negatively correlated ($r = -0.232$, $p < 0.01$, $n = 136$), as were those of ants and *C. capensis* ($r = -0.352$, $p < 0.01$). *S. cyclostigma* numbers were positively correlated with those of ants ($r = 0.379$, $p < 0.01$). When crop 5 was removed, again only the relationship between *C. capensis* and ant number remained significant ($r = -0.346$, $p < 0.01$, $n = 89$).

8.3.2 Variability in the effects of ants on wasp progeny production

Mean ant numbers per fig on the unbanded branches of individual trees ranged from 0.05 to 4.63 over the sampling period (Table 8.4). For the combined sample (data from the eight trees) a mean number of 1.29 ants per fig was present on unbanded branches, and of 2.65 ants per fig on the unbanded branches of the HDB sample. The mean number of ants per dissected fig for the combined sample (banded: 0.049 ± 0.117 ants per fig, n = 77; unbanded: 1.302 ± 2.41 ants per fig, n = 70) was very similar to that calculated over the monitoring period because similar numbers of figs were dissected in each crop.

Ant numbers changed through crop development, in a manner similar to that described in Chapter 4. *P. megacephala* was present on most trees (Table 8.4), and comprised the majority of the ants. Apart from trees on which only *Acantholepis capensis* or *P. megacephala* were present, it was not possible to separate the effects of individual ant species. However, the numerical dominance of *P. megacephala* places it as the most important ant species in the interaction, without invoking interspecific differences in ant behaviour towards wasps. Attempts to obtain data on a wider range of ant species failed largely due to fig abortion or predation. For example, site 3, with the highest number of ant species present, also experienced the highest frugivory rate on premature figs. Ant species other than *P. megacephala* also often disappeared early during fig development.

Although *H. patruelis* was not the only ant attractant, it differed from, for example, attractive exudates in that it persisted usually throughout the figs' development. Ants which tended *H. patruelis* (mainly *P. megacephala*) therefore tended to be consistently present through the figs' developmental period.

Wasp progeny numbers and the proportions represented by different species varied between branches and trees (Fig. 8.1; Table 8.5, 8.6). All figs contained some pollinator progeny, and although *A. guineensis* was absent from a few figs, it was present on all trees. *S. cyclostigma* and *Apocryptophagus* spp. were absent from figs on one tree each. On unbanded branches for the combined sample a mean of 275.5 ± 239.4 wasps of internally and 94.5 ± 81.1 wasps of externally ovipositing species per fig were present (Table 8.5). Total numbers of wasps per fig ranged from 82.8 ± 52.9 on unbanded branches of tree 7 to 620.9 ± 339.0 on those of tree 5 with a mean of 370.0 ± 248.5 on unbanded branches for the combined sample. In general, the proportions of wasps appeared more similar between branches on the same trees than between trees (Fig. 8.1), emphasising the importance of variation in numbers and species of wasps present at different times in determining the wasp progeny profile of the crop. Only on the unbanded branch of tree 6 did *Apocryptophagus* comprise the majority of wasps (Table 8.6). High *C. capensis*, *S. cyclostigma* or *A. guineensis* numbers were characteristic of the other trees. For the combined sample, *C. capensis* made up the most wasps, followed by *A. guineensis*, *S. cyclostigma* and *Apocryptophagus* (Fig. 8.1).

Wasp numbers and proportions varied in a complex manner on banded versus unbanded branches on individual trees. On seven of the eight trees, as well as for the whole sample and eight branch pairs with highest ant numbers, *C. capensis* numbers and proportions were approximately equal or higher on unbanded than banded branches (Table 8.5, 8.6). Tree 6 cannot be considered representative, as wasp counts were made on only two figs from the unbanded branch, both of which had high *Apocryptophagus* numbers, limiting *C. capensis* oviposition and preventing emergence (unpubl. data). Only on trees 3 and 5 were *C. capensis* numbers significantly different for banded versus unbanded branches (Table 8.3), while on tree 1 the proportion of *C. capensis* present was significantly higher on unbanded than banded branches (Table 8.4).

S. cyclostigma did not vary consistently in numbers or proportions between banded and unbanded trees (Table 8.5, 8.6), nor were significant differences between banded and unbanded branches present on any trees. Very similar values were also obtained for banded and unbanded branches for the combined and HDB samples.

The proportions of *A. guineensis* were higher on banded than unbanded branches on six of the eight trees, as well as for the combined and HDB samples. Absolute numbers were less consistently elevated by ant exclusion (Table 8.5, 8.6). On tree 1, with the highest ant numbers, significantly lower numbers and proportions of *A. guineensis* were present on unbanded than banded branches.

Apocryptophagus numbers and proportions were significantly higher on banded than unbanded branches for tree 2 (Table 8.5, 8.6). On no other trees were differences significant. For both the combined and HDB samples, the numbers and proportions were higher on banded than unbanded branches, although this difference was not significant.

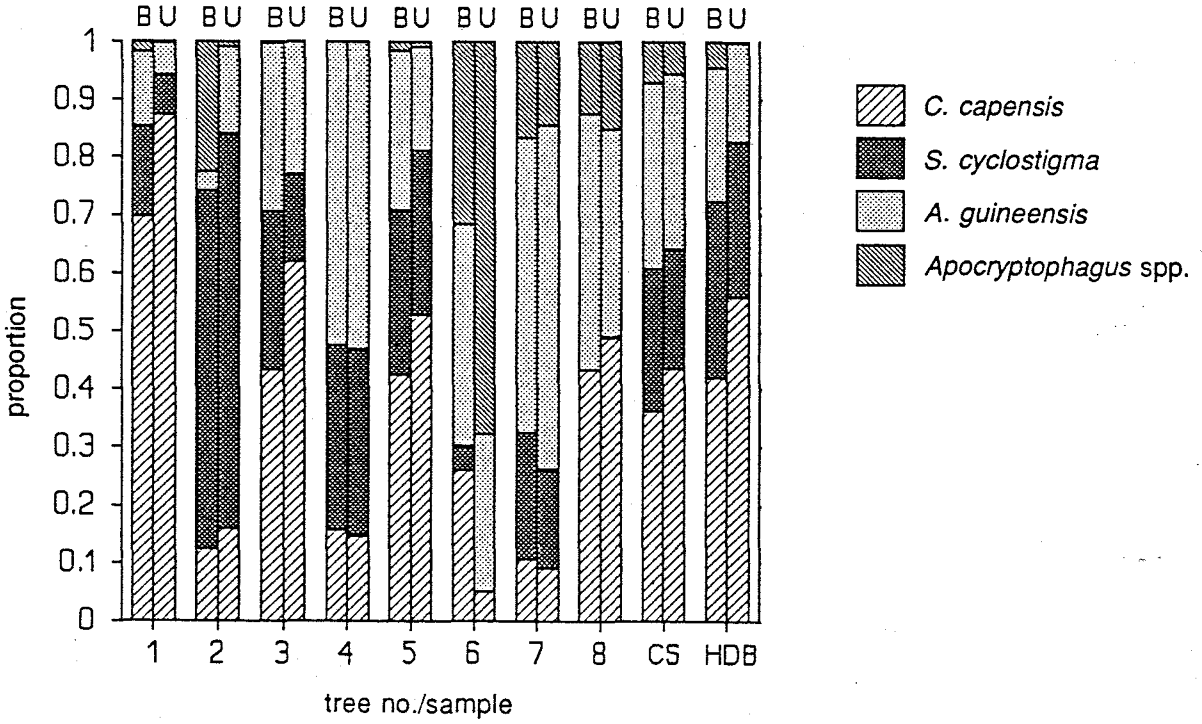


Figure 8.1. Proportions of the wasp progeny of each species emerging from figs on banded (B) and unbanded (U) branches on each of the eight trees, the combined sample (CS) and the eight highest density branches (HDB).

Table 8.4. Mean ant densities on figs on banded (B) and unbanded (U) branches, and the total percentage of visiting ants of each species, on the 8 trees monitored and for the combined sample, and the eight branch pairs with highest ant numbers (HDB). Ant species present were *A. capensis* (Ac), *Camponotus* nr *postoculatus* (Cp), *Camponotus* sp.1 (C1), *Cataulacus intrudens* (Ci), *Crematogaster* spp. (Cr), and *Pheidole megacephala* (Pm). Note that only *P. megacephala* percentages were calculated for these last two samples.

tree no. /sample	no. sample dates	no. branch pairs	mean no. ants per fig		% individuals					
			B	U	Ac	Cp	C1	Ci	Cr	Pm
1	7	4	0.153 (0.642)	4.593 (6.599)				0.1		99.9
2	7	1	0 (0)	1.144 (1.414)						100
3	7	3	0.085 (0.310)	0.611 (0.822)						100
4	9	3	0.007 (0.023)	0.428 (0.592)		2.6				97.4
5	5-6	3	0.007 (0.030)	0.185 (0.253)	53.0					47.0
6	8	1	0 (0)	0.158 (0.161)	100					
7	4	3	0.008 (0.026)	0.121 (0.180)	4.2		3.6		92.6	
8	10	1	0 (0)	0.05 (0.121)	100					
combined		19	0.050 (0.324)	1.288 (3.533)	-	-	-	-	-	96.9
HDB		8	0.081 (0.442)	2.650 (4.894)	-	-	-	-	-	99.6

Table 8.5. Numbers of wasp progeny emerging from figs on banded (B) and unbanded (U) branches, on eight trees, the combined sample, and the eight highest ant-density branch pairs (HDB).

species	tree no. /sample	no. figs		no. wasps		Mann-Whitney U	
		B	U	B	U	Z	p
C. capensis	1	16	15	324.1 (110.9)	375.1 (153.4)	0.771	0.441
	2	5	5	30.4 (14.3)	38.2 (38.5)	-0.314	0.753
	3	12	12	157.5 (99.4)	273.1 (196.8)	2.165	0.0304
	4	12	12	45.1 (38.2)	49.4 (41.7)	0.404	0.686
	5	12	8	141.4 (71.6)	314.1 (190.5)	1.967	0.0491
	6	4	2	73.0 (34.9)	3.50 (3.54)	-1.620	0.105
	7	12	12	7.33 (5.55)	8.08 (13.5)	-0.934	0.351
	8	4	4	167.8 (50.3)	362.3 (318.8)	0.144	0.885
	combined	77	70	136.6 (132.0)	196.5 (208.4)	0.919	0.358
	HDB	33	32	184.1 (161.5)	235.5 (197.8)	0.991	0.322
S. cyclostigma	1	16	15	75.5 (91.3)	28.1 (58.9)	-1.687	0.0917
	2	5	5	154.5 (70.4)	183.2 (40.4)	0.836	0.403
	3	12	12	108.6 (76.4)	72.2 (112.4)	-1.184	0.236
	4	12	12	105.0 (54.8)	125.0 (86.3)	0.491	0.624
	5	12	8	86.8 (54.4)	207.6 (234.8)	1.043	0.297
	6	4	2	16.2 (31.4)	0 (0)	-0.822	0.411
	7	12	12	15.9 (12.9)	14.0 (18.4)	-0.838	0.402
	8	4	4	0 (0)	0 (0)	-	-
	combined	77	70	75.9 (73.9)	79.0 (120.7)	-1.417	0.157
	HDB	33	32	107.8 (80.7)	99.0 (103.3)	-0.529	0.597

Table 8.5. *continued*

species	tree no. /sample	no. figs		no. wasps		Mann-Whitney U	
		B	U	B	U	Z	p
internal ovipositors	1	16	15	399.6 (104.0)	403.1 (146.8)	-0.257	0.797
	2	5	5	184.9 (77.2)	221.5 (25.7)	1.044	0.296
	3	12	12	266.1 (83.5)	345.3 (224.9)	0.375	0.707
	4	12	12	150.1 (64.8)	174.5 (104.2)	0.404	0.686
	5	12	8	228.2 (103.1)	521.8 (336.1)	2.199	0.0279
	6	4	2	89.2 (63.0)	3.50 (3.54)	-1.620	0.105
	7	12	12	23.2 (16.5)	22.1 (23.2)	-0.636	0.525
	8	4	4	167.8 (50.3)	362.3 (318.8)	0.144	0.885
	combined	77	70	212.4 (144.9)	275.5 (239.4)	0.983	0.326
	HDB	33	32	291.9 (140.2)	334.5 (172.7)	0.702	0.483
A. guineensis	1	16	15	67.1 (57.6)	28.1 (28.1)	-2.196	0.0281
	2	5	5	9.0 (9.69)	44.6 (47.2)	1.152	0.249
	3	12	12	119.2 (92.8)	90.5 (84.9)	-0.722	0.470
	4	12	12	165.8 (59.3)	181.4 (51.4)	0.577	0.564
	5	12	8	81.3 (42.5)	92.5 (52.2)	0.116	0.908
	6	4	2	101.8 (48.2)	27.0 (24.0)	-1.620	0.105
	7	12	12	37.3 (17.4)	49.0 (30.8)	0.895	0.371
	8	4	4	179.5 (73.1)	192.3 (63.4)	0.144	0.885
	combined	77	70	92.0 (74.0)	86.5 (76.9)	-0.720	0.472
	HDB	33	32	91.9 (79.8)	64.8 (72.9)	-1.542	0.123

Table 8.5. *continued*

species	tree no. /sample	no. figs		no. wasps		Mann-Whitney U	
		B	U	B	U	Z	p
Apocryptophagus spp.	1	16	15	10.2 (23.9)	0.53 (1.25)	-1.053	0.292
	2	5	5	49.1 (35.4)	2.56 (3.51)	-2.115	0.0345
	3	12	12	0.86 (2.97)	0 (0)	-0.917	0.359
	4	12	12	0 (0)	0.13 (0.46)	0.917	0.359
	5	12	8	5.35 (9.16)	6.63 (18.7)	-1.046	0.295
	6	4	2	90.5 (88.9)	58.5 (10.6)	-0.231	0.817
	7	12	12	13.3 (11.6)	11.8 (10.0)	-0.260	0.795
	8	4	4	46.8 (38.3)	56.5 (51.8)	0	1.0
	combined	77	70	15.5 (33.1)	7.99 (20.5)	-1.694	0.0902
	HDB	33	32	12.4 (26.3)	0.70 (1.74)	-1.484	0.138
external ovipositors	1	16	15	77.3 (70.1)	28.6 (27.9)	-2.334	0.0196
	2	5	5	58.1 (28.7)	47.1 (47.4)	-0.209	0.835
	3	12	12	120.0 (93.8)	90.5 (84.9)	-0.722	0.470
	4	12	12	165.8 (59.3)	181.5 (51.6)	0.577	0.564
	5	12	8	86.7 (43.2)	99.1 (60.4)	0.116	0.908
	6	4	2	192.3 (72.7)	85.5 (34.6)	-1.620	0.105
	7	12	12	50.5 (24.7)	60.8 (35.5)	0.837	0.403
	8	4	4	226.3 (89.4)	248.8 (52.7)	0.433	0.665
	combined	77	70	107.5 (79.3)	94.5 (81.1)	-1.257	0.209
	HDB	33	32	104.3 (77.1)	65.5 (72.8)	-2.310	0.0209

Table 8.5. *continued*

species	tree no. /sample	no. figs		no. wasps		Mann-Whitney U	
		B	U	B	U	Z	p
total wasps	1	16	15	476.9 (135.9)	431.7 (168.3)	-0.929	0.353
	2	5	5	243.0 (57.5)	268.6 (45.5)	0.627	0.531
	3	12	12	386.2 (120.3)	435.8 (435.8)	0.202	0.840
	4	12	12	315.8 (108.7)	356.0 (134.4)	0.838	0.402
	5	12	8	314.9 (117.8)	620.9 (339.0)	2.199	0.0279
	6	4	2	281.5 (111.3)	89.0 (31.1)	-1.620	0.105
	7	12	12	73.8 (24.7)	82.8 (52.9)	0.087	0.931
	8	4	4	394.0 (101.6)	611.0 (290.1)	0.722	0.470
	combined	77	70	319.9 (163.8)	370.0 (248.5)	0.564	0.573
	HDB	33	32	396.2 (141.6)	400.0 (174.4)	-0.308	0.758

Table 8.6. Proportions of the progeny of each species of wasp emerging from figs on banded (B) and unbanded (U) branches on eight trees, the combined sample, and the eight highest ant-density branch pairs (HDB).

species	tree no. /sample	no. figs		proportion wasps (SD)		Mann-Whitney U	
		B	U	B	U	Z	p
C. capensis	1	16	15	0.698 (0.200)	0.876 (0.169)	2.511	0.0120
	2	5	5	0.124 (0.047)	0.159 (0.172)	-0.418	0.676
	3	12	12	0.433 (0.251)	0.620 (0.236)	1.934	0.0531
	4	12	12	0.156 (0.137)	0.147 (0.139)	-0.087	0.931
	5	12	8	0.424 (0.206)	0.528 (0.174)	0.964	0.335
	6	4	2	0.260 (0.086)	0.050 (0.057)	-1.620	0.105
	7	12	12	0.105 (0.085)	0.090 (0.094)	-0.664	0.507
	8	4	4	0.434 (0.112)	0.490 (0.291)	0	1.0
	combined	77	70	0.363 (0.273)	0.436 (0.350)	0.913	0.361
	HDB	33	32	0.421 (0.322)	0.560 (0.372)	1.634	0.102
S. cyclostigma	1	16	15	0.156 (0.195)	0.067 (0.067)	-1.594	0.111
	2	5	5	0.618 (0.153)	0.682 (0.111)	0.418	0.676
	3	12	12	0.274 (0.189)	0.151 (0.250)	-1.548	0.122
	4	12	12	0.319 (0.100)	0.322 (0.130)	0.375	0.707
	5	12	8	0.285 (0.174)	0.285 (0.216)	-0.116	0.908
	6	4	2	0.042 (0.077)	0 (0)	-0.822	0.411
	7	12	12	0.221 (0.163)	0.172 (0.134)	-0.665	0.506
	8	4	4	0 (0)	0 (0)	-	-
	combined	77	70	0.246 (0.203)	0.206 (0.231)	-1.583	0.113
	HDB	33	32	0.302 (0.226)	0.267 (0.049)	-0.823	0.410

