ASPECTS OF THE ECOLOGY OF NAMIB DESERT ANTS

by

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ABSTRACT

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Thirty-six species of ants were collected in the central Namib Desert, Namibia during the period 1981 to 1985. The ant fauna was dominated by the Myrmicinae, comprising 29 species, followed by the Formicinae, comprising six species and the Pseudomyrmecinae with one species. The dominance of the ant fauna by these subfamilies was in part attributed to the abilities of certain members of these ant groups to store food. The majority of ant species occurred on the gravel plains where species richness was strongly correlated with mean annual rainfall, an index of primary productivity. Certain species were strongly associated with perennial vegetation reflecting the ants' requirements for honeydew, nectar and/or nesting sites. The vast majority of ant species were not dependent on perennial vegetation and relied primarily on seeds, insects or both for food.

Thirteen ant species occurred sympatrically in a 16 ha plot situated on the flat, barren gravel plains in a region receiving on the average ~87 mm of rain per year. The numerical density of foragers fluctuated markedly during the 17 month study period with all species exhibiting similar patterns of change. Fluctuations in forager abundance were partly in response to variations in food availability. Community structure was reasonably robust through time but rank order of species was not entirely static. Seed-harvesting species comprised 96.7 % of the total forager biomass. The ants were opportunistic feeders exhibiting large fluctuations in dietary niche breadth and in intra- and interspecific dietary niche overlap. There was no clear relationship between ant body size and food particle size utilization.

Eight of the most common species in the ant community showed increases in forager activity after rainfall and with increases in food availability. Variations in ambient temperature and humidity explained a significant amount of the observed variation in activity levels. There was a shift towards increased diurnalism during winter. Nocturnal species had lower Critical Thermal limits than diurnal species. No species exploited the entire range of thermal conditions of which it was physiologically capable.

The two dominant species in the community, *Messor denticornis* and *Tetramorium rufescens*, differed markedly in size. *Tetramorium rufescens*, the smaller species, was a diffuse forager, had a relatively high nest density and small foraging range. *Messor denticornis* was predominantly a trunk-trail forager with a low nest density and large foraging range. Food items were patchy and *M. denticornis* trunk-trails led to rich food patches. There was considerable dietary overlap during a year when seeds were apparently superabundant, both species primarily taking seeds of the grass *Enneapogon brachystachyus*. When food was scarce both species became opportunistic but *T. rufescens* exhibited larger and more frequent fluctuations in dietary niche breadth. The community patterns are not readily reconciled to competition theory and it is suggested that competitive interactions may not be important determinants of the structure of this Namib Desert ant community.

In the dry Kuiseb River bed, *Ocymyrmex barbiger* foragers were active on the insolated surface between sand surface temperatures (T_s) of 27-67 °C. At $T_s > \sim 51$ °C foragers periodically paused in relatively cooler thermal refuges, such as shade, or climbed above the desert floor on any available object. The frequency and length of pauses in thermal refuges increased with increasing T_s. Workers, because of their small size, ~4 mg live mass, had low thermal inertia, as evidenced by high cooling rates in a range of air speeds, and were therefore efficient heat exchangers, equilibrating rapidly to ambient temperature. Through measurements of operative environmental temperature in pertinent positions in the ant's habitat and a knowledge of wind-related cooling rates it was possible to

estimate the body temperature of foraging ants. Foragers experienced periods when body temperature would have equalled or exceeded their Critical Thermal Maximum (CTM) of 51.5°C. Laboratory experiments indicated that ants could tolerate temperatures > CTM for short periods and that short but frequent thermal respites facilitated survival at temperatures = CTM.

Ocymyrmex barbiger was a diurnal arthropod scavenger. The number of successful foraging excursions per colony per day increased with increasing daily vapour pressure deficits. The ants apparently made use of prey items which had succumbed to thermal and desiccation stress. Forager running speed was a function of surface temperature but progressively less time was spent searching for prey beyond a critical surface temperature with the result that the optimal search temperature for individual foragers was 52.4 °C. Maximal foraging activity of colonies occurred at surface temperatures corresponding to this optimal search temperature.