Figure 8.6. *continued*

species	tree no. /sample	no. figs		proportion wasps (SD)		Mann-Whitney U	
		B	U	B	U	Z	p
internal ovipositors	1	16	15	0.855 (0.114)	0.943 (0.045)	2.511	0.0120
	2	5	5	0.742 (0.139)	0.841 (0.150)	1.044	0.296
	3	12	12	0.707 (0.187)	0.771 (0.217)	0.837	0.403
	4	12	12	0.475 (0.084)	0.468 (0.115)	-0.202	0.840
	5	12	8	0.710 (0.140)	0.813 (0.077)	1.813	0.0698
	6	4	2	0.301 (0.127)	0.049 (0.057)	-1.620	0.105
	7	12	12	0.326 (0.227)	0.262 (0.158)	-0.260	0.795
	8	4	4	0.433 (0.112)	0.490 (0.291)	0	1.0
	combined	77	70	0.610 (0.245)	0.642 (0.301)	1.117	0.264
	HDB	33	32	0.724 (0.199)	0.827 (0.197)	2.507	0.0122
A. guineensis	1	16	15	0.128 (0.097)	0.056 (0.046)	-2.313	0.0207
	2	5	5	0.032 (0.033)	0.150 (0.151)	1.253	0.210
	3	12	12	0.291 (0.185)	0.229 (0.217)	-0.837	0.403
	4	12	12	0.525 (0.084)	0.531 (0.115)	0.202	0.840
	5	12	8	0.276 (0.147)	0.179 (0.076)	-1.504	0.132
	6	4	2	0.382 (0.161)	0.273 (0.175)	-0.694	0.487
	7	12	12	0.508 (0.161)	0.595 (0.100)	0.953	0.341
	8	4	4	0.443 (0.065)	0.359 (0.156)	-0.722	0.470
	combined	77	70	0.321 (0.207)	0.304 (0.239)	-0.719	0.472
	HDB	33	32	0.234 (0.213)	0.171 (0.197)	-1.595	0.111

Figure 8.6. *continued*

species	tree no. /sample	no. figs		proportion wasps (SD)		Mann-Whitney U	
		B	U	B	U	Z	p
Apocryptophagus spp.	1	16	15	0.017 (0.037)	0.002 (0.004)	-1.053	0.292
	2	5	5	0.225 (0.162)	0.009 (0.012)	-2.115	0.0345
	3	12	12	0.002 (0.006)	0 (0)	-0.917	0.359
	4	12	12	0 (0)	0.0002 (0.0007)	0.917	0.359
	5	12	8	0.014 (0.021)	0.008 (0.023)	-1.046	0.295
	6	4	2	0.316 (0.261)	0.678 (0.117)	1.157	0.247
	7	12	12	0.167 (0.140)	0.143 (0.147)	-0.260	0.795
	8	4	4	0.124 (0.010)	0.151 (0.180)	0.144	0.885
	combined	77	70	0.070 (0.129)	0.054 (0.142)	-1.493	0.135
	HDB	33	32	0.043 (0.101)	0.002 (0.006)	-1.449	0.147
external ovipositors	1	16	15	0.145 (0.114)	0.057 (0.045)	-2.511	0.0120
	2	5	5	0.258 (0.139)	0.159 (0.150)	-1.044	0.296
	3	12	12	0.293 (0.187)	0.229 (0.217)	-0.837	0.403
	4	12	12	0.525 (0.084)	0.532 (0.115)	0.202	0.840
	5	12	8	0.290 (0.140)	0.187 (0.077)	-1.813	0.0698
	6	4	2	0.699 (0.127)	0.951 (0.951)	1.620	0.105
	7	12	12	0.674 (0.227)	0.738 (0.158)	0.260	0.795
	8	4	4	0.567 (0.112)	0.510 (0.291)	0	1.0
	combined	77	70	0.390 (0.245)	0.358 (0.301)	-1.117	0.264
	HDB	33	32	0.276 (0.199)	0.173 (0.197)	-2.507	0.0122

For most trees, as well as the combined and HDB samples, total wasp numbers were lower on banded than on unbanded branches, although only on tree 5 was this difference significant (Table 8.5). No significant difference in total wasp numbers was present for tree 1, which had the highest ant numbers.

When wasp species were grouped as internal and external ovipositors, differences between banded and unbanded branches were more consistent, particularly on trees with higher ant densities. The numbers of internal ovipositor progeny were higher on unbanded and externals on banded branches (Table 8.5, 8.6), and this was also true for the combined and HDB samples. On tree 1 the numbers of external ovipositors were significantly higher on the banded than the unbanded branches (Table 8.5) and the proportions of both internal and external ovipositors were also significantly different (Table 8.6). The numbers of external ovipositors were significantly higher on the banded than unbanded branches for the HDB sample, while the proportions of both internal and external ovipositors were significantly different.

Plots of the proportion contributed by each wasp species per fig (Fig. 8.2) against ant numbers for the whole data set (n = 147 figs) indicate that on the majority of individual figs an average of zero to two ants was present. A positive relationship between *C. capensis* proportions and ant numbers, and between combined internal ovipositors and ant numbers, was evident. A negative relationship between the proportions of the two external species (separately and combined) and ant numbers, and a wide scatter in the relationship between the proportions of *S. cyclostigma* proportion and ant numbers, were also evident. The use of absolute numbers rather than proportions of wasps does not result in as clear a pattern due to the variable of fig size.

Partial correlations of ants with each wasp species, and between wasp species, were conducted for the whole data set, in order to test relationships between the various species

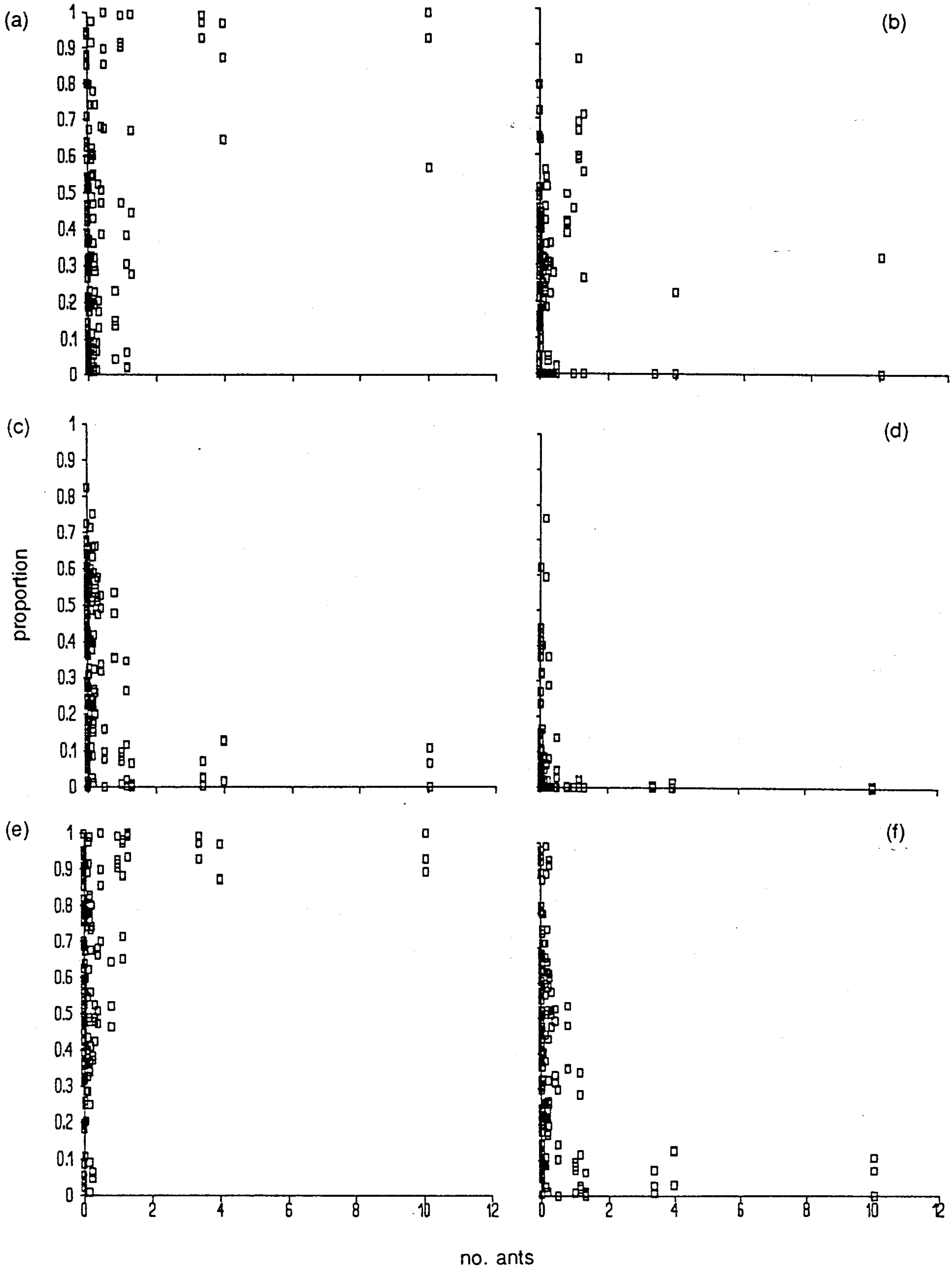


Figure 8.2. Proportions of wasp species against ant number for individual figs (n = 147). a) *C. capensis.* b) *S. cyclostigma.* c) *A. guineensis.* d) *Apocryptophagus* spp.. e) internal ovipositors. f) external ovipositors.

pairs independently of other interactions. Data from figs from all banded and unbanded branches were combined (n = 147 figs) and a $\sqrt{(x+1)}$ transformation applied to adjust the count data from a Poisson towards a Normal distribution (Snedecor & Cochran 1980). Ant numbers were significantly positively correlated with numbers of *C. capensis* and the combined internal ovipositors per fig, and significantly negatively correlated with those of *A. guineensis*, *Apocryptophagus* and the combined external ovipositor numbers (Table 8.7). These results are in agreement with the trends indicated by the previous analyses.

On the basis of the plots of wasp proportions against ant numbers (Fig. 8.2), data were divided into figs with 0-2 and those with 2-10 ants per fig, and partial correlations were conducted on the two separate data sets (Table 8.7). In the first category ant numbers were significantly correlated with individual and combined internal ovipositor numbers, and significantly negatively correlated with *A. guineensis* and combined external ovipositor numbers. At higher than two ants per fig no significant correlations existed between wasps and ants.

For the whole data set, or figs with 0-2 ants, no significant inter-correlations were present between the four wasp species except between *S. cyclostigma* and *Apocryptophagus* (Table 8.7). However, the signs of correlation coefficients between potential competitors (*C. capensis*, *S. cyclostigma* and *Apocryptophagus*) were all negative and between the parasitoid *A. guineensis* and its hosts were positive (except for one case). On figs with 2-10 ants present, a significant positive correlation between the numbers of *A. guineensis* and the two internal ovipositors was present. Presumably, figs with large numbers of hosts produce large numbers of *A. guineensis*, but these do not reduce host numbers sufficiently to reverse the positive association, which would result in a negatively density dependent relationship.

The relationship between the proportions of the wasp progeny contributed by each species in individual figs and mean ant numbers on the figs was also investigated for the whole data

Table 8.7. Partial correlations between the progeny numbers of the various wasp species, and between ant numbers and wasp numbers.

correlated data pair	whole data set (n = 147)		0-2 ants/fig (n = 136)		2-10 ants/ fig (n = 11)	
	r	p	r	p	r	p
C. capensis vs *S. cyclostigma*	-0.136	NS	-0.129	NS	-0.599	NS
C. capensis vs *A. guineensis*	0.102	NS	0.108	NS	0.708	*
C. capensis vs *Apocryptophagus*	-0.138	NS	-0.118	NS	-0.074	NS
S. cyclostigma vs *A. guineensis*	0.124	NS	0.113	NS	0.780	**
S. cyclostigma vs *Apocryptophagus*	-0.327	**	-0.310	**	-0.217	NS
A. guineensis vs *Apocryptophagus*	-0.019	NS	0.041	NS	0.061	NS
C. capensis vs ants	0.309	**	0.178	*	-0.072	NS
S. cyclostigma vs ants	-0.082	NS	0.178	*	0.216	NS
A. guineensis vs ants	-0.309	**	-0.204	*	-0.202	NS
Apocryptophagus vs ants	-0.173	*	-0.134	NS	0.071	NS
internal vs external ovipositors	0.088	NS	-0.110	NS	0.704	*
internal ovipositors vs ants	0.299	**	0.304	**	-0.135	NS
external ovipositors vs ants	-0.365	**	-0.249	**	-0.068	NS

p: * < 0.05, ** < 0.01

set. Proportions were transformed by arcsine($\sqrt{p}$) in order to make the variance independent of the mean (Sokal & Rohlf 1981) and ant numbers were transformed by $\sqrt{(x+1)}$. Ant numbers were positively correlated with the proportions of *C. capensis* ($r = 0.460$, $p < 0.0001$, $n = 147$ figs) and combined internal ovipositors ($r = 0.441$, $p < 0.0001$), and negatively correlated with those of *S. cyclostigma* ($r = -0.172$, $p = 0.0368$), *A. guineensis* ($r = -0.430$, $p < 0.0001$) and *Apocryptophagus* spp. ($r = -0.201$, $p = 0.0148$), as well as external ovipositors ($r = -0.441$, $p < 0.0001$).

In order to determine whether ant presence resulted in changes in the sex ratios of wasp species, a Spearman Rank correlation was conducted on the whole data set ($n = 147$ figs) between ant numbers per fig and the sex ratio (no. females/(no. males + females)) for each wasp species. No significant correlations were present (*C. capensis*: $r = 0.122$, $p = 0.140$; *S. cyclostigma*: $r = 0.148$, $p = 0.146$; *A. guineensis*: $r = -0.116$, $p = 0.170$; *Apocryptophagus*: $r = 0.172$, $p = 0.198$). There were also no significant differences in the sex ratios of each wasp species between banded ($n = 77$) and unbanded ($n = 70$) figs for the combined sample (Table 8.8).

The relationship between the numbers of the two externally ovipositing wasp species recorded on the outside of figs during the monitoring period and the numbers of their progeny from these figs, as well as between the former and ant numbers on the figs, was examined. Mean wasp numbers were calculated for each branch ($n = 38$ branches) for use in the analysis. No significant correlation was present between *A. guineensis* numbers recorded on the figs and progeny numbers (Spearman Rank: $r = 0.278$, $p = 0.0912$), nor between ants and *A. guineensis* on figs ($r = -0.240$, $p = 0.144$), although the former approached significance. *Apocryptophagus* numbers on the figs were significantly correlated with both their progeny numbers ($r = 0.648$, $p = 0.0001$) and ant numbers ($r = -0.442$, $p = 0.0072$). The correlation between total numbers of external ovipositors on the figs approached significance ($r = -0.281$, $p = 0.0878$).

Table 8.8. Sex ratios of wasp species from figs in which they were present on banded (B) and unbanded (U) branches. Sex ratio = (no. females/(no. males + females)).

wasp species	no. figs		sex ratio (SD)		Mann-Whitney U	
	B	U	B	U	Z	p
C. capensis	77	70	0.723 (0.203)	0.724 (0.212)	0.180	0.857
S. cyclostigma	58	39	0.720 (0.153)	0.706 (0.173)	-0.239	0.811
A. guineensis	75	67	0.470 (0.149)	0.451 (0.179)	-1.091	0.275
Apocryptophagus spp.	34	23	0.690 (0.164)	0.692 (0.169)	-0.122	0.903

8.4 DISCUSSION

8.4.1 Effects of ants on foundress numbers of internally ovipositing species

When considering the whole data set, *P. megacephala* had a slight, non-significant negative effect on the number of *C. capensis* foundresses entering female-phase figs on *F. sur*, and a positive effect (or no effect, if a tree with low *S. cyclostigma* and ant numbers was excluded from the analysis) on numbers of *S. cyclostigma*. However, on only one individual crop were *C. capensis* foundresses present in significantly higher numbers in figs on banded than unbanded branches, while *S. cyclostigma* was present in significantly higher numbers on unbanded branches on three of the five trees. A difference in behaviour between the two internally ovipositing species when searching for an ostiole may result in *C. capensis* being more vulnerable to predation by ants than *S. cyclostigma*. A direct positive relationship between *S. cyclostigma* and ants seems unlikely, but ants may have benefitted this species indirectly by preying on *C. capensis*, although no correlations were present between numbers of the two species.

Although Nefdt (1989) estimated that a maximum of four foundress pollinators carried an adequate number of eggs to utilise all accessible ovules, Gardiner (1986) showed that *C. capensis* progeny number carried on increasing with the foundress number of this species up to 11 foundresses in *F. sur*, unlike in *F. burtt-davyi*. In *F. sur* there is therefore a high critical number of foundresses above which progeny number is virtually constant and if ants reduced numbers from, for example, ten to eight, progeny numbers could still be affected.

8.4.2 Ant effects on wasp progeny production

The results obtained from correlation analyses of wasp and ant numbers using the entire data set were supported by the comparison of wasp progeny production in figs on banded and unbanded branches. However, the trends appearing from this second analysis were not always strong, and varied from tree to tree.

Ant numbers were negatively related to the numbers of *A. guineensis* and *Apocryptophagus* progeny produced. Thus ants disturbed and preyed on externally ovipositing species, resulting in a reduction in oviposition events. However, although directly ants had a negative effect on *Apocryptophagus spp.*, indirectly they benefitted these species by reducing parasitism - the net effect on *Apocryptophagus* depends on the relative magnitude of direct versus indirect effects.

Reflecting the absence of parasitoids and competitors, ant numbers were positively related to those of *C. capensis* and the internal ovipositor progeny combined. The slight negative effects of ants on *C. capensis* foundresses were therefore more than offset by their positive effects on the pollinator through the reduction of parasitism and competition. However, the relationship between ant presence and changes in *S. cyclostigma* numbers was very variable. Compton & Robertson (1988, 1991) found similar variability in the relationship between ant and *S. cyclostigma* numbers. The possible advantage gained by *S. cyclostigma* foundresses in the presence of ants was thus not reflected in the numbers of their progeny produced. Ants therefore affected *C. capensis* and *S. cyclostigma* differently not only during the female phase but also during the interfloral phase of fig development. A possible reason for the difference in effects during the interfloral phase is discussed later.

At densities of between zero and two ants per fig, ants had an increasing effect on wasp numbers as ant numbers increased. At densities greater than two ants per fig no correlations between ant and wasp numbers were present. However, the sample size may be too small at this level to draw definitive conclusions, and Compton & Robertson (1991) recorded a decreasing effect between eight and four ants per fig (although this may be due in part to ant species effects). Compton & Robertson (1988, 1991) showed similar but generally stronger effects of ants on the numbers of wasp progeny produced than were found in this study. However, their studies employed higher mean ant numbers (8, 7.92 and 7 ants/fig) and sometimes different ant species. Compton & Robertson (1988) also used much larger fig sample sizes. At ant densities similar to those in this study, they found equivalent effects on wasp numbers.

The ant species present on a particular tree must also affect the outcome of the interaction in that the number of wasps which are caught or disturbed per ant per unit time must depend partly on the size and behaviour of the workers (the species' effectiveness as a predator). *Anoplolepis custodiens* and *P. megacephala* are highly aggressive towards other ant species (Steyn 1954) but this does not necessarily reflect their ability as predators. Probably the *Tetraponera* species and *Polyrhachis schistacea* found occasionally on *F. sur* are also efficient fig wasp predators. However, for this study system the overwhelming numerical dominance of *P. megacephala* places it as the most important species by far, although *A. custodiens* also had an effect on one tree in Compton & Robertson's (1991) study. *P. megacephala* is also the most important species throughout southern Africa (Cushman *et al.* in prep.).

The total numbers of wasp progeny emerging from figs on banded branches tended to be lower than the numbers from unbanded branches. This supports Compton & Robertson's (1988) suggestion that parasitoids may destroy more host larvae than they replace with their own, through, for example, probing activity. Some cases of lower numbers of progeny on banded branches could also be due to the presence of higher *Apocryptophagus* numbers on these branches, resulting in a disproportionate decrease in internal ovipositor number through the limitation of oviposition site accessibility. Alternatively, the use of Formex may have reduced the numbers of progeny produced on banded branches by damaging phloem vessels and thus decreasing the availability of nutrients for larval growth. No evidence of plant pathological effects were evident, however, although Formex is a polybutene and wax compound which can severely damage citrus bark when applied directly (Samways & Tate 1984). In addition, *H. patruelis* feeding removes more phloem from unbanded than banded branches, although this apparently has no detrimental effects in terms of progeny or seed reduction (Chapter 5). A decrease in progeny production could also result in false positive correlations between ant and *C. capensis* number, but this possibility cannot be tested directly as only one unbanded branch had zero ants. However, if banding did affect progeny production, we would expect only wasp numbers and not proportions to change between banded and unbanded branches, unless reduced phloem flow affected species differentially, which seems unlikely. In fact, proportionality patterns are similar to those of absolute numbers, so that a banding effect is unlikely.

The finding of S. Compton & H. Robertson (unpubl. data) that *A. guineensis* sex ratios were male biased (greater than 50% males) in the absence of ants, but more female biased when ants were present and the *A. guineensis* wasp densities were greatly reduced, was not reflected in this study. This is possibly due to the lower overall *A. guineensis* densities in this study, which resulted in a move away from superparasitism, and therefore male bias, even in the absence of ants.

Several complementary factors can be invoked to explain the frequently erratic patterns of change in wasp numbers in the presence of ants, both within and between trees, obtained in this and Compton & Robertson's (1988, 1991) studies. Patchiness in the spatial distribution of ants within a branch was often high, as ants frequently clustered with *H. patruelis* on only a few figs, so that some figs received high "protection" while neighbouring figs received little. Although *H. patruelis* and consequently ants shifted around over the fruiting period, ants are only useful in providing protection against externally ovipositing species during the periods in fig development when these species oviposit. Thus only those figs with high ant numbers during these critical periods (which vary between wasp species) were likely to benefit. Much larger sample sizes are necessary at each ant density to reduce variance caused by the patchiness of effects sufficiently to elucidate trends. Alternatively, individual figs should be monitored through their development.

Considerable variability is also induced by the biology of the fig and its wasps. Intraspecific variability in fig size and floret number has been recorded for a number of species, including *F. sur* (Galil & Eisikowitch 1968; Berg 1990; Bronstein 1992; pers. obs.). The numbers and proportions of all wasp species arriving at a tree vary (Bronstein 1991) as a function of the presence of male-phase trees in the vicinity, the prevailing weather conditions and other such factors.

Finally, there is much that we do not understand about the inter-relationships between the wasp species within the figs, and very little is known about the ecology of the non-pollinating fig wasps although they are very important to the pollinator-fig mutualism (Bronstein 1991). Without knowing how the relationships between wasp species change with wasp density and similar variables, it is difficult to predict the exact patterns of change with changes in ant density. Many parasitoids can determine the species, age, density, size and state of parasitism of potential hosts before ovipositing (van Alphen & Vet 1986). It is therefore reasonable that externally ovipositing fig wasps, both parasitic and other, can assess the suitability of a fig before they oviposit (Bronstein 1991). For example, Bronstein (1991) found that the probability of oviposition by *Idarnes* sp. in *F. pertusa* was correlated with the pollination status of the figs: unpollinated figs abort and therefore represent wasted eggs to *Idarnes*. Aggregation of large numbers of *A. guineensis* on certain figs (pers. obs.) may indicate that they can determine the correct host stage for parasitism. This is also supported by evidence that eggs are not laid into figs immediately after pollination and for a week or two before the progeny emerge (S. Compton pers. comm.). It is feasible that parasitism rates by *A. guineensis* are density dependent with respect to host number, i.e. that a large fig has a different percentage of parasitism to a small fig. In field experiments parasitism levels by various species have been shown to be density independent, or positively or inversely density dependent with respect to host numbers (Lessells 1985; Walde & Murdoch 1988). This relationship can vary within a single species pair (Lessells 1985). The possibility that *A. guineensis* may prefer one host species over another can also not be ruled out. This preference may change with changing relative abundances of the host species (Van Alphen & Vet 1986) and explain variation in the effects on *C. capensis* versus *S. cyclostigma*, for example. Certain *Apocryptophagus* species, with very large body sizes, might also be preferred hosts, because they produce very large female *Apocrypta* progeny, which should have advantages in terms of egg load and longevity.

8.4.3 Implications for the fitness of the tree

The pollinating wasp of *F. sur*, *C. capensis*, gathers pollen before it leaves its natal fig, and carries it to a female-phase fig on the same or another tree. It thus affects the male fitness of its natal tree. By reducing parasitism by *A. guineensis* and competition by *Apocryptophagus*, ants increase the numbers of pollinator progeny produced, and therefore the male fitness of the tree. The effects of ants on the female fitness of the tree (seed production) are potentially ambigious, as they reduce *Apocryptophagus* numbers and thus competition for pollination sites, but promote *S. cyclostigma*, which also competes for pollination sites. However, this was not investigated in the present study.

By reducing parasitism by *A. guineensis* and competition by *Apocryptophagus*, ants not only benefit the pollinators, but also the pollinators' competitors. The benefits accruing to the pollinators and the tree vary as a function of on the numbers and proportions of the non-pollinating wasp species in relation to *C. capensis*. For example, if few pollinators and mainly

S. cyclostigma are present, as in tree 2 in this study, then a decrease in external ovipositors will benefit a *C. capensis* competitor. Similarly, if *A. guineensis* parasitism rates are very low, as in tree 1, benefits of ants to *C. capensis* will also be small. They may even have a negative effect on *C. capensis* if reduction in foundress number cannot be offset by reduction in parasitism.

In conclusion, we can expect a gradient of benefit of ant presence, in terms of both male and possibly female tree fitness, as a function of ant species and density, as well as of the wasp progeny composition. Ants have an increasingly positive effect at between zero and two ants per fig and possibly at higher densities. The 2.65 ants per fig on high density branches corresponded to an increase of 28% in pollinator numbers, while that of 1.30 per fig on unbanded branches for the combined data from the eight trees corresponded to a 44% increase (although neither of these differences was statistically significant due to high variances). The latter ant density is not much higher than that of the average ant density at the study sites of 0.93 ants/fig at 2m height calculated for the whole monitoring period (Chapter 4). Although *P. megacephala* numbers at 2m height are overestimates of mean numbers per fig over the whole tree (Chapter 4), ants must nevertheless have a positive effect on the male fitness of *F. sur* trees in the population as a whole, by preying on competitors and parasitoids of the trees' pollinators. This must be balanced against the negative effects of ant predation on emerging wasp progeny, which are quantified in the following chapter.

9 THE EMERGENCE OF WASP PROGENY FROM MALE-PHASE FIGS: EMERGENCE BIOLOGY AND PREDATION BY *PHEIDOLE MEGACEPHALA*

9.1 INTRODUCTION

Ants are attracted to plants by various types of food, as well as by nesting sites (Beattie 1985; Hölldobler & Wilson 1990). Depending on the species, plants provide ants with both solid prey, in the form of arthropods and seeds, and liquid nutrients, mainly in the form of honeydew secreted by homopterans and extrafloral nectar produced directly by the plants. These liquid nutrients provide one of the few stationary and persistent food sources available to ants (Carroll & Janzen 1973) and therefore often result in the long term presence of high ant numbers on the plant. Ants tending homopterans commonly affect plants negatively, as they promote growth rates and population numbers of the homopterans, resulting in increased sap loss and often pathogen transmission (Beattie 1985; Buckley 1987b). However, in a few recent studies ants have been shown to indirectly benefit the plants on which they tend homopterans, by opportunistically preying on other plant herbivores (Laine & Niemelä 1980; Messina 1981; Bach 1991; Ito & Higashi 1991). Very few of these studies assess the relative costs and benefits to plants of ant presence, i.e. which set of conditions there is an indirect ant-plant mutualism operating. The importance of such conditionality in mutualisms has only recently been emphasised (Cushman & Addicott 1991).

In the genus *Ficus*, the larvae of all species of agaonine fig wasps develop in the galled ovules and then pupate. The details of wasp behaviour during the male phase of fig development differ between fig species (Galil & Eisikowitch 1974; Frank 1984) but has been described by Galil & Eisikowitch (1968, 1974) for *F. sycomorus*, which is closely related to

F. sur. At the beginning of this phase male pollinators (*C. arabicus* Mayr in *F. sycomorus*) chew their way out of their galls and enter the lumen. They locate female wasps in galls, chew a hole into the gall, and mate. As the females emerge the male pollinators are detaching the anthers, which now contain ripe pollen. The anthers fall to the floor of the lumen, from where the female pollinators fill their pollen bags. The male pollinators then bore one or more tunnels through the ostiole, and the females exit the fig and fly away in search of a female-phase fig in which to oviposit and pollinate. In *F. sur*, males of the pollinator, *C. capensis*, usually bore the exit tunnels. Galil & Eisikowitch (1968) found that in *F. sycomorus*, *Sycophaga sycomori* L. females were also capable of this task. Although *S. cyclostigma* males were never recorded boring exit tunnels in the current study, this species frequently occurs without pollinators in *F. sur* figs in Natal (S. Compton pers. comm.), suggesting that they may be able to escape from the figs themselves. However, Baijnath & Ramcharun (1983) stated that in the absence of the pollinator, no wasps could escape from *F. sur* figs. Once wasps have emerged from the fig it ripens and the seeds are dispersed by various vertebrates and ants (Breitwisch 1983; Thomas 1988; Kaufmann *et al.* 1991).

Ants have been recorded preying on fig wasps both arriving at and leaving fig trees (Frank 1984; Bronstein 1988, 1991; Compton & Robertson 1988, 1991; pers. obs.), as have dragonflies, birds, staphylinid beetles and phorid and asilid flies (Janzen 1979; Bronstein 1988; Compton & Disney 1991; S. Compton pers. comm.). On *F. sur*, ants, and particularly *Pheidole megacephala*, are attracted to figs by the honeydew-producing homopteran *Hilda patruelis*. They prey on *C. capensis* and *S. cyclostigma* females as they enter the ostioles of female-phase figs, and on ovipositing *Apocryptophagus* and *A. guineensis* on the outside of the figs. They have been shown to have a greater effect on the externally ovipositing species, thus reducing competition and parasitism and increasing the number of pollinators produced (Compton & Robertson 1988, 1991; Chapter 8). The reduction in *Apocryptophagus* also probably increases seed set by making available more ovules for pollination. Thus ants can indirectly have a positive effect on the male and possibly the female fitness of the tree. The presence of *H. patruelis*, which is dependent on ants (Chapter 6), produces no detectable effect on seed or wasp progeny production (Chapter 5). Therefore ants have so far been shown to have no negative effects on the tree. However, they also prey on all species of wasp progeny emerging from male-phase figs. It is the object of this chapter to quantify these negative effects and to assess their importance in decreasing the survivorship of wasps of the next generation. *P. megacephala* is the only ant predator considered, as it is by far the most frequently observed ant on the trees, both in Grahamstown (Chapter 4) and throughout southern Africa (Cushman *et al.* in prep.). The chapter also characterises the biology of wasp emergence and ant predation and addresses the question of whether male wasps emerging from the fig keep the ants occupied by sacrificing themselves and thus decrease predation on female wasps. For convenience figs from which wasps are emerging or have emerged are referred to as "emerging" and "emerged" figs.

9.2 MATERIALS AND METHODS

Male-phase figs from four crops on three trees, all at site 1, were monitored for emergence patterns and predation of the emerging wasps by ants. Large crops with varying numbers of *P. megacephala* present on figs were selected. Figs from which wasps are to emerge the following day are usually identifiable as they change colour from dark to olive green, and become shiny and slightly softer. On each occasion figs were individually marked on the afternoon before the day they were predicted to emerge. The numbers and activities of *P. megacephala* workers on the figs were recorded, as were their numbers on the whole fruiting branch on which marked figs were growing and the numbers and developmental stages of all figs on the fruiting branch. The following morning the numbers and activities of ants on marked figs were again recorded at regular intervals before and during wasp emergence, and for up to two hours after emergence. The numbers of ants on whole fruiting branches were recorded at longer intervals. The timing and duration of the different stages of wasp emergence, the numbers of each species, the sexes of emerging wasps, and their behavioural activities were recorded for selected marked figs. *C. capensis* and *S. cyclostigma* females were indistinguishable under the observational conditions and were recorded together. Ant activities, the numbers of each species, the sexes of wasps captured by ants and the numbers of ants occupied with these wasps were also noted. Temperatures at the time of emergence were also recorded for crops 3 and 4. On the afternoon of the same day as emergence (or for crops 1 and 2, the following day) ant numbers and activities were again recorded on marked, emerged figs. These were then split open and the number of ants in the lumen counted. Fig developmental stages were again recorded at this time.

Data on ant predation rates and numbers of ants occupied with male and female wasps were collected from other marked and non-marked figs, both on the four crops and a fifth at site 1. Numbers of ants on several emerged versus non-emerged figs were recorded for crops 3 and 4. On a sixth crop, at site 2, the length of time between wasp capture and removal was recorded for male *C. capensis* and female internal ovipositors.

9.3 RESULTS

9.3.1 Biology of wasp emergence

A total of 15 figs was monitored fully: three from each of crops 1 and 3, and four from each of crops 2 and 4. Emergence times ranged from 05h55 to 07h46 for crops 3 and 4 in the summer months of December and February respectively, and from 07h41 to 09h52 for crops 1 and 2 in April (autumn). On crops 3 and 4, wasps began to emerge from figs at temperatures ranging from 15°C to 23°C. Male *C. capensis* bored one or two common exit tunnels through the bracts of the ostiole. These tunnels reached the outer surface of the ostiole in the morning. The length of time between the appearance of the tunnels and the emergence of the first male wasp was often only a few seconds but on occasion stretched to over an hour. A number of male *C. capensis* crawled from the tunnels onto the fig surface (Table 9.1), and in the absence of ant predation they remained on the fig near the ostiole, or fell off if the ostiole was angled towards the ground. Males emerged from the tunnels at an increasing rate and were usually followed by a burst of female emergence after a variable length of time (Table 9.1). The females of all species were interspersed with one another as they emerged, and emerging wasps often appeared to be pushed out by pressure from wasps inside the lumen. For most figs the interval between the appearance of the first female and the point at which less than five females per minute were emerging was an accurate measure of peak female emergence time (Table 9.1). After a few minutes of peak emergence activity by females, among which there were usually interspersed a few more male *C. capensis*, the emergence rate usually tailed off rapidly, but small numbers of wasps continued to appear for a few minutes. An average of 27.23 ± 9.79 *C. capensis* males emerged over the whole wasp emergence period (male 1 to < 5 wasps/min), but very few non-pollinator males exited the fig.

Females of internally ovipositing species therefore emerged at a mean rate of 0.651 ± 0.210 wasps per second during the second interval (female 1 to < 5 wasps/min), and emergence rates ranged between 0.392 and 1.0 wasps per second. In the initial burst of females emergence, however, rates were higher. Variation in the emergence rate and length of the emergence period for females varied partly as a function of the ease of exit - some figs had convoluted bracts or narrow exit tunnels - and probably also the number of wasps in the lumen and ambient temperature. Females flew away immediately or a few seconds after emergence - this again depended partly on the angle of the ostiole to the ground and on the temperature. Under cold conditions females tended to remain on the fig surface longer. In order to determine whether *A. guineensis* females tended to emerge after those of internally ovipositing species, the numbers of *A. guineensis* emerging during the first half of the female emergence interval were compared to those emerging during the second half using a Wilcoxon Signed-Ranks Test; no significant difference was present ($Z = 1.079$, $p = 0.281$; $n = 6$ pairs).

Although the wasps from most figs were observed to emerge in the morning, this was not always the case. Wasps were observed emerging from figs of a fifth crop in January (summer) at about 16h00 at an extremely slow rate (0.0167 and $0.0593s^{-1}$ respectively for two figs), although the time of male emergence was unknown for these figs, and it is possible the tunnel had been cut early that morning.