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SECTION ONE

INTRODUCTION

Ants are among the most ubiquitous and abundant terrestrial organisms. They occur in habitats from the equator to the arctic circle (Brian, 1978; Pisarski, 1978) and, in any given ecosystem, have a biomass that exceeds that of all the vertebrates (Wilson, 1971). In general, ants are polyphagous (Carroll & Janzen, 1973; Petal, 1978) but select food with a high protein or carbohydrate content (Stradling, 1978). They are important factors in energy flow exceeding the importance of homeothermic vertebrates (Petal, 1978). They are major predators on other insects (Wilson, 1971) and frequently deplete prey populations markedly (Stradling, 1978). They are major earth movers (Wilson, 1971) and modify the chemical and physical properties of soil (Petal, 1978).

In hot deserts ants are the most abundant animals (Crawford, 1981; Pisarski, 1978). In these arid ecosystems they play an important role in the conservation, localization and turnover of nutrients (Crawford, 1981). They are major consumers of seeds (Stradling, 1978) and have a significant impact on the seed reserves of certain species, frequently consuming more than 70% of the production of preferred species (see references in Whitford, 1978b).

Despite their importance, ecological studies of ants in the deserts of southern Africa are conspicuously absent from the literature. The recent study of Curtis (1983), which focused on the ecological relationships and adaptations of Camponotus detritus in the central Namib Desert, was the first of its kind in a southern African desert. Thus at the outset of the present study virtually nothing was known about Namib Desert ants. Because of this void in our knowledge, the scope of this thesis is deliberately broad in order to gain an overall perspective of Namib Desert ant ecology. Inevitably there was a compromise between acquiring detailed information on specific topics and gaining a broader perspective. A broader perspective was considered to be a more valuable contribution to knowledge in that it would stimulate further work by identifying fruitful areas for research.

An adaptationist philosophy was adopted in this enquiry. The unifying question posed throughout the study was "how do the ants make a living in the central Namib Desert?". With respect to individual species this question was primarily concerned with how the organisms coped with the harsh physical environment, particularly high diurnal temperatures. With respect to community ecology the question was concerned more with coexistence.

By far the majority of quantitative ecological studies of desert ants have been carried out in North America. As most readers will probably be familiar with North American deserts it is appropriate at this stage to briefly emphasize those features of the central Namib Desert which set it apart from the North American situation. The central Namib Desert is a narrow coastal desert, having an average width of approximately 120 km. It embraces two major habitats, the dune-sea and gravel plains, and has a very steep climatic gradient across its width (Louw & Seely, 1982). It is comparatively arid; mean annual rainfall increasing progressively from ~15 mm at the coast to ~87 mm approximately 100 km inland (Lancaster et al., 1984). Vast areas, particularly on the flat gravel plains, are devoid of photosynthetically active plant life for most of the time (Robinson, 1978). Effective rain, that is sufficient to enable annual and perennial plants to grow and produce seed, does not occur on a regular predictable basis, and may be absent for several consecutive years (Lancaster et al., 1984).

To a large extent the physical environment determined the direction of the present enquiry. At the outset the proposal was to compare the structure and function of ant communities on the gravel plains across the rainfall, and hence productivity, gradient. Before such a study could occur, however, it was necessary to select comparable sites and this involved amongst other considerations a survey to establish which ant species occurred in the desert and where they occurred. The survey revealed that ant abundance, in terms of individuals and species, was very low for much of the area and that comparative community studies would therefore be relatively unproductive. On the basis of this it was felt that a more thorough examination of the structure and function of one relatively species rich community would be more profitable.

One of the major problems encountered in the study of this community related to the particular period in which it occurred. For most of the study no effective rain fell and the ant populations were largely inactive. In view of this difficulty, emphasis was shifted toward a study of the foraging ecology of the two most dominant species in the community. These two species were therefore studied more intensively and more regularly than the remaining, rarer species. One of the dominant species was strictly nocturnal and the other crepuscular to nocturnal thus further confounding the collection of data and effectively limiting what could be investigated.

One diurnal species, Ocymyrmex barbiger, was conspicuously active throughout the year but not at the major study site. In the dry Kuiseb River bed near the Desert Ecological Research Unit foragers of this species were regularly observed during the heat of the day. Because this appeared to be an unusually arid-adapted species a study was initiated to elucidate how and why the foragers occupied this thermal niche.