9.3.2 Ant predation on emerging wasps

Ant densities on the 15 figs were calculated for five time intervals relating to wasp emergence (Table 9.2) as well as for the whole of each monitoring event. Initial ant densities (including data from the previous afternoons until half an hour before emergence) of *P. megacephala* workers were 5.58 ± 6.28 ants per fig, with a range from 0.5 to 20.3. Over the whole monitoring period a mean of 10.08 ± 9.22 ants per fig were present. The ants were either tending *H. patruelis* or, on a few figs, simply walking around on the fig surface.

On figs on which a large number of ants were initially present, the wasp exit tunnel was often discovered by them as soon as it appeared, whereas on some figs on which no ants or

Table 9.1. Duration of wasp emergence and numbers of wasps emerging from male-phase figs.

parameter	no. crops	no. figs	interval	
			male 1-female 1	female 1-<5/min
duration ± SD (min,s) (range)	4	15	7,57 ± 9,26[1,2] (0,38-101)	8,42 ± 2,47 (5-15)
no. male *C. capensis* ± SD	4	15	17.60 ± 7.75	9.57 ± 7.36
no. female internal ovipositors ± SD	4	15	-	327.2 ± 124.7
no. *A. guineensis* ± SD	2	6	-	11.7 ± 18.9

1: n = 8 figs (crops 3 & 4) for mean ± SD
2: median value = 3min (n = 15 figs)

Table 9.2. Numbers of *P. megacephala* workers on male-phase figs before, during and after wasp emergence. The emergence interval is from the appearance of the first male until less than five females per minute.

crop	no. figs	no. ants at each interval (SD)					
		>30min pre-emergence	30-0min pre-emergence	emergence	0-30min post-emergence	>30min post-emergence	total
1	3	7.21 (11.3)	10.9 (15.0)	12.9 (19.8)	16.5 (26.4)	11.6 (15.8)	12.1 (17.7)
2	4	2.80 (2.91)	3.92 (2.12)	8.63 (5.94)	10.3 (7.09)	7.55 (6.15)	6.22 (3.35)
3	3	2.0 (1.50)	2.25 (2.54)	3.30 (2.62)	3.50 (1.80)	8.92 (11.6)	3.40 (2.60)
4	5	8.97 (5.71)	14.6 (7.83)	19.6 (5.96)	19.1 (8.10)	11.3 (5.31)	15.9 (5.89)
total	15	5.58 (6.28)	8.56 (8.97)	12.1 (10.7)	14.0 (13.0)	9.90 (8.60)	10.1 (9.22)

Table 9.3. Numbers of ants on emerged (E) and non-emerged (NE) figs.

crop	sample	no. figs		no. ants per fig (SD)		Mann-Whitney U	
		NE	E	NE	E	Z	p
3	1	5	5	0.40 (0.55)	31.1 (15.8)	2.546	0.0109
	2	5	5	0.40 (0.55)	5.0 (3.32)	1.844	0.0652
4	3	4	4	10.0 (5.42)	14.5 (5.0)	1.016	0.309
	4	5	4	7.20 (2.49)	20.8 (7.14)	2.337	0.0194

only one ant was present, it was not discovered at all. Ants frequently became excited, sometimes attempting to enter the tunnel and occasionally reversing rapidly from it, as if they had been bitten. Once male wasps had emerged from the tunnel they were attacked and "subdued" by one or more ants and eventually carried off the figs. As female wasps emerged they were treated in the same way. However, as the females were more agile and left the fig surface soon after they had emerged, ants had more difficulty in capturing them. Recruitment of ants onto the figs occurred in proportion to the initial number on the figs. On the 15 figs monitored, ant numbers increased from what was usually their lowest value in the sequence to a peak during emergence or in the half-hour following the event (Table 9.2), and then slowly decreased. The mean ant density in the half-hour after emergence was 2.5 times that of initial ant numbers for the whole sample. Initial ant number was highly significantly correlated with numbers during these following two periods (Spearman Rank Correlation: $r = 0.930$, $p = 0.0008$; $r = 0.879$, $p = 0.0015$ respectively), indicating that the number of ants recruited was related to their initial numbers on the figs. The attraction of ants to emerging or emerged figs was confirmed by comparing numbers of ants on emerged and non-emerged figs for two samples on each of crops 3 and 4 (Table 9.3). There was often great activity on the part of the ants during emergence, with large numbers moving onto and off the fig, and attacking, subduing and carrying wasps.

Ants sometimes removed male *C. capensis* from inside the exit tunnel after emergence, and over the next few hours entered the lumen and removed male wasps, mainly those of *S. cyclostigma*, *Apocryptophagus* spp. and *A. guineensis* (see Chapter 7). Ants entering the figs also removed any female wasps that remained, as well as loose plant parts such as anthers, and they cleaned and widened the exit tunnel.

Ants captured between one and 28 male *C. capensis* per fig, representing 3.3-68.4% of those emerging, with a mean of 9.13 ± 10.02 (33.5%) males. They captured between zero and 33 female internal ovipositors, representing 0-12.7% of these females emerging, with a mean of 9.87 ± 11.89 (3.02%) females (Fig. 9.1a, b). Only one *A. guineensis* female was observed to be captured, on the fig with the highest mean number (32.5) of ants. The number of male *C. capensis* and females of the internally ovipositing wasps captured by ants was significantly positively correlated with overall ant numbers over the whole period on the fig (Spearman Rank Correlation: r = 0.756, p = 0.0047 for males; r = 0.722, p = 0.0069 for females) as were the proportions of the total wasps caught while emerging (Spearman Rank: r = 0.668, p = 0.0125 for males; r = 0.749, p = 0.0051 for females).

There was no significant correlation between the number of ants on a whole fruiting branch over the entire period and initial ant numbers on individual figs on the branch (Spearman Rank: r = 0.270, p = 0.313) or between the former and those at emergence on individual figs on the branch (r = 0.301, p = 0.279). This confirms the observation that ant distribution on fruiting branches was patchy and that recruitment to emerging figs was very localised, so that a fig at the end of a branch on which there was a large number of ants closer to the base might have no or few ants on it, and no recruitment as its wasps emerged. This patchiness in the effects of ants on the wasps was also detected during the experiments discussed in Chapter 8.

The number of ants in the lumens of figs on the afternoon of the day on which wasps had emerged from them, or the following afternoon, varied from zero to 20. On crops 1, 2 and 3 very few ants were present (0.33 ± 0.58, 0.14 ± 0.38 and 1.50 ± 1.78 respectively) while on crops 4 and 5 18.33 ± 1.53 and 9.64 ± 4.50 ants were counted per lumen. The number of ants in the lumen were significantly positively correlated with the initial numbers on the fig (Spearman Rank: r = 0.820, p = 0.0021).

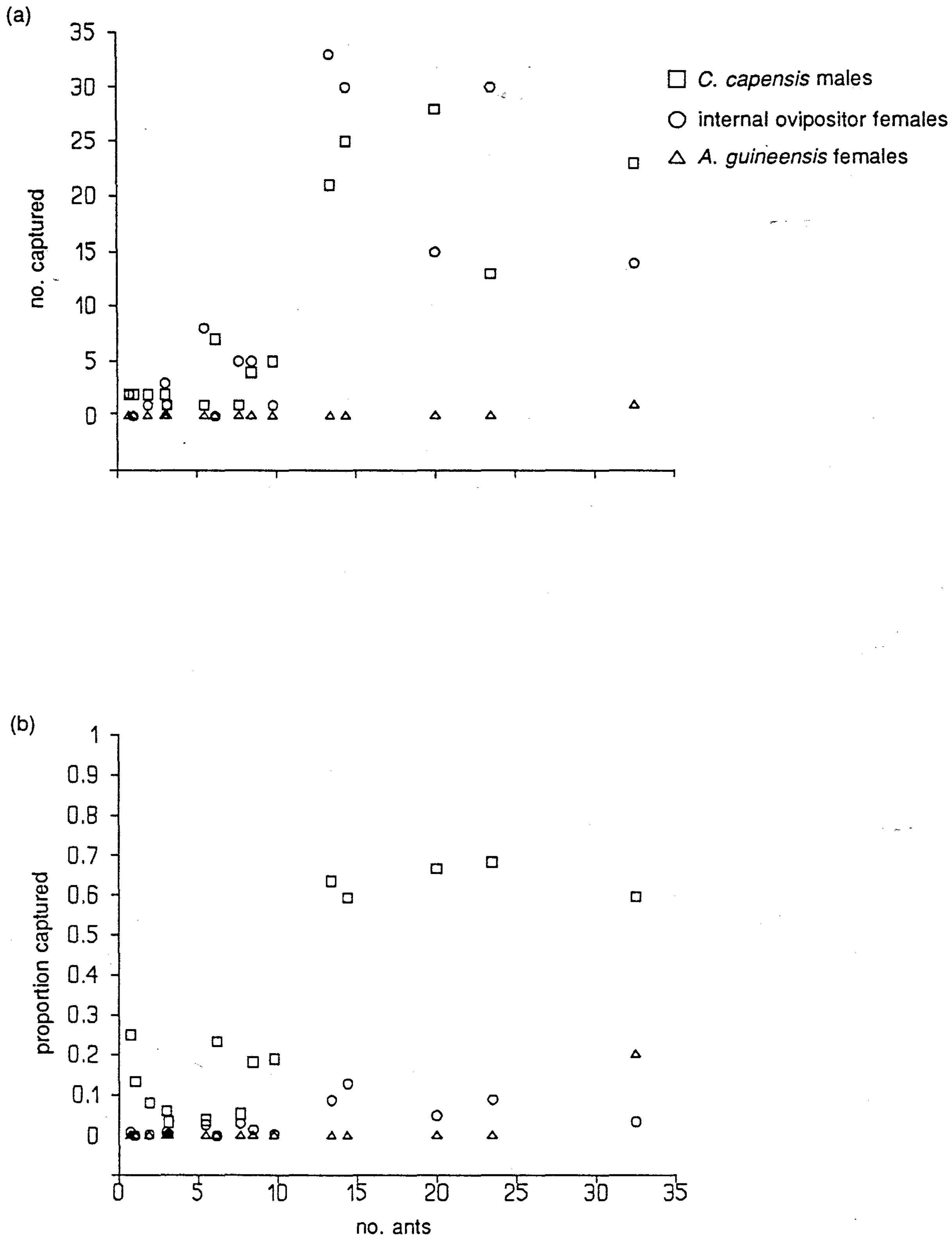


Figure 9.1. Numbers of ants on monitored *F. sur* figs (means for whole monitoring period) versus a) numbers and b) proportions of male *C. capensis*, female internal ovipositors and female *A. guineensis* captured while emerging from male-phase figs.

9.3.3 Factors affecting predation of female wasps by ants

The previous observations and results suggested that several possible factors reduced females' chances of being attacked by ants. Females were more agile than males and left the fig as soon as they had emerged; they usually emerged from the fig in a burst and therefore saturated the ant predators present, thus avoiding the higher recruitment and predation which would probably occur over a longer, slower emergence event; they usually emerged in the early morning when ant activity was at its lowest (Chapter 7); and finally the male *C. capensis* which emerged onto the fig surface could "mop up" and occupy ants which would otherwise be free to prey on females. Several of these possibilities were investigated further.

No significant correlation was present between the rate of female emergence and the proportion of the total number of emerging females that were captured (Spearman Rank: $r = 0.152$, $p = 0.570$, $n = 15$). However, none of the 15 figs monitored had very low emergence rates, and therefore the wasps probably saturated the ant predators in all the figs. A positive correlation between emergence rate and the proportion of wasps captured would only be expected for a much lower emergence rate. Very low emergence rates were recorded for the last few wasps emerging from figs on crops 1 to 4 and for the fifth crop monitored, where all of the seven females from one fig were captured by ants as they emerged at a rate of $0.0167s^{-1}$. On a second fig on this crop, wasps emerged at $0.0593s^{-1}$ and 54.7% of the 64 emerging females were captured. However, these high capture rates were also partly due to the high ant numbers on these figs during wasp emergence (30 on fig 1 and 100 on fig 2).

The first male wasps to emerge onto the fig surface occupied any *P. megacephala* which were present on the fig at the time. Only when the ants removed the wasps from the fig and came into contact with other ants could recruitment occur. Thus, after the ants initially on the fig became occupied with wasps, and before more ants had been recruited, wasps were not preyed upon. The importance of this effect was a function of both the time lag before recruitment occurred as well as the duration of wasp emergence.

Male *C. capensis* were usually attacked initially by three to four ants and females by one to two, possibly both because males were stronger and needed more attention and because ants rapidly became saturated with emerging females. As the wasps were subdued the number of ants in contact with each wasp frequently decreased, and often a single ant carried the wasp off the fig and up the branch. A single male *C. capensis* occupied a mean of 2.63 ± 1.36 *P. megacephala* (n = 254 counts) while it was on the fig, in comparison to 2.08 ± 0.91 ants (n = 176 counts) occupied by one female internal ovipositor. This difference in ant number attacking a male *C. capensis* versus a female internal ovipositor was highly significant (Mann-Whitney U: Z = -3.947, p = 7.93×10^{-5}). A single count of four ants was recorded for *A. guineensis* but this was for an initial attack. The time taken between the capture and removal of a single male *C. capensis* was 91.6 ± 18.7s (n = 5 wasps) and of a female 64.3 ± 81.3s (n = 12 wasps), again indicating that males were harder to subdue. The length of this period was especially variable for females (from 10s to 4min 39s). Nonetheless, all five males but only three females took more than a minute to be removed. The other nine females were removed after 24.1 ± 11.6s. If the three former females are included, the difference in timing is non-significant (Mann-Whitney U: Z = -1.528, p = 0.126) but it becomes significant (Z = -2.933, p = 3.35×10^{-3}) once they are removed. It appears therefore that, although most females are removed after a much shorter time than males, some females occupy ants for a long period. That this difference may reflect a dichotomy between *C. capensis* and *S. cyclostigma* cannot be ruled out.

One female internal ovipositor occupied an average of 2.08 ants for 64.3s; the product of this is 133.7 "ant seconds". One male *C. capensis* occupied 2.63 ants for 91.6s, resulting in a product of 240.9 "ant seconds". Therefore in terms of ant occupancy with captured wasps on the fig, one male is equivalent to 1.8 females. The calculated mean for the 15 figs of 9.13 males captured therefore translates to 16.4 females saved per fig, or 5.01% of the females emerging. This figure is greater than the 3.02% of females captured by ants in the presence of males and suggests that the males cut ant predation of females by about 65%. However, this calculation assumes that a female is as easy to catch as a male. While it is doubtful that this is so, this parameter was not measured, and could only be assessed by determining the percentage of successful capture attempts for males versus females and the length of time taken to capture a male versus a female. However, "mopping up" by males is probably still significant in reducing predation by ants on female progeny emerging from a fig.

For each fig the estimated numbers of females saved due to the presence of *C. capensis* males was determined by multiplying the number of males captured by 1.8. There was a significant correlation between this value and the number of ants on the figs at emergence (Spearman Rank: $r = 0.714$, $p = 0.010$, $n = 15$), so that the presence of males became more valuable to the females as ant densities increased. However, no significant correlation was present between the savings and the sex ratios of emerging wasps for each fig (no. males/(no. males+females)) ($r = 0.213$, $p = 0.425$). Therefore the numbers of females saved were not necessarily greater when a higher fraction of males was present. These results may have been confounded by the presence of *S. cyclostigma* females, however.

9.4 DISCUSSION

9.4.1 Emergence biology

The wasp progeny from most of the male-phase *F. sur* figs monitored in this study emerged during the morning. Wasps from *F. burtt-davyi* Hutch. also emerged largely during the morning in Grahamstown (Ware & Compton 1994), whereas in Kenya, wasps from *F. sycomorus* emerged in the early evening (Galil & Eisikowitch 1974), and in Zululand *Ceratosolen galili* Wiebes, also from *F. sycomorus*, emerged in the early afternoon (Compton *et al.* 1991). For *F. burtt-davyi*, the time at which wasps emerged from their figs was strongly correlated with temperature, particularly that of the previous evening. Female pollinators (*Elizabethiella baijnathi* Wiebes) flew in the laboratory at 15°C but at lower ambient temperatures in the field, probably due to direct solar irradiation (Ware & Compton 1994). It is therefore probable that temperature is the most important cue for pollinator emergence, although additional cues such as changing light intensity cannot be ruled out. Ware & Compton (1994) concluded that the timing of emergence optimised conditions for wasps searching for a receptive tree in which to oviposit, in terms of environmental factors such as wind speed and temperature. In addition, *E. baijnathi* (Ware & Compton 1994) and *C. capensis*, like most fig wasp species, are diurnal, so that emerging early in the day would allow a greater length of searching time. *Ceratosolen arabicus* Mayr, the pollinator of *F. sycomorus*, is specifically a nocturnal flier, however (Ware & Compton 1994) - this may be related to the environmental conditions under which the tree grows. In Zululand, *C. galili* is diurnal, and Compton *et al.* (1991) suggested that this may have resulted in its apparent rarity in dry habitats, through being prone to dehydration. The importance of pollinators emerging at an optimal time is increased by their short lifespan. Compton *et al.* (1994) found that *C. capensis* lived for 1-3 days in the laboratory, and Kjellberg *et al.* (1988) recorded a maximum longevity of at least 48 hours for *Blastophaga psenes* (L.) in the field.

Virtually all the wasps had emerged from the monitored *F. sur* figs within 10-15 minutes of the start of emergence. By comparison, one hour after the exit hole had been cut 90% of pollinators but only 25% of interlopers had emerged from *F. pertusa* L. figs (Bronstein 1988). The behaviour of *Pegoscapus assuetus* Grandi and *P. jimenezi* Grandi, the respective pollinators of *F. aurea* Nuttall and *F. citrifolia* P. Miller, two species in the section *Urostigma*, during the male phase of fig development is different from that in *F. sur* and *F. sycomorus*. Male pollinators create the exit hole before females emerge from their galls (Frank 1984); a much slower, longer emergence can therefore be expected. *F. pertusa* is also in the section *Urostigma* and is pollinated by *Pegoscapus silvestrii* Grandi. Similar male-phase behaviour would explain the slow emergence rate of these wasps. Similarly, wasp emergence in *F. sycomorus* can be expected to be similar to *F. sur* as both are pollinated by *Ceratosolen* species and are in the section *Sycomorus*.

9.4.2 Ant predation on emerging wasps

Male pollinators played a significant role in protecting females from ants by reducing predation on them by up to more than 50%. Males are therefore involved in all parts of the male phase of fig development: they mate with females through holes they cut in the females' galls, thereby facilitating the females' emergence from the galls, they detach anthers, they bore an exit hole and finally they mop up ants. At this point males have zero direct reproductive fitness because they have finished mating and have bored the exit tunnel, but by reducing predation of those females with which they have mated they can indirectly increase their fitness, as well as that of the females (and the tree). Such behaviour might therefore be potentially adaptive. Interestingly, the presence of *S. cyclostigma* females could be expected to have the same effect, namely occupying ants that would otherwise attack *C. capensis* females.

Ants were shown in this study to remove up to 68.4% of emerging male pollinators emerging and up to 12.7% of female internal ovipositors with respective means of 33.5% and 3.02%. These predation rates were at an initial ant density of 5.58 ants per fig, which is high compared to the means of 1.30 for Chapter 8 and 0.93 calculated at 2m for the whole *F. sur* population studied (Chapter 4). The results presented here therefore show the potential for male reduction of female predation, but are not typical for the population as a whole.

The importance of predation by ant species other than *P. megacephala* on *F. sur* (Chapter 4) was not examined, but can be expected to be a function of their abundance, predatory behaviour and to a small extent size: larger ants cannot enter the lumen to prey on wasps, but will need fewer workers per prey item.

If we consider unbanded branches with a mean density of 1.30 ants per fig to be the norm, *C. capensis* numbers decreased by 30.5% and those of internal ovipositors by 22.9% in the absence of ants, due to pressure from the parasitoid *Apocrypta guineensis* and the *Apocryptophagus* competitors (Chapter 8). Female wasps comprised 73.4% of *C. capensis* and 74.3% of internal ovipositors (unpubl. data) on unbanded branches. Therefore *C. capensis* females are reduced by 27.2% and those of the combined internal ovipositors by 20.6% on branches without ants, as compared to branches with 1.30 ants per fig. During progeny emergence, ants (at a mean of 5.88 per fig) removed a mean of 9.87 female internal ovipositors per fig. In the absence of ants, therefore, 3.13% more females would successfully leave the fig. Thus the net effect of removing ants from figs over the entire developmental period is a reduction of 17.5% in female internal ovipositor production, i.e. the positive effect of ants to internal ovipositors in removing parasitism and competitive pressure from external ovipositors far outweighs their negative effects as predators on emerging wasps and their impact on foundress females. If ant numbers per fig for Chapter 8 (1.30) and Chapter 9 (5.88) had been standardised, ant predation rates on emerging wasps may have been even lower, and the benefits of ants even greater.

Our main interest is in *C. capensis* as it is the pollinator of *F.sur*, and is affected far more than *S. cyclostigma* by ants via changes in parasitism pressure (Chapter 8). *C. capensis* comprised 70.5% of the combined internally ovipositing females on unbanded branches (Chapter 8). If we assume that ants prey on the two species of emerging internal ovipositor females in proportion to the numbers emerging, then ants remove a mean of 6.96 *C. capensis* per fig. In the absence of ants, therefore, there is a net reduction of 24.2% in *C. capensis* numbers produced per fig, so that the negative effects of ant removal throughout the figs' developmental period are even higher for *C. capensis* than for the internally ovipositing species combined.

It is possible that ants prey differentially on different species of emerging female wasps either because some species are easier to catch than others or because they differ in their emergence time and rate. Bronstein (1988) found indirect evidence in *F. pertusa* that interlopers, which left at a slower rate than pollinators, were more heavily preyed on by staphylinid beetles which entered the lumen via the exit tunnel - pollinators escaped before the beetles arrived. No differences between the timing of female emergence were detected in this study, but *A. guineensis* may be stronger and more difficult to catch than *C. capensis* or *S. cyclostigma.*

Predation by ants on females emerging from *F. sur* figs was reduced in several ways: males "mopped up" ants; females emerged at a high rate, were very agile and spent only a short time on the fig surface; and wasps emerged at a time of day when ant numbers were at their lowest (Carnegie 1960; Chapter 7). How likely is it that these traits have been selected in response to wasp predation by ants? More simple explanations can be found for most traits: emergence time can be related to success in finding receptive figs; males necessarily emerge onto the fig surface after boring an exit tunnel; and the pressure of females in the fig may cause rapid emergence. The strongest argument against these traits being selected to decrease ant predation of females is that in the whole fig population ant predation pressure on emerging wasps is very low, especially in comparison to other mortality factors during the free-living phase. Possibly in fig species with lower emergence rates the predation rate by ants and other insects would be more significant, although Bronstein (1988) believes that even for *F. pertusa* in-flight mortality is more important than that on the trees.

No quantitative measures have been made of the percentage mortality between leaving a natal fig and arriving at a receptive female-phase fig for wasps from *F. sur*. However, an estimated 95% of emergent female *E. baijnathi* from *F. burtt-davyi* fail to enter receptive figs (Compton & Robertson in prep.). Herre (1989) and Berg (1990) assumed a constant number of figs producing wasps and becoming receptive, and expressed pollinator success rate as the ratio of mean foundress number per fig to mean number of females produced per fig. The success rate ranged from one in 20 for *F. mathewsii* to one in 120-180 for *F. ottoniifolia* (Miq.) Miq. (Berg 1990). For *F. sur*, using a mean of 144.2 female pollinator progeny produced per fig and 3.25 foundress pollinators per fig (Chapter 8) results in one in 44.4 pollinators (2.25%) entering a receptive fig - this encompasses ant predation on both emergent and receptive figs and the in-flight mortality between (Fig. 9.2). At a mean of 3.02% ant predation of emerging *C. capensis* females, 139.8 females successfully leave each fig. Therefore a success rate of 2.32% after predation on emerging wasps is necessary to produce a mean of 3.25 foundresses per receptive fig on trees with ants present through their entire developmental cycle. If ants were absent from emerging figs, and assuming that density dependent mortality does not occur, a 2.32% success rate would yield 3.35 foundresses per fig, an increase of 2.94% (Fig. 9.2). However, an absence of ants on the producing crop over its entire developmental period would result in the production of only 104.9 *C. capensis* females per fig due to increased parasitism or competition (Chapter 8). At a 2.59% success rate (which takes into account the absence of ants on receptive female-phase figs (Chapter 8)) this translates to 2.71 foundresses. This represents a substantial reduction of 19.1% from the 3.35 foundresses when ants were absent only at emergence (Fig. 9.2). Thus, the decrease in

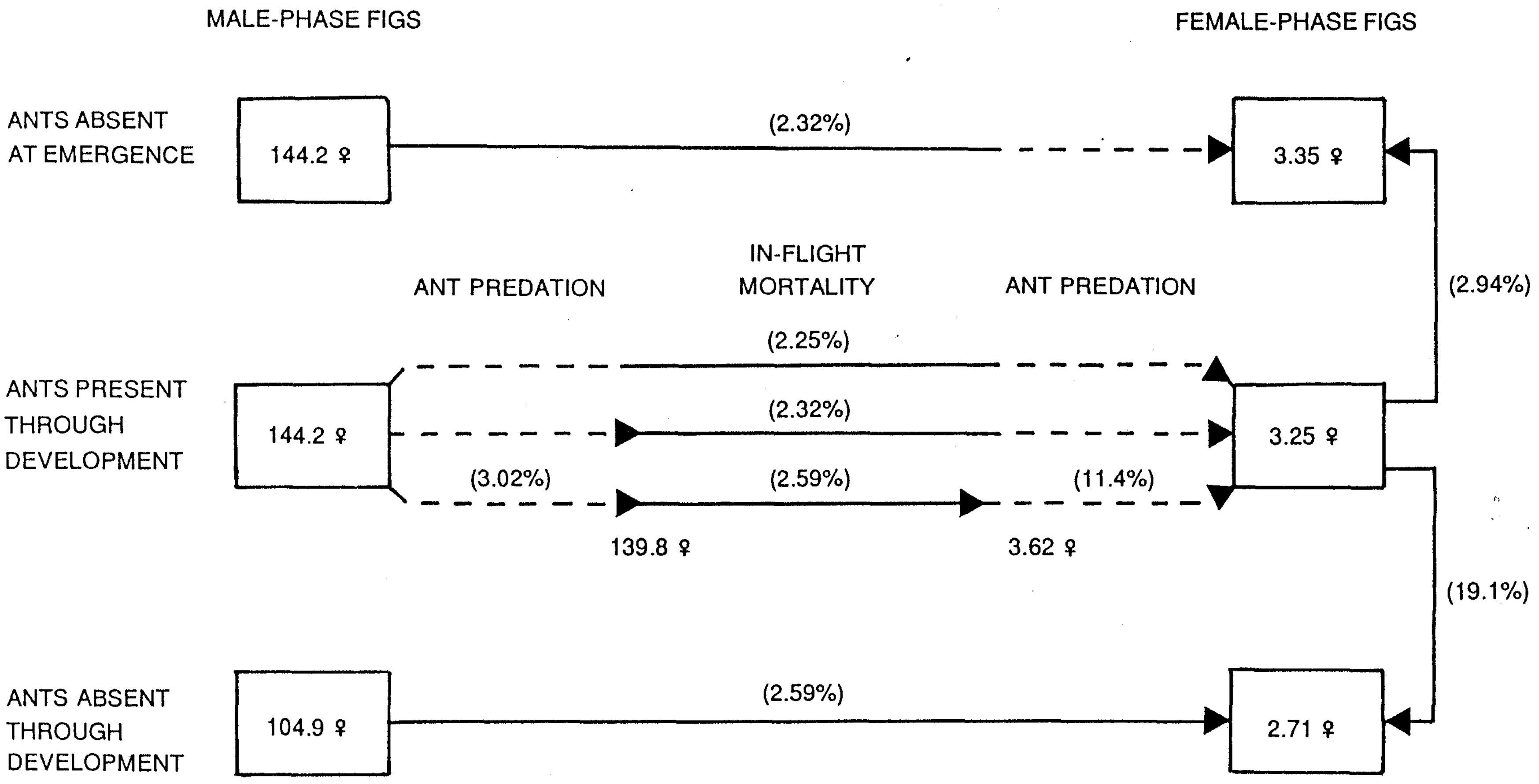


Figure 9.2. Success rates of *C. capensis* females between leaving their natal figs and arriving at receptive figs. Solid lines between male- and female-phase figs represent in-flight mortality, broken lines mortality due to ant predation on figs. Percentages in parentheses represent the change in wasp numbers between arrowheads.

the number of pollinator females available to receptive figs due to their predation by ants on emergence from male-phase figs (and on arrival at receptive figs) is much less than the increase in pollinator numbers which results from the presence of ants on the figs during development. Again, ant numbers were not standardised, so that the actual predation effects are probably even smaller relative to the increase in foundress numbers due to a reduction in parasitism.

The results of this chapter and the previous one thus provide strong evidence that the interaction of ants on the figs of *F. sur* with its fig wasps are beneficial to the pollinators, and therefore indirectly beneficial for the tree.

10 DISCUSSION

THE FAUNA ASSOCIATED WITH *FICUS SUR*

The arthropod fauna of *F. sur* in the Grahamstown area is diverse and the species interact with the tree and one another in various ways. Fifty-nine phytophagous species in eight orders and seven feeding guilds were recorded feeding on the fruit, stems and leaves of the plant as both immatures and adults. One phytophagous species, *Ceratosolen capensis,* also acted as the pollinator of *F. sur.* One or more psocopteran species probably fed on epiphytes such as algae and lichens growing on *F. sur.* Phytophages were attacked by a number of species of arthropod predators, such as coccinellids, neuropterans and spiders, and various parasitoid species. Nineteen species of ants were recorded on *F. sur*, foraging for food in the form of honeydew, exudates from wounds and animal prey, and some of them occupying nesting sites in dead twigs and branches. Finally, a large number of species acted as "tourists" or incidentals, using the tree for mating, resting and sexual displays. A number of vertebrates, particularly birds and mammals, also foraged at *F. sur* trees, feeding mainly on ripe and unripe figs and probably on a variety of arthropods.

Interactions between insects and the tree and between the insect species can be divided into a number of broad categories based on their outcomes (Boucher *et al.* 1982). Direct herbivore-tree interactions on the tree can generally be classified as +/-, where herbivores benefit from feeding on the tree but damage it by decreasing the photosynthetic area, phloem and xylem availability and seed, pollen and pollinator production. Predators and parasitoids have a similar +/- interaction with their prey or hosts. Interactions between species of the same trophic level, such as those between phytophages, predators, parasitoids or ants, can often be classified as -/- or -/0, i.e. competitive/amensal. It is likely that some commensal interactions (+/0) occur also, as when insects use the tree for pupation or overwintering. Finally, a number of mutualisms (+/+) are operating on the *F. sur* trees, both directly and indirectly, between pollinators, the tree, ants and tended homopterans and lepidopterans. The relative magnitude of each interaction and its importance to the ecology of the tree is dependent on the species pair involved and their abundance. Within a given interaction, magnitude and even sign may vary depending on ecological context, so that although it is convenient to categorise an interaction as being either mutualistic or not, in some cases this may not be useful or valid (Thompson 1988; Cushman & Addicott 1991).

INTERACTIONS BETWEEN SPECIES

The aim of this study was to assess and quantify the insect community on *F. sur*, looking particularly at some of the more important and interesting interactions, and especially those between ants visiting the tree, the polyphagous homopteran *Hilda patruelis* and the tree and its pollinating wasps.

H. patruelis was the most abundant homopteran on the figs of *F. sur* around Grahamstown (Chapter 3). It fed almost exclusively on or near developing figs, disappearing in the absence of a crop and very rarely appearing on leafy branches. On trees continously producing figs, *H. patruelis* was often permanently present. Populations of the bug in this study peaked in late summer and autumn and were at their lowest in late winter (Chapter 3). *H. patruelis* was almost ubiquitously tended by ants for its honeydew, but only once were ants observed removing *H. patruelis* eggs. The most important ant species on the trees, in terms of both abundance and its activities, was *Pheidole megacephala* (Chapter 4). *P. megacephala* was found mainly tending *H. patruelis* on fruiting branches, and was rare on leafy branches. It achieved its maximum numbers on trees in late summer and fell to its lowest numbers in late winter. The ants *Crematogaster* spp. and *Acantholepis capensis* were also widespread, but usually appeared in low numbers, while *Polyrhachis schistacea* and *Anoplolepis custodiens* were localised but appeared in high numbers where they occurred. Ant species and numbers varied between sites, between and within trees, and seasonally (Chapter 4). The species also varied in their behavioural activities and the resources on the tree they utilised.

H. patruelis was not shown to have any short-term negative effects on trees on which it fed, either in terms of numbers of pollinator wasps produced or seed production and viability (Chapter 5). No pathogen transmission was obvious. However, long-term reductions in fitness are difficult to detect, so that it is premature to conclude that *H. patruelis* did not damage the tree at all, especially as the variability in pollinator numbers and fig size may also have obscured any subtle effects.

No benefits to *H. patruelis* of being tended by *P. megacephala* were detected (Chapter 6); nymphs are mobile and were probably able to escape the local build-up of their honeydew which occurs when ants are absent, except on small crops. Honeydew may also be removed by other insects such as wasps and flies in the absence of ants (Hespenheide 1985). Ants did not protect *H. patruelis* against its only recorded parasitoid, *Psyllechthrus oophagus*, and may have formed a mutualism with one of its predators, *Lachnocnema bibilus*. However, *H. patruelis* was virtually always associated with ants and disappeared in their absence, implying the presence of a fairly obligate need for their presence. The behaviour of *H. patruelis*, and in particular its attraction to ant rich sites possibly evolved in a different ecological context, where a mutualism was established. Ants may still occasionally protect *H. patruelis* from generalist invertebrate, and in the case of aggressive ant species, from vertebrate predators (Thomas 1988). Honeydew output may have evolved in the ancestors of *H. patruelis* in order to attract ants and therefore decrease attack from predators, including the ants themselves.

The ants benefitted from tending *H. patruelis* in terms of the energy they gained from honeydew as well as the prey items which they opportunistically acquired while tending *H. patruelis* (Chapter 7). The scale of the benefit to each ant colony clearly depends on the size of the tended *H. patruelis* population as well as that of the ant colony and the presence of ant competitors and alternative food sources, but it appears that foraging on a fruiting *F. sur* tree can provide a substantial proportion of the nutritive needs of a *P. megacephala* colony. On trees which did not fruit continuously this resource would only be available intermittently, however, and when a tree was not fruiting, it would be necessary for the ants to use alternative food sources. A possible indication of the importance of *H. patruelis* to *P. megacephala* was the frequent presence of nests below *F. sur* trees, but as no assessment of the costs of tending *H. patruelis* or of colony fitness gain in terms of reproductive output was made, the absolute significance of *H. patruelis* to the ants was not determined.

The P. megacephala attracted to the trees by *H. patruelis* slightly decreased the numbers of female foundress wasps of *Ceratosolen capensis* entering the figs but had no, or possibly a positive, effect on *Sycophaga cyclostigma* females entering the figs to oviposit (Chapter 8). However, both *P. megacephala* and probably other ant species resulted in an overall increase in the numbers and proportions of both internally ovipositing wasp species progeny, and particularly *C. capensis*, by disturbing and preying on *Apocrypta guineensis* and *Apocryptophagus* spp. females ovipositing from the fig surface and thus reducing parasitism and competition (Chapter 8). Again the observed effects depended on ant numbers, as well as on the relative proportions and absolute numbers of wasp species initially arriving at the fig to oviposit. Ants also preyed on fig wasp progeny emerging from their natal figs (Chapter 9). However, this had a small effect on the number of female wasps leaving the figs in comparison to the increase in numbers due to ant predation or disturbance of externally ovipositing females.