Each section of this thesis has been written to be comprehensible on its own. As a consequence there are occasional repetitive statements, particularly in the introductory parts of some sections. The first section describes the species composition of the central Namib Desert ant fauna, indicates where the species occur and, where possible, provides brief notes on their trophic roles and activity patterns. The following section examines the quantitative relationship between species richness and climatic gradient. Three sections are then devoted to community structure and function describing activity patterns of eight relatively abundant species, patterns of abundance and trophic relationships of the community as a whole and the foraging ecology of the two dominant species. This is followed by two sections concerning the behavioural and physiological ecology of O. barbiger. One of these sections describes how the ants forage during thermally stressful periods and the body temperatures foraging ants attain. The other section is concerned with the reason why this species occupies its unusual thermal niche. During the community study it was demonstrated that pitfall trapping was not a relaible way of quantifying relative abundances of ant species and a published paper describing this work has been appended at the end of the thesis. The major conclusions to emerge from this study are expressed in the final section.

SECTION TWO

CHECKLIST, BIOLOGICAL NOTES AND DISTRIBUTION OF ANTS IN THE CENTRAL NAMIB DESERT

2.1 INTRODUCTION

Ants play an important role in the ecology of most terrestrial habitats. Indeed, it is a little appreciated fact that "their biomass and energy consumption exceed those of vertebrates in most terrestrial habitats" (Wilson, 1971). In desert ecosystems, although ant species richness is comparatively low, they have a dominant position due to their numerical abundance (Crawford, 1981; Pisarski, 1978). For example, in the western Sahara desert ants comprise 75 % of the total fauna (Bernard, 1972). Ants play numerous roles in the economy of desert ecosystems but undoubtedly their most prominent, and probably most important, is that of a seed predator (eg Buckley; 1982).

Despite the established importance of ants in other deserts almost nothing is known about the ants of the Namib Desert. Here the results of an ant survey of the central Namib Desert are presented. A list and short description of all the species known to occur in the dune field, Kuiseb River and gravel plains is given, accompanied where possible with brief biological notes concerning their trophic role, habitat and activity period. To facilitate future ant research in the Namib Desert a generic key has been provided, a key to species level being inappropriate at present in view of the taxonomic confusion which exists for certain groups and the fact that certain genera are currently being revised (Bolton, pers. comm.).

2.2 PROCEDURE

Ants were collected using pitfall traps and searching by eye. Bait was occasionally used in both techniques. On the gravel plains sampling sites were restricted to areas accessible by road. In the dune-field, sampling sites coincided with the work sites of other scientists. With the exception of one study (see section 3), the intensity of sampling, and the techniques used, were not identical at each site. The data obtained therefore give reliable presence but unreliable absence information. Most sampling occurred from 1981 to 1983.

Data on the habits of the ants were obtained in a similar opportunistic manner. Certain species were the focus of other studies and considerably more information is available on them than on some of the rarer species. Where possible the literature has been referred to for confirmation of chance observations. However, as ant studies in southern Africa have been predominantly restricted to taxonomic and agricultural problems, published information is limited or absent for many species. Members of each species have been classified as either individual or group foragers. Individual foraging refers to ants which predominantly searched for and retrieved food objects on their own. Group foraging refers to those species which regularly used trunk-trails to reach localized food sources. Total lengths (TL) are given in mm and refer to the length of individuals, from the mandibular apex to the gastral apex. Voucher specimens of all species have been lodged at the British Museum of Natural History, London and at the Desert Ecological Research Unit, Gobabeb, Namibia. Where it was not possible to give reliable specific names, alphabetical codes have been used.

2.3 RESULTS AND DISCUSSION

A map of the central Namib Desert showing major habitats and place names is shown in Fig. 2.1. Thirty-six species belonging to three subfamilies and ten genera were collected in the central Namib Desert (Table 2.1). The ant fauna was dominated taxonomically by the Myrmicinae, comprising 6 genera and 29 species, followed by the Formicinae, comprising 3 genera and 6 species and lastly the Pseudomyrmecinae with only one representative.

2.3.1 Generic key

The Namib ants can be separated to genus level with the key which follows. The key is based on worker characters and relevant morphological features are illustrated in Fig. 2.2.