THE ANT-FIG-*H. PATRUELIS* INTERACTION

A large number of both direct and indirect interactions characterise this system (Fig. 10.1). A direct mutualism between *H. patruelis* and ants probably exists, as the former appears to be behaviourally dependent on the latter, although benefits to *H. patruelis* were not conclusively shown (see Cushman & Beattie 1991). Several indirect interactions in the ant-fig-homopteran system are also mutualistic. Ants benefit from the fig tree indirectly through the presence of *H. patruelis* which provides them with food. The fig tree benefits indirectly from ants through their attraction to *H. patruelis* and their subsequent removal of seed predatory wasps and those parasitic on the tree's pollinators, as well as other herbivores. Consequently the tree also benefits indirectly from *H. patruelis* through the attraction of ants. These indirect interactions are beneficial to the tree because the ant-promoted *H. patruelis* causes no detectable damage to the tree and because ant presence results in a net increase in pollinator numbers.

The benefits to the tree from ants and *H. patruelis* are conditional on there being sufficiently high ant densities and significant densities of seed predatory and parasitoid fig wasps present. In the absence of externally ovipositing fig wasps the ants will have a negative effect, however slight. Similarly, on crops where only *S. cyclostigma* is present, other trees in the area (or the same tree if it is continuously fruiting), may be negatively affected. Indirect ant-plant mutualisms are likely to be generally conditional, due to the balance between costs to the plant of ants tending and promoting homopterans (and preying on the plants pollinators in this system) versus benefits to the plant of ants removing other herbivores (or pollinator parasitoids and competitors). Nevertheless, assuming that the wasp profiles of the eight trees from which ants were excluded (Chapter 8) are fairly representative of the population, the mean outcome of the interaction can be expected to be beneficial for *F. sur* on a high proportion of trees, particularly as ant densities on the experimental trees were shown to be representative of ant densities on figs in the whole *F. sur* population. Only a few studies (e.g. Messina 1981; Ito & Higashi 1991) have previously shown that a similar overall increase in plant reproductive output can occur in the presence of ants.

Although the mean effect on *F. sur* of ant and *H. patruelis* presence was found to be beneficial, the substantial temporal and spatial variability which exists in the system must affect the strength (and occasionally the sign) of the interaction. Wasp numbers and relative proportions vary from crop to crop (Chapter 8), due to differences in fig sizes between trees and wasp availability. Ant numbers, as well as *H. patruelis* numbers per fig, vary seasonally, being at their lowest in late winter and highest in late summer. However, we cannot directly assess the significance of this in terms of changes in ant protection of figs, as fig developmental times and possibly relative wasp abundance also varies seasonally. The numbers of ants also change at a diel scale, which may affect predation rates on wasps (Chapter 9).

The strength of the benefits accruing from the mutualism to the tree and its pollinator also varies spatially, at an inter-site level (*P. megacephala* was most common at site 1 and rarest at site 3), an inter-tree level (some trees have more ants than others), and a within-tree level (densities of *P. megacephala*, at least, were much higher in the lower branches of the trees (Chapter 4)).

Furthermore, within a fruiting branch ants were often patchily distributed and their densities on individual figs changed over the developmental time of the figs, resulting in differential and varying protection of the figs and their occupants. Ant numbers usually peaked late in the developmental period of the figs of each crop, due to the slow buildup of *H. patruelis* numbers (Chapter 4) - they may therefore provide more protection against *A. guineensis* than *Apocryptophagus* species, which oviposit earlier.

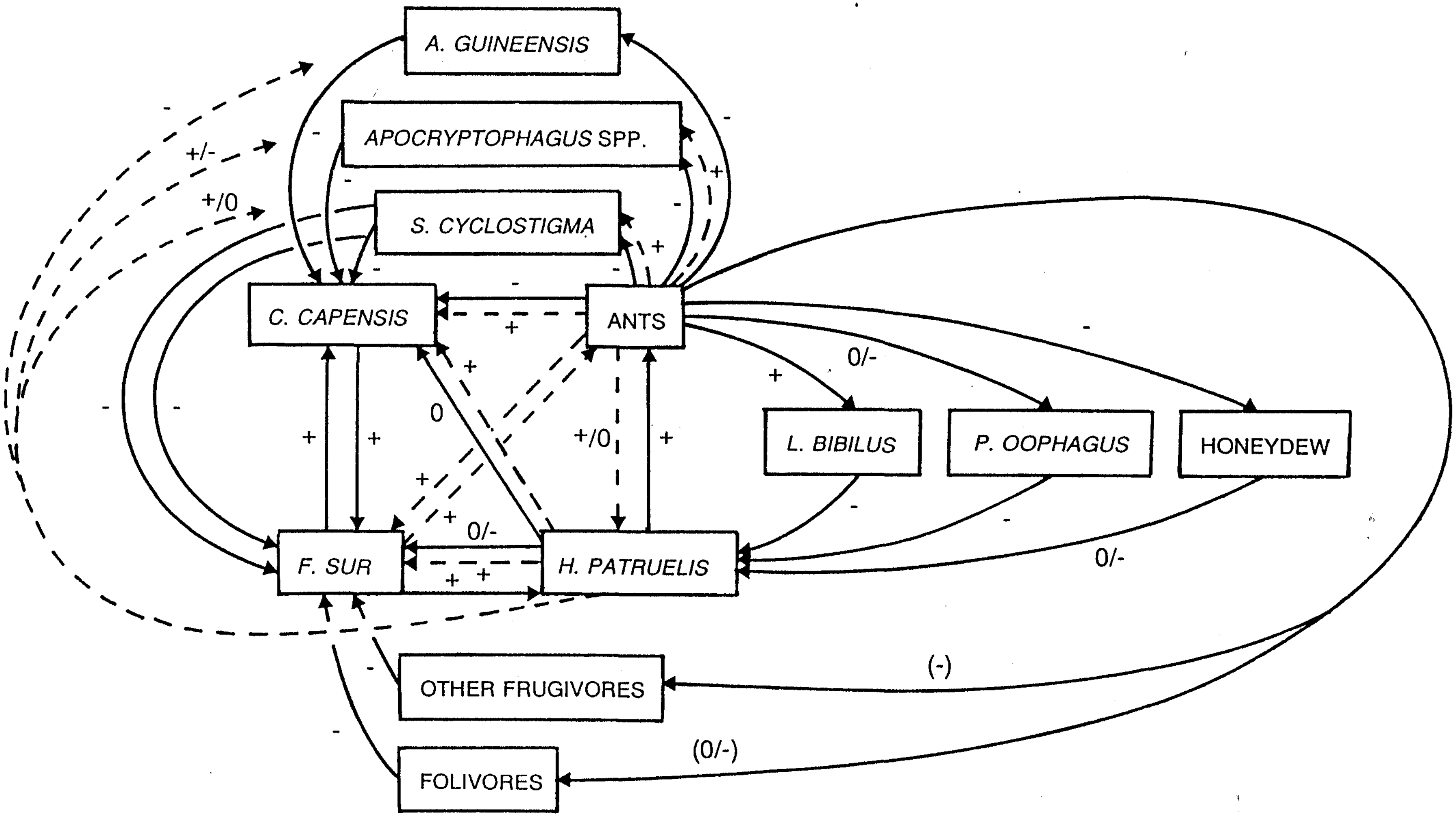


Figure 10.1. Some of the interactions involving *Ficus sur* and its associated insects examined in this study. Direct interactions are indicated by solid lines, indirect interactions by broken lines. The signs of the interactions are also indicated. Unconfirmed interactions are shown by signs in parentheses. Interactions among insects other than *C. capensis*, *F. sur*, *H. patruelis* and ants are omitted.

Both the ant-*H. patruelis* and ant-*H. patruelis-F. sur* interactions probably also vary somewhat over the geographical range of *F. sur* and *H. patruelis*, as species combinations and densities change - these include *H. patruelis* predators and parasitoids, ant species and fig wasp species. However, throughout southern Africa the *P. megacephala-H. patruelis* interaction on fig trees of the *Sycomorus* group has been found to be highly consistent and important (Cushman *et al.* in prep.). In Madagascar and Cameroon other species of tettigometrids and ants have been observed in abundance on figs (S. Compton pers. comm.; pers. obs.). The fig wasp fauna of *F. sur* (Baijnath & Ramcharun 1983; Compton *et al.* 1994) and other fig species also become richer further north in Africa, so that the protective value to pollinators of ants tending tettigometrids could become more important. At the same time, however, some of these wasp species might be relatively immune to ants, and Hawkins and Compton (1992) have also shown that local parasitoid community richness declines towards the tropics.

THE IMPORTANCE OF ANTS AND *H. PATRUELIS* FOR *F. SUR* REPRODUCTIVE SUCCESS

What is the importance of the ant-tree-*H. patruelis* interaction to the overall biology and reproductive fitness of *F. sur*? Taking into account ant predation of emerging pollinator females as well as of pollinator parasitoids during the interfloral phase of the fig, a reduction in ant numbers from 1.3 to 0.05 per fig resulted in a net reduction of 24.2% in the number of pollinator females leaving male-phase figs (Chapter 9). This translates to a net decrease of 17.5% female pollinators for the *F. sur* population around Grahamstown in the absence of the mean population level of 0.93 ants per fig at 2m height. The benefit to the male reproductive component of the *F. sur* trees of having ants present on their fruiting branches is therefore substantial. Benefits to female fitness (seed production) are more ambigious, as ants benefit one competitor for pollination sites (*S. cyclostigma*) but decrease the numbers of others (*Apocryptophagus* spp.).

How does this ant-mediated change in reproductive success compare to other factors? The reproduction of *Ficus* is characterised by great wastage of both pollinators, representing male fitness (Herre 1989; Berg 1990; Compton & Robertson in prep.) and seeds, representing female fitness (Janzen 1979; Jordano 1983; Roberts & Heithaus 1986). Pollinator larvae developing in the fig are destroyed by parasitoids and predators, and less than 5% of adult females leaving a natal fig may reach their destination in a receptive one (Compton & Robertson in prep.). Pollinating wasp larvae (Janzen 1979) and lygaeid bugs destroy seeds on the tree (Slater 1972), while weevils and lepidopteran larvae bore into figs and destroy both wasps and seeds (Janzen 1979; Bronstein 1988). On *F. sur* the weevil *Omophorus* sp. and the pyralids *Cirrhochrista convoluta* and *Botyodes hirsutalis* can cause huge fig losses. While *C. convoluta* does not destroy seeds or wasps (with the possible exception of *Apocryptophagus* spp.) because it oviposits before the female phase, the other two species can destroy entire crops of interfloral-phase figs with all their seeds and wasps. Particular trees (especially at site 3) were consistently more heavily attacked than others and produced virtually no figs during the entire period in which they were monitored. This may mean that they are phenotypically more susceptible to attack or that the herbivorous insects were extremely localised in their movements. Site 3 as a whole was characterised by high herbivory rates by these three insects, and by low ant numbers. As site 3 is the least disturbed site, its natural history may be more representative of wild *F. sur* populations than that of sites 1 or 2.

Despite the variety of seed mortality factors during fig development, huge numbers of seeds reach maturity. For *F. sur*, a mean of 1175 seeds per fig was recorded (n = 40) (Chapter 5), which in a moderately sized crop of 500 figs translates to more than half a million seeds per crop. Seeds are destroyed after leaving the tree by terrestrial lygaeids, often in huge numbers (Slater 1972) and, in other fig species at least, by birds (Jordano 1983; Lambert 1989). As with most plants, a very low recruitment rate of young trees in relation to the number of seeds produced is therefore evident.

Clearly a great many factors affect male and female fitness of *F. sur*, some of which have effects that are equal to or greater than the ant-induced changes in seed predation by fig wasps, and parasitism of and competition with the fig trees' pollinator. Whether the ant-fig-*H. patruelis* interaction is reflected at the *F. sur* population level, in terms of the recruitment of young trees, cannot therefore be predicted, and will depend on its magnitude relative to the many other factors which affect reproductive output.

FUTURE RESEARCH

It is important and would be very interesting to quantify the effects of ants on the major invertebrate frugivores of *F. sur* (Fig. 10.1). All are potentially disturbed from ovipositing or feeding by ant presence. *Omophorus* sp. adults and young *B. hirsutalis* larvae, whose eggs are laid on the fruiting branches near figs, are both attacked by *P. megacephala* (pers. obs.). Ito & Higashi (1991) similarly showed that weevils were significantly reduced by ants on oak trees. On the other hand, ants may also attack the braconid larval and eulophid egg parasitoids of *Omophorus* sp. and *B. hirsutalis*. The reduction of *F. sur* folivores by ants is probably less important both because of the lower ant numbers on leafy branches and the indirect and usually lower effects which folivores have on tree fitness, although Crawley (1985) showed that even low levels of defoliation could significantly affect reproductive output. This could also be examined.

Several other interesting and important areas of future research could be undertaken with this ant-fig-bug system. These include a more detailed investigation of the patchiness of ant densities on figs and the resultant patchiness of protection, by following the fates of individual developing figs; vertebrate and generalist invertebrate predation of *H. patruelis* and the effects of ants on this; the effects of ant presence on the growth and persistence of *H. patruelis* populations; and the role of ants in secondary seed dispersal as well as the importance of the rewards they obtain from foraging on fig trees.

CONCLUSIONS

Although the term "mutualism" has been in use for over a century (Boucher *et al.* 1982), it is mostly in recent years that apparently mutually beneficial interactions between species have been critically evaluated, from both ecological and evolutionary perspectives, in terms of the benefits that each species accrues (Cushman & Beattie 1991), and in terms of variability in the strengths and signs of interactions under different intrinsic and extrinsic conditions (Addicott 1984, 1986; Howe 1984; Thompson 1988; Cushman & Addicott 1991). The potential importance of indirect interactions between species (in mutualistic as well as other contexts) for population dynamics and the structuring of communities has also been recognised recently (Boucher *et al.* 1982; Beattie 1985; Strauss 1991). Ant-plant-homopteran and -lepidopteran systems have proved interesting and useful tools for studying both conditional and indirect interactions, because they are easy to manipulate experimentally, and because the interactions they encompass vary between mutualism and antagonism, with many factors causing variability. The conditionality of indirect interactions within the ant-fig-homopteran system investigated in this study, and in particular the indirect benefits accruing to the tree through the presence of ants and *H. patruelis*, supports the growing evidence that variability in the outcomes of interactions is typical of mutualisms. Nonetheless, the rarity of a change of sign from positive or zero to negative in the indirect ant-fig-*H. patruelis* interactions means that selection pressures, although weak, are in a consistent direction. This lends credence to the idea that indirect interactions are potentially important to the success of those species involved.

11 REFERENCES

Abe, Y. (1988) Trophobiosis between the gall wasp, *Andricus symbioticus*, and the gall-attending ant, *Lasius niger*. Applied Entomology and Zoology **23**:41-44.

Abe, Y. (1992) The advantage of attending ants and gall aggregation for the gall wasp *Andricus symbioticus* (Hymenoptera: Cynipidae). Oecologia **89**:166-167.

Addicott, J.F. (1979) A multispecies aphid-ant association: density dependence and species-specific effects. Canadian Journal of Zoology **57**:558-569.

Addicott, J.F. (1981) Stability properties of 2-species models of mutualism: simulation studies. Oecologia **49**:42-49.

Addicott, J.F. (1984) Mutualistic interactions in population and community processes. *In* A New Ecology. Novel Approaches to Interactive Systems. (eds Price, P.W., C.N. Slobodchikoff and W.S. Gaud), pp. 437-455. John Wiley and Sons, New York.

Addicott, J.F. (1986) On the population consequences of mutualism. *In* Community Ecology. (eds Diamond, J. and T.J. Case), pp. 425-436. Harper and Row, New York.

Andersen, A.N. (1983) Species diversity and temporal distribution of ants in the semi-arid mallee region of northwestern Victoria. Australian Journal of Ecology **8**:127-137.

Andersen, A.N. (1986) Diversity, seasonality and community organization of ants at adjacent heath and woodland sites in south-eastern Australia. Australian Journal of Zoology **34**:53-64.

Andersen, A.N. (1988) Insect seed predators may cause far greater losses than they appear to. Oikos **52**:337-340.

Andersen, A.N. (1992) Regulation of "momentary" diversity by dominant species in exceptionally rich ant communities of the Australian seasonal tropics. American Naturalist **140**:401-420.

Arnold, G. (1915) A monograph of the Formicidae of South Africa. Annals of the South African Museum **14**:1-766.

Attygale, A.B. and E.D. Morgan (1985) Ant trail pheromones. Advances in Insect Physiology **18**:1-30.

Auclair, J.L. (1963) Aphid feeding and nutrition. Annual Review of Entomology **8**:439-490.

Bach, C.E. (1991) Direct and indirect interactions between ants (*Pheidole megacephala*), scales (*Coccus viridis*) and plants (*Pluchea indica*). Oecologia **87**:233-239.

Baijnath, H. and S. Ramcharun (1983) Aspects of pollination and floral development in *Ficus capensis* Thunb. (Moraceae). Bothalia **14**:883-888.

Baker, E.W. and G.W. Wharton (1952) An Introduction to Acarology. The Macmillan Company, New York.

Basset, Y. (1990) The arboreal fauna of the rainforest tree *Argyrodendron actinophyllum* as sampled with restricted canopy fogging: composition of the fauna. Entomologist **109**:173-183.

Basset, Y. (1991a) Leaf production of an overstorey rainforest tree and its effects on the temporal distribution of associated insect herbivores. Oecologia **88**:211-219.

Basset, Y. (1991b) The seasonality of arboreal arthropods foraging within an Australian rainforest tree. Ecological Entomology **16**:265-278.

Basset, Y., H-P. Aberlenc and G. Delvare (1992) Abundance and stratification of foliage arthropods in a lowland rain forest of Cameroon. Ecological Entomology **17**:310-318.

Basset, Y. and A.H. Arthington (1992) The arthropod community of an Australian rainforest tree: abundance of component taxa, species richness and guild structure. Australian Journal of Ecology **17**:89-98.

Beattie, A.J. (1985) The Evolutionary Ecology of Ant-Plant Mutualisms. Cambridge University Press, Cambridge.

Behle, R.W. and G.J. Michels (1993) Greenbug (Homoptera: Aphididae) feeding affects nonstructural carbohydrate levels in seedling sorghum. Journal of Economic Entomology **86**:363-368.

Belsky, A.J. (1986) Does herbivory benefit plants? A review of the evidence. American Naturalist **127**:870-892.

Bentley, S., J.B. Whittaker and A.J.C. Malloch (1980) Field experiments on the effects of grazing by a chrysomelid beetle (*Gastrophysa viridula*) on seed production and quality in *Rumex obtusifolius* and *Rumex crispus*. Journal of Ecology **68**:671-674.

Berg, C.C (1989) Classification and distribution of *Ficus*. Experientia **45**:605-611.

Berg, C.C. (1990) Reproduction and evolution in *Ficus* (Moraceae): traits connected with the adequate rearing of pollinators. Memoirs of the New York Botanical Garden **55**:169-185.

Boucher, D.H., S. James and K.H. Keeler (1982) The ecology of mutualism. Annual Review of Ecology and Systematics **13**:315-347.

Bourgoin, T. and A. Dejean (1994) Trophobiosis behaviour between *Euphyonarthex phyllostoma* (Hemiptera, Fulgomorpha, Tettigometridae) and two species of *Camponotus* (Hymenoptera, Formicidae), submitted.

Breitwisch, R. (1983) Frugivores at a fruiting *Ficus* vine in a southern Cameroon tropical wet forest. Biotropica **15**:125-128.

Brian, M.V., M.D. Mountford, A. Abbott and S. Vincent (1976) The changes in ant species distribution during ten years post-fire regeneration of a heath. Journal of Animal Ecology **45**:115-133.

Briese, D.T. and B.J. Macauley (1980) Temporal structure of an ant community in semi-arid Australia. Australian Journal of Ecology **5**:121-134.

Bristow, C.M. (1983) Treehoppers transfer parental care to ants: a new benefit of mutualism. Science **220**:532-533.

Bristow, C.M. (1984) Differential benefits from ant attendance to two species of Homoptera on New York ironweed. Journal of Animal Ecology **53**:715-726.

Bristow, C.M. (1991) Are ant-aphid associations a tritrophic interaction? Oleander aphids and Argentine ants. Oecologia **87**:514-521.

Broad, G.H. (1966) Groundnut pests. Rhodesia Agricultural Journal **2427**:1-4.

Broekhuysen, G.J. (1948) The brown house ant (*Pheidole megacephala*, Fabr.) in South Africa. Union of South Africa, Department of Agriculture Bulletin **266**:1-40.

Bronstein, J.L. (1988) Predators of fig wasps. Biotropica **20**:215-219.

Bronstein, J.L. (1989) A mutualism at the edge of its range. Experientia **45**:622-637.

Bronstein, J.L. (1991) The nonpollinating wasp fauna of *Ficus pertusa*: exploitation of a mutualism? Oikos **61**:175-186.

Bronstein, J.L. (1992) Seed predators as mutualists: ecology and evolution of the fig/pollinator interaction. *In* Insect-Plant Interactions. Volume 4. (ed. Bernays, E.), pp. 1-44. CRC Press, Boca Raton.

Bronstein, J.L. and A. Patel (1992) Causes and consequences of within-tree phenological patterns in the Florida strangling fig, *Ficus Aurea* (Moraceae). American Journal of Botany **79**:41-48.

Buckley, R.C. (1983) Interactions between ants and membracid bugs decreases growth and seed set of host plant bearing extrafloral nectaries. Oecologia **58**:132-136.

Buckley, R.C. (1987a) Interactions involving plants, Homoptera and ants. Annual Review of Ecology and Systematics **18**:111-135.

Buckley, R. (1987b) Ant-plant-homopteran interactions. Advances in Ecological Research **16**:53-85.

Carayon, J. (1964) Un cas d'offrande nuptiale chez les Hétéroptères. Comptes Rendus, Academie de Sciences (Paris) **259**:4815-4818.

Carmin, J. and D. Scheinkin (1931) The fauna of Palestinian plants: 2. *Ficus sycomorus* Linné. Bulletin de la société royale entomologique d'Egypte. **15**:164-187.

Carnegie, A.J.M. (1960) Effects of temperature variations on the activities of the brown house ant, *Pheidole megacephala* F. race *punctulata* Mayr. (Hymenopt.:Formicidae). Journal of the Entomological Society of Southern Africa **23**:304-311.

Carroll, C.R. and D.H. Janzen (1973) Ecology of foraging by ants. Annual Review of Ecology and Systematics **4**:231-257.

Carver M., G.F. Gross and T.E. Woodward (1991) Hemiptera (Bugs, leafhoppers, cicadas, aphids, scale insects etc.). *In* The Insects of Australia, 2nd Edition. Volume 1. (ed. CSIRO), pp. 429-509. Melbourne University Press, Carlton.

Claridge, M.F. and M.R. Wilson (1976) Diversity and distribution patterns of some mesophyll-feeding leafhoppers of temperate woodland canopy. Ecological Entomology **1**:231-250.

Clark, G.C. and C.G.C. Dickson (1971) Life Histories of the South African Lycaenid Butterflies. Purnell, Cape Town.

Clark, J.M. and R.L. Switzer (1977) Experimental Biochemistry, 2nd Edition. W.H. Freeman and Company, New York.

Cochrane, M. (1989) A new silkworm at the Cape. Sagittarius **4**:16-17.

Compton, S.G. (1987) *Aganais speciosa* and *Danaus chrysippus* (Lepidoptera) sabotage the latex defences of their host plants. Ecological Entomology **12**:115-118.

Compton, S.G. (1989) Sabotage of latex defenses by caterpillars feeding on fig trees. South African Journal of Science **85**:605-606.

Compton, S.G. and R.H.L. Disney (1991) New species of *Megaselia* (Diptera: Phoridae) whose larvae live in fig syconia (Urticales: Moraceae), and adults prey on fig wasps (Hymenoptera: Agaonidae). Journal of Natural History **25**:203-219.

Compton, S.G., K.C. Holton, V.K. Rashbrook, S. van Noort, S. Vincent and A.B. Ware (1991) Studies of *Ceratosolen galili*, a non-pollinating agaonid fig wasp. Biotropica **23**:188-194.

Compton, S.G. and R.J.C. Nefdt (1990) The figs and fig wasps of *Ficus burtt-davyi*. Mitteilungen aus dem Institut für Allgemeine Botanik, Hamburg **23a**:441-450.

Compton, S.G., J.-Y. Rasplus and A.B. Ware (1994) African fig wasp parasitoid communities. *In* Parasitoid Community Ecology. (eds Hawkins, B.A. and W. Sheenan), in press.

Compton, S.G. and H.G. Robertson (1988) Complex interactions between mutualisms: ants tending homopterans protect fig seeds and pollinators. Ecology **69**:1302-1305.

Compton, S.G. and H.G. Robertson (1991) Effects of ant-homopteran systems on fig-figwasp interactions. *In* Ant-Plant Interactions. (eds Huxley, C.R. and D.F. Cutler), pp. 120-130. Oxford University Press, Oxford.

Compton, S.G. and A.B. Ware (1991) Ants disperse the elaiosome-bearing eggs of an African stick insect. Psyche **98**:207-213.

Corlett, R.T. (1984) The phenology of *Ficus benjamina* and *Ficus microcarpa* in Singapore. Journal of the Singapore National Academy of Science **13**:30-31.

Corlett, R.T. (1987) The phenology of *Ficus fistulosa* in Singapore. Biotropica **19**:122-124.

Cottrell, C.B. (1984) Aphytophagy in butterflies: its relationship to myrmecophily. Zoological Journal of the Linnean Society **79**:1-57.

Crawley, M.J. (1983) Herbivory. The Dynamics of Animal-Plant Interactions. Blackwell Scientific Publications, Oxford.

Crawley, M.J. (1985) Reduction of oak fecundity by low-density herbivore populations. Nature **314**:163-164.

Cudjoe, A.R., P. Neuenschwander and M.J.W. Copland (1993) Interference by ants in biological control of the cassava mealybug *Phenacoccus manihoti* (Hemiptera: Pseudococcidae) in Ghana. Bulletin of Entomological Research **83**:15-22.

Cushman, J.H. (1991) Host-plant mediation of insect mutualisms: variable outcomes in herbivore-ant interactions. Oikos **61**:138-144.

Cushman, J.H. and J.F. Addicott (1989) Intra- and interspecific competition for mutualists: ants as a limited and limiting resource for aphids. Oecologia **79**:315-321.

Cushman, J.H. and J.F. Addicott (1991) Conditional interactions in ant-plant-homopteran mutualisms. *In* Ant-Plant Interactions. (eds Cutler, D.F. and C.R. Huxley), pp. 92-103. Oxford University Press, Oxford.

Cushman, J.H. and A.J. Beattie (1991) Mutualisms: assessing the benefits to hosts and visitors. Trends in Ecology and Evolution **6**:193-195.

Cushman, J.H. and T.G. Whitham (1989) Conditional mutualism in a membracid-ant association: temporal, age-specific, and density-dependent effects. Ecology **70**:1040-1047.

Cushman, J.H. and T.G. Whitham (1991) Competition mediating the outcome of a mutualism: protective services of ants as a limiting resource for membracids. American Naturalist **138**: 851-865.

Degen, A.A., M. Gersani, Y. Avivi and N. Weisbrot (1986) Honeydew intake of the weaver ant *Polyrhachis simplex* (Hymenoptera: Formicidae) attending the aphid *Chaitophorous populialbae* (Homoptera: Aphididae). Insectes Sociaux **33**:211-215.

Dixon, A.F.G. (1973) Biology of Aphids. Studies in Biology No. 44. Arnold, London.

Fellers, J.H. (1989) Daily and seasonal activity in woodland ants. Oecologia **78**:69-76.

Fletcher, M.J. and M. Carver (1991) Superfamily Fulgoroidea. *In* The Insects of Australia, 2nd Edition. Volume 1. (ed. CSIRO), pp. 474-479. Melbourne University Press, Carlton.

Frank, S.A. (1984) The behavior and morphology of the fig wasps *Pegoscapus assuetus* and *P. jimenezi*: descriptions and suggested behavioral characters for phylogenetic studies. Psyche **91**:289-308.

Fritz, R.S (1983) Ant protection of a host plant's defoliator: consequence of an ant-membracid mutualism. Ecology **64**:789-797.

Fürsch, H. (1985) Coccinellidae. *In* Insects of Southern Africa (eds Scholtz, C.H. and E. Holm), pp. 250-251. Butterworths, Durban.

Galil, J. (1977) Fig biology. Endeavour **1**:52-56.

Galil, J. and D. Eisikowitch (1968) On the pollination ecology of *Ficus sycomorus* in East Africa. Ecology **49**:259-269.

Galil, J. and D. Eisikowitch (1974) Further studies on pollination ecology in *Ficus sycomorus*. New Phytologist **73**:515-528.

Gardiner, A.J. (1986) Sex ratios in fig wasps and why so many daughters. Unpublished Honours Thesis, Rhodes University, South Africa.

Ghesquière, J. (1968) Ethologie, biogéographie et brachyptérisme de *Psyllechthrus oophagus* Ghesquière. Revue de Zoologie et de Botanique Africaines **78**:47-52.

Grant, S. and V.C. Moran (1986) The effects of foraging ants on arboreal insect herbivores in an undisturbed woodland savanna. Ecological Entomology **11**:83-93.

Greenslade, P.J.M. (1971a) Interspecific competition and frequency changes among ants in Solomon Islands coconut plantations. Journal of Applied Ecology **8**:323-352.

Greenslade, P.J.M. (1971b) Phenology of three ant species in the Solomon Islands. Journal of the Australian Entomological Society **10**:241-252.

Greenslade (1972) Comparative ecology of four tropical ant species. Insectes Sociaux **19**:195-212.

Greenslade, P.J.M. and P. Greenslade (1977) Some effects of vegetation cover and disturbance on a tropical ant fauna. Insectes Sociaux **24**:163-182.

Haines, G.C. (1927) The fig curculio. Department of Agriculture, Union of South Africa. Entomological Notes **Series 35**:1-3.

Hanks, L.M. and C.S. Sadof (1990) The effects of ants on nymphal survivorship of *Coccus viridis* (Homoptera: Coccidae) Biotropica **22**:210-213.

Hawkins, B.A. and S.G. Compton (1992) African fig wasp communities: undersaturation and latitudinal gradients in species richness. Journal of Animal Ecology **61**:361-372.

Herre, E.A. (1989) Coevolution of reproductive characteristics in twelve species of new world figs and their pollinator wasps. Experientia **45**:637-647.

Hespenheide, H.A. (1985) Insect visitors to extrafloral nectaries of *Byttneria aculeata* (Sterculiaceae): relative importance and roles. Ecological Entomology **10**:191-204.

Hiller, N. (1985) The geology of the Grahamstown area. *In* Grahamstown and Its Environs. (eds Daniel, J.B.McI., W. Holleman and A. Jacot Guillarmod), pp. 11-17. Albany Museum, Grahamstown.

Hölldobler, B. and E.O. Wilson (1990) The Ants. Belknap Press of Harvard University Press, Cambridge, Massachusetts.

Howe, H.F. (1984) Constraints on the evolution of mutualisms. American Naturalist **123**:764-777.

Inouye, D.W. (1982) The consequences of herbivory: a mixed blessing for *Jurinea mollis* (Asteraceae). Oikos **39**:269-272.

Ito, F. and S. Higashi (1991) An indirect mutualism between oaks and wood ants via aphids. Journal of Animal Ecology **60**:463-470.

Jackson, D.A. (1984) Ant distribution patterns in a Cameroonian cocoa plantation: investigation of the ant mosaic hypothesis. Oecologia **62**:318-324.

Jacot Guillarmod, A. (1985) Vegetation of the Grahamstown area. *In* Grahamstown and Its Environs. (eds Daniel, J.B.McI., W. Holleman and A. Jacot Guillarmod), pp. 18-25. Albany Museum, Grahamstown.

Janzen, D.H. (1979) How to be a fig. Annual Review of Ecology and Systematics **10**:13-51.

Janzen, D.H. (1980) When is it coevolution? Evolution **34**:611-612.

Jensen, T.F. (1978a) Annual production and respiration in ant populations. Oikos **31**:207-213.

Jensen, T.F. (1978b) An energy budget for a field population of *Formica pratensis* Retz. (Hymenoptera: Formicidae). Natura Jutlandica **20**:203-226.

Jerath, M.L. (1967) An encyrtid parasite of *Hilda undata* Walk. (Homoptera: Tettigometridae) in Ibadan. Nigerian Entomologists' Magazine **1**:43.

Jordano, P. (1983) Fig-seed predation and dispersal by birds. Biotropica **15**:38-41.

Kansky, R. (1988) Variation in ant activity and its consequences for the Cape fig tree *Ficus sur* Forssk.. Unpubl. Honours Thesis, Rhodes University, South Africa.

Kaufmann, S., D.B. McKey, M. Hossaert-McKey and C.C. Horvitz (1991) Adaptations for a two-phase seed dispersal system involving vertebrates and ants in a hemiepiphytic fig (*Ficus microcarpa*: Moraceae). American Journal of Botany **78**:971-977.

Keeler, K.H. (1981) A model of selection for facultative nonsymbiotic mutualism. American Naturalist **118**:488-498.

Kjellberg, F., B. Doumesche and J.L. Bronstein (1988) Longevity of a fig wasp (*Blastophaga psenes*). Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Series C **91**:117-122.

Kjellberg, F.G. Michaloud and G. Valdeyron (1987) The *Ficus Ficus*-pollinator mutualism: how can it be evolutionary stable? *In* Insects-Plants (eds Labeyrie, V., G. Fabres and G. Lachaise), pp. 335-340. W. Junk, Dordrecht.

Klingauf, F.A. (1987) Feeding, adaptation and excretion. *In* Aphids. Their Biology, Natural Enemies and Control. Volume A. (eds Minks, A.K. and P. Harrewijn), pp. 225-253. Elsevier, Amsterdam.

Lachaise, D. (1977) Niche separation of African *Lissocephala* within the *Ficus* drosophilid community. Oecologia **31**:201-214.

Lachaise, D., L. Tsacas and G. Couturier (1982) The Drosophilidae associated with tropical African figs. Evolution **36**:141-151.

Laine, K.J. and P. Niemelä (1980) The influence of ants on the survival of mountain birches during an *Oporinia autumnata* (Lep., Geometridae) outbreak. Oecologia **47**:39-42.

Lambert, F.R. (1989) Pigeons as seed predators and dispersers of figs in a Malaysian lowland forest. Ibis **131**:521-527.

Larsen, K.J., S.E. Heady and L.R. Nault (1992) Influence of ants (Hymenoptera: Formicidae) on honeydew excretion and escape behaviors in a myrmecophile, *Dalbulus quinquenotatus* (Homoptera: Cicadellidae), and its congeners. Journal of Insect Behavior **5**:109-122.

Lawton, J.H. (1978) Host-plant influences on insect diversity: the effects of space and time. Symposia of the Royal Entomological Society of London **9**:105-125.

Lei, H. and R. Xu (1993) Studies on honeydew excretion by greenhouse whitefly, *Trialeurodes vaporariorum* (Westw.) on its host plant, *Cucumis sativus*. Journal of Applied Entomology **115**:43-51.

Lessells, C.M. (1985) Parasitoid foraging: should parasitism be density dependent? Journal of Animal Ecology **54**:27-41.

Leston, D. (1978) A neotropical ant mosaic. Annals of the Entomological Society of America **71**:649-653.

Lighton, J.R.B., G.A. Bartholomew and D.H. Feener (1987) Energetics of locomotion and load carriage and a model of the energy cost of foraging in the leaf-cutting ant *Atta colombica* Guer. Physiological Zoology **60**:524-537.

Louw, J.F. (1968) Die ekologie van die malmier, *Anoplolepis custodiens* (Smith) (Hymenoptera: Formicidae), in die sentrale Oranje-Vrystaat - I. Die bogrondse aktiwiteitspeil van die werkers. Journal of the Entomological Society of Southern Africa **31**:241-248.

Lubke, R.A. and Y. van Wijk (1988) Terrestrial plants and coastal vegetation. *In* A Field Guide to the Eastern Cape Coast. (eds Lubke, R.A., F.W. Gess and M.N. Bruton), pp. 167-240. Wildlife Society of Southern Africa, Grahamstown.

Mahdi, T. and J.B. Whittaker (1993) Do birch trees (*Betula pendula*) grow better if foraged by wood ants? Journal of Animal Ecology **62**:101-116.

Majer, J.D. (1972) The ant mosaic in Ghana cocoa farms. Bulletin of Entomological Research **62**:151-160.

Majer, J.D. (1976a) The maintenance of the ant mosaic in Ghana cocoa farms. Journal of Applied Ecology **13**:123-144.

Majer, J.D. (1976b) The ant mosaic in Ghana cocoa farms: further structural considerations. Journal of Applied Ecology **13**:145-155.

Majer, J.D. (1985) Recolonization by ants of rehabilitated mineral sand mines on North Stradbroke Island, Queensland, with particular reference to seed removal. Australian Journal of Ecology **10**:31-48.

Majer (1990) The abundance and diversity of arboreal ants in Northern Australia. Biotropica **22**:191-199.

Majer, J.D. and A.E. de Kock (1992) Ant recolonization of sand mines near Richards Bay, South Africa: an evaluation of progress with rehabilitation. South African Journal of Science **88**:31-36.

Markin, G.P. (1970) Food distribution within laboratory colonies of the Argentine ant, *Iridomyrmex humilis* (Mayr). Insectes Sociaux **17**:127-158.

Marquis, R.J. (1984) Leaf herbivores decrease fitness of a tropical plant. Science **226**:537-539.

Maschinski, J. and T.G. Whitham (1989) The continuum of plant responses to herbivory: the influence of plant association, nutrient availability, and timing. American Naturalist **134**:1-19.

Maschwitz, U., M. Schroth, H. Hänel and T.Y. Pong (1984) Lycaenids parasitizing symbiotic plant-ant partnerships. Oecologia **64**:78-80.

Maschwitz, U. and H. Hänel (1985) The migrating herdsman *Dolichoderus* (*Diabolus*) *cuspidatus*: an ant with a novel mode of life. Behavioral Ecology and Sociobiology **17**:171-184.

Maurizio, A. (1975) How bees make honey. *In* Honey. A Comprehensive Study. (ed. Crane, E.), pp. 77-105. Heinemann, London.

Messina, F.J. (1981) Plant protection as a consequence of an ant-membracid mutualism: interactions on goldenrod (*Solidago* sp.). Ecology **62**:1433-1440.

Meyer, G.A. (1993) A comparison of the impacts of leaf- and sap-feeding insects on growth and allocation of goldenrod. Ecology **74**:1101-1116.

Meyer, G.A. and R.B. Root (1993) Effects of herbivorous insects and soil fertility on reproduction of goldenrod. Ecology **74**:1117-1128.

Meyer, G.A. and T.H. Whitlow (1993) Effects of leaf and sap feeding insects on photosynthetic rates of goldenrod. Oecologia **92**:480-489.

Migdoll, I (1987) Field guide to the butterflies of southern Africa. Struik, Cape Town.

Millar, I.M. (1990) The aphids (Homoptera: Aphidoidea) of South Africa. An identification guide. Department of Agricultural Development, Pretoria, South Africa. Entomology Memoir **78**:1-105.

Milton. K., D.M. Windsor, D.W. Morrison and M.A. Estribi (1982) Fruiting phenologies of two neotropical *Ficus* species. Ecology **63**:752-762.

Milton, K. (1991) Leaf change and fruit production in six neotropical Moraceae species. Journal of Ecology **79**:1-26.

Mittler, T.E. (1958) Studies on the feeding and nutrition of *Tuberolachnus salignus* (Gmelin) (Homoptera, Aphididae) II. The nitrogen and sugar composition of ingested phloem sap and excreted honeydew. Journal of Experimental Biology **35**:74-84.

Moran, V.C. and T.R.E. Southwood (1982) The guild composition of arthropod communities in trees. Journal of Animal Ecology **51**:289-306.

Nefdt, R.J.C. (1989) Interactions between fig wasps and their host figs. Unpublished MSc Thesis, Rhodes University, South Africa.

Newbery, D.McC. (1980a) Interactions between the coccid, *Icerya seychellarum* (Westw.), and its host tree species on Aldabra atoll I. *Euphorbia pyrifolia* Lam.. Oecologia **46**:171-179.

Newbery, D.McC. (1980b) Interactions between the coccid, *Icerya seychellarum* (Westw.), and its host tree species on Aldabra atoll II. *Scaevola taccada* (Gaertn.) Roxb.. Oecologia **46**:180-185.

Perrin, H. (1991) Biosystématique et écologie évolutive des Curculio (Coleoptera: Curculionidae). Double radiation sur *Ficus* (Moraceae) et sur Fagales. Unpublished Ph.D. Thesis, Université Paris-VI.

Pettey, F.W. (1924) South African psyllids. Department of Agriculture, Union of South Africa. Entomology Memoir **2**:21-30.

Pierce, N.E. and M.A. Elgar (1985) The influence of ants on host plant selection by *Jalmenus evagoras*, a myrmecophilous lycaenid butterfly. Behavioral Ecology and Sociobiology **16**:209-222.

Pierce, N.E. and P.S. Mead (1981) Parasitoids as selective agents in the symbiosis between lycaenid butterfly larvae and ants. Science **211**:1185-1187.

Pierce, N.E., D.R. Nash, M. Baylis and E.R. Carper (1991) Variation in the attractiveness of lycaenid butterfly larvae to ants *In* Ant-Plant interactions. (eds Huxley, C.R. and D.F. Cutler), pp. 131-142. Oxford University Press, Oxford.

Pinhey, E.C.G. (1975) Moths of southern Africa. Tafelberg, Cape Town.

Ramirez, W.B. (1969) Fig wasps: mechanism of pollen transfer. Science **163**:580-581.

Ramirez, W.B. (1970) Host specificity of fig wasps. Evolution **24**:680-691.

Ramirez, W.B. (1989) Dispersal and colonisation of *Ficus* in the New World. *In* Evolution, Systematics and Fossil History of the Hamamelidae. Volume 2. "Higher" Hamamelidae. (eds Crane, P.R. and S. Blackmore), pp. 279-284. Clarendon Press, Oxford.

Rapisarda, C. (1989) Presenza in Sicilia della psilla verde del fico (*Homotoma viridis* Klimaszewski) e descrizione della sua ninfa di ultima età. Bollettino della Soccietà Entomologica Italiana, Genova **121**:13-18.

Rausher, M.D. and P. Feeny (1980) Herbivory, plant density, and plant reproductive success: the effect of *Battus philenor* on *Aristolochia reticulata*. Ecology **61**:905-917.

Rico-Gray, V. and L.da S.L. Sternberg (1991) Carbon isotopic evidence for seasonal change in feeding habits of *Camponotus planatus* Roger (Formicidae) in Yucatan, Mexico. Biotropica **23**:93-95.

Roberts, J.T. and E.R. Heithaus (1986) Ants rearrange the vertebrate-generated seed shadow of a neotropical fig tree. Ecology **67**:1046-1051.

Rockwood, L.L. (1973) The effect of defoliation on seed production of six Costa Rican tree species. Ecology **54**:1363-1369.

Rogers, L., R. Lavigne and J.L. Miller (1972) Bioenergetics of the western harvester ant in the shortgrass plains ecosystem. Environmental Entomology **1**:763-768.

Room, P.M. (1971) The relative distributions of ant species in Ghana's cocoa farms. Journal of Animal Ecology **40**:735-751.

Room, P.M. (1975) Relative distributions of ant species in cocoa plantations in Papua New Guinea. Journal of Applied Ecology **12**:47-61.

Root (1973) Organisation of plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). Ecological Monographs **43**:95-124.

Rozario, S.A., R.A. Farrow and P.J. Gullan (1993) Effects of ant attendance on reproduction and survival of *Eurmeloides punctata* (Signoret) and *Eurymela distincta* Signoret (Hemiptera: Eurymelidae) on eucalypts. Journal of the Australian Entomological Society **32**:177-186.

Sacchi, C.F., P.W. Price, T.P. Craig and J.F. Itami (1988) Impact of shoot galler attack on sexual reproduction in the Arroyo willow. Ecology **69**:2021-2030.

Samways, M.J. (1990) Species temporal variability: epigaeic ant assemblages and management for abundance and scarcity. Oecologia **84**:482-490.

Samways, M.J. and B.A. Tate (1984) Evaluation of several trunk barriers used to prevent the movement of the pugnacious ant [*Anoplolepis custodiens* (Smith)] into citrus trees. Citrus and Subtropical Fruit Journal :9-26.

Savolainen, R. and K. Vepsäläinen (1988) A competition hierarchy among boreal ants: impact on resource partitioning and community structure. Oikos **51**:135-155.

Skead, C.J. and G.A. Ranger (1958) A contribution to the biology of the Cape Province white-eyes (*Zosterops*). Ibis **100**:319-333.

Skinner, G.J. (1980) The feeding habits of the wood-ant, *Formica rufa* (Hymenoptera: Formicidae), in limestone woodland in north-west England. Journal of Animal Ecology **49**:417-433.

Slansky, F. and J.M. Scriber (1985) Food consumption and utilization. *In* Comprehensive Insect Physiology, Biochemistry and Pharmacology. Volume 4. Regulation: Digestion, Nutrition, Excretion. (eds Kerkut, G.A. and L.I. Gilbert), pp. 87-163. Pergamon Press, Oxford.

Slater, J.A. (1971) The biology and immature stages of South African Heterogastrinae, with the description of two new species (Hemiptera: Lygaeidae). Annals of the Natal Museum **20**:443-465.

Slater, J.A. (1972) Lygaeid bugs (Hemiptera: Lygaeidae) as seed predators of figs. Biotropica **4**:145-151.

Snedecor, G.W. and W.G. Cochran (1980) Statistical Methods, 7th Edition. Iowa State University Press, Ames.

Sokal, R.R. and F.J.Rohlf (1981) Biometry, 2nd Edition. W.H. Freeman and Co., New York.

Southwood, T.R.E., V.C. Moran and C.E.J. Kennedy (1982) The richness, abundance and biomass of the arthropod communities on trees. Journal of Animal Ecology **51**:635-649.

Stephenson, A.G. (1980) Flower and fruit abortion: proximate causes and ultimate functions. Annual Review of Ecology and Systematics **12**:253-279.

Stephenson, A.G. (1981) Fruit set, herbivory, fruit reduction, and the fruiting strategy of *Catalpa speciosa* (Bignoniaceae). Ecology **61**:57-64.

Steyn, J.J. (1954) The pugnacious ant (*Anoplolepis custodiens* Smith) and its relation to the control of citrus scales at Letaba. Memoirs of the Entomological Society of Southern Africa **3**:1-96.

Stone, A.W. (1988) Climate and weather. *In* A Field Guide to the Eastern Cape Coast. (eds Lubke, R.A., F.W. Gess and M.N. Bruton), pp. 19-30. Wildlife Society of Southern Africa, Grahamstown.

Stork, N.E. (1987) Guild structure of arthropods from Bornean rain forest trees. Ecological Entomology **12**:69-80.

Strauss, S.Y. (1991) Indirect effects in community ecology: their defenition, study and importance. Trends in Ecology and Evolution **6**:206-210.

Strong, D.R., J.H. Lawton and T.R.E. Southwood (1984) Insects on plants. Community patterns and mechanisms. Blackwell Scientific Publications, Oxford.

Strong, F.E. (1965) Detection of lipids in the honeydew of an aphid. Nature **205**:1242.

Sudd, J.H. (1987) Ant aphid mutualism *In* Aphids. Their Biology, Natural Enemies and Control. Volume A. (eds Minks, A.K. and P. Harrewijn), pp. 355-365. Elsevier, Amsterdam.

Sudd, J.H. and M.E. Sudd (1985) Seasonal changes in the response of wood-ants (*Formica lugubris*) to sucrose baits. Ecological Entomology **10**:89-97.

Swain, V.M. and G.L. Prinsloo (1986) A list of phytophagous insects and mites on forest trees and shrubs in South Africa. Department of Agriculture and Water Supply. Entomological Memoir **66**:1-91.

Takada, H. and Y. Hashimoto (1985) Association of the root aphid parasitoids *Aclitus sappaphis* and *Paralipsis eikoae* (Hymenoptera, Aphidiidae) with the aphid-attending ants *Pheidole fervida* and *Lasius niger* (Hymenoptera, Formicidae). Kontyû **53**:150-160.

Taylor, B. (1977) The ant mosaic on cocoa and other tree crops in Western Nigeria. Ecological Entomology **2**:245-255.

Taylor, B. and S.F. Adedoyin (1978) The abundance and inter-specific relations of common ant species (Hymenoptera: Formicidae) on cocoa farms in western Nigeria. Bulletin of Entomological Research **68**:105-121.

Tedders, W.L. and B.W. Wood (1985) Estimate of the influence of feeding by *Monelliopsis pecanis* and *Monellia caryella* (Homoptera: Aphididae) on the fruit, foliage, carbohydrate reserves, and tree productivity of mature "Stuart" pecans. Journal of Economic Entomology **78**:642-646.

Thomas, D.W. (1988) The influence of aggressive ants on fruit removal in the tropical tree, *Ficus capensis* (Moraceae). Biotropica **20**:49-53.

Thompson, J.N. (1982) Interaction and Coevolution. John Wiley and Sons, New York.

Thompson, J.N. (1988) Variation in interspecific interactions. Annual Review of Ecology and Systematics **19**:65-87.

Torres, J.A. (1984) Niches and coexistence of ant communities in Puerto Rico: repeated patterns. Biotropica **16**:284-295.

Traniello, J.F.A. (1989) Foraging strategies of ants. Annual Review of Entomology **34**:191-210.

Tsacas, L. and D. Lachaise (1979) La radiation africaine des *Lissocephala* inféodées aux *Ficus* (Dipt. Drosophilidae). Annales Société entomologique de France **15**:589-603.

Tsuiki, S., Y. Hashimoto and W. Pigman (1963) The oligosaccharides. *In* Comprehensive Biochemistry. Volume 5. The Carbohydrates. (eds Florkin, M. and E.H. Stotz), pp. 153-184. Elsevier, Amsterdam.

Ueckermann, E.A. (1991) African *Aceria* (Acari: Eriophyidae): species associated with plants of the family Moraceae. Phytophylactica **23**:1-7.

Van Alphen, J.J.M. and L.E.M. Vet (1986) An evolutionary approach to host finding and selection. *In* Insect Parasitoids (eds Waage, J. and D. Greathead), pp. 23-61. Academic Press, London.

Vanderplank, F.L. (1960) The bionomics and ecology of the red tree ant, *Oecophylla* sp., and its relationship to the coconut bug *Pseudotheraptus wayi* Brown (Coreidae). Journal of Animal Ecology **29**:15-33.

Van Hook, R.I., M.G. Nielsen and H.H. Shugart (1980) Energy and nitrogen relations for a *Macrosiphum liriodendri* (Homoptera: Aphididae) population in an east Tennessee *Liriodendron tulipifera* stand. Ecology **61**:960-975.

Van Noort, S., A.B. Ware and S.G. Compton (1989) Pollinator-specific volatile attractants released from the figs of *Ficus burtt-davyi*. South African Journal of Science **85**:323-324.

Verkerke, W. (1988) Sycone morphology and its influence on the flower structure of *Ficus sur* (Moraceae). Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Series C **91**:319-344.

Verkerke, W. (1989) Structure and function of the fig. Experientia **45**:612-622.

Vincent, S. (1991) Polymorphism and fighting in male fig wasps. Unpublished PhD Thesis, Rhodes University, South Africa.

Völkl, W. (1992) Aphids or their parasitoids: who actually benefits from ant-attendance? Journal of Animal Ecology **61**:273-281.

Völkl, W. and M. Mackauer (1993) Interactions between ants attending *Aphis fabae* ssp. *cirsiiacanthiodis* on thistles and foraging parasitoid wasps. Journal of Insect Behavior **6**:301-312.

Walde, S.J. and W.W. Murdoch (1988) Spatial density dependence in parasitoids. Annual Review of Entomology **33**:441-466.

Ware, A.B. and S.G. Compton (1994) Dispersal of adult female fig wasps I. Arrivals and departures. Entomologia Experimentalis et Applicata, in press.

Washburn, J.O. (1984) Mutualism between a cynipid gall wasp and ants. Ecology **65**: 654-656.

Way, M.J. (1963) Mutualism between ants and honeydew-producing Homoptera. Annual Review of Ecology and Systematics **8**:307-344.

Wearing, C.H. and K. McCarthy (1992) Predation of codling moth *Cydia pomonella* L. by the silvereye *Zosterops lateralis* (Latham). Biocontrol Science and Technology **2**:285-295.

Weaving, A.J.S. (1980) Observations on *Hilda patruelis* Stal. (Homoptera: Tettigometridae) and its infestation of the groundnut crop in Rhodesia. Journal of the Entomological Society of Southern Africa **43**:151-167.

Wheeler, W.M. (1922) Ants of the American Museum Congo expedition. A contribution to the myrmecology of Africa. Bulletin of the American Museum of Natural History **45**:1-256.

Whitford, W.G. (1978) Structure and seasonal activity of Chihuahua Desert ant communities. Insectes Sociaux **25**:79-88.

Whittaker, J.B. (1991) Effects of ants on temperate woodland trees. *In* Ant-Plant Interactions. (eds Cutler, D.F. and C.R. Huxley), pp. 67-79. Oxford University Press, Oxford.

Whittaker, J.B. and S. Warrington (1985) An experimental field study of different levels of insect herbivory induced by *Formica rufa* predation on sycamore (*Acer pseudoplatanus*) III. Effects on tree growth. Journal of Applied Ecology **22**:797-811.

Wiebes, J.T. (1979) Co-evolution of figs and their insect pollinators. Annual Review of Ecology and Systematics **10**:1-12.

Wilson, E.O. (1987) The arboreal ant fauna of Peruvian Amazon forests: a first assessment. Biotropica **19**:245-251.

Wolda, H. (1992) Trends in abundance of tropical forest insects. Oecologia **89**:47-52.

Wood, T.K. (1977) Role of parent females and attendant ants in the maturation of the treehopper, *Entylia bactriana* (Homoptera: Membracidae). Sociobiology **2**:257-272.