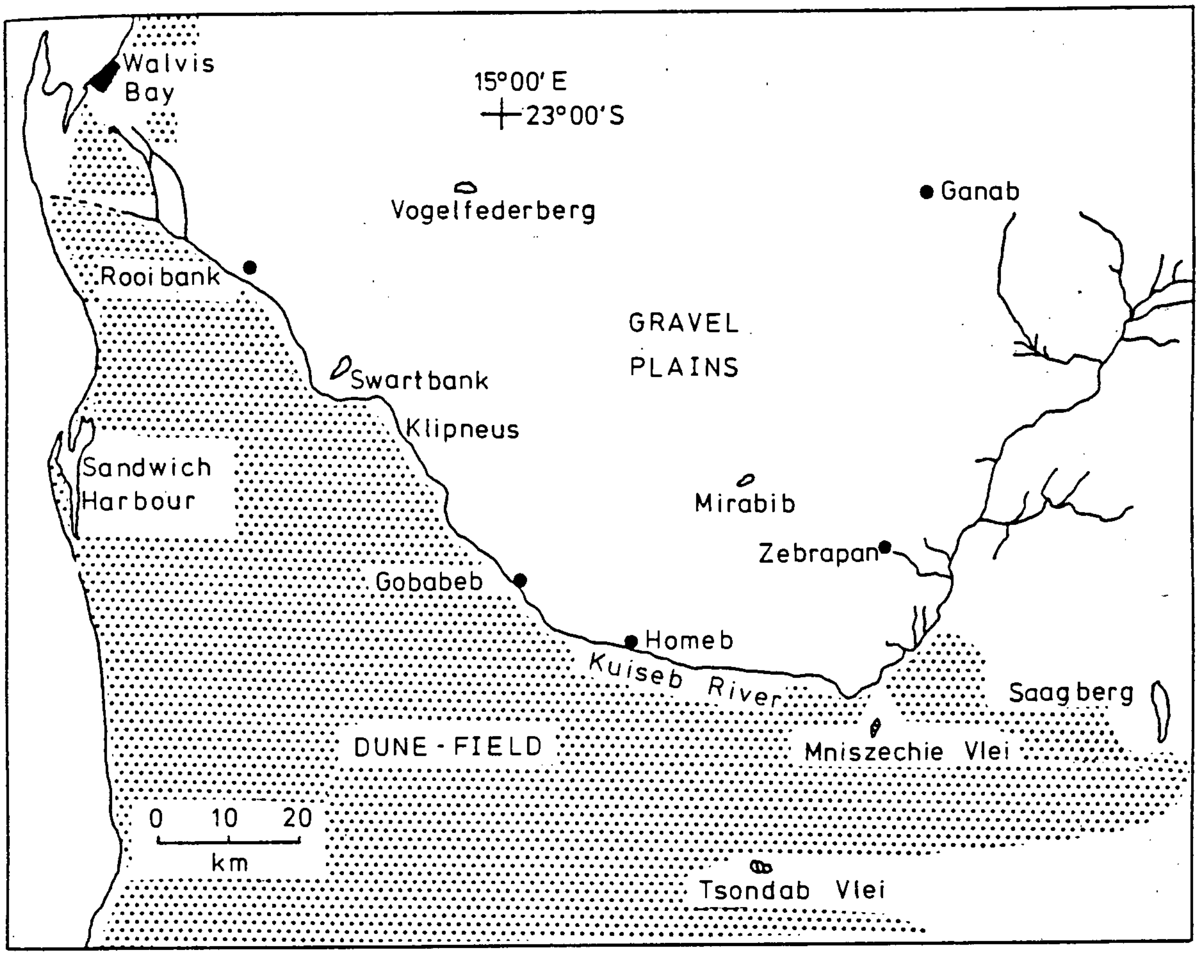

Figure 2.1. Map of the central Namib Desert indicating major geographic features.

Table 2.1. Ant species occurring in the central Namib Desert.

MYRMICINAE

Tetramorium rufescens Stitz

Tetramorium jordani Santschi

Tetramorium pogonion Bolton

Tetramorium solidum Emery

Tetramorium grandinode Santschi

Tetramorium peringueyi Arnold

Tetramorium sericeiventre Emery

Tetramorium sp. near *caldarium* (Roger)

Monomorium viator Santschi

Monomorium damarense Forel)

Monomorium spp. (10 species)

Pheidole tenuinodis Mayr

Messor denticornis Forel

Ocymyrmex barbiger Emery

Ocymyrmex turneri Donisthorpe

Ocymyrmex velox Santschi

Crematogaster spp. (3 species)

FORMICINAE

Anoplolepis steingroeveri (Forel)

Anoplolepis sp.

Acantholepis sp.

Camponotus detritus Emery

Camponotus fulvopilosus (De Geer)

Camponotus maculatus (F.)

Camponotus mystaceus Emery

PSEUDOMYRMECINAE

Tetraponera ambigua (Emery)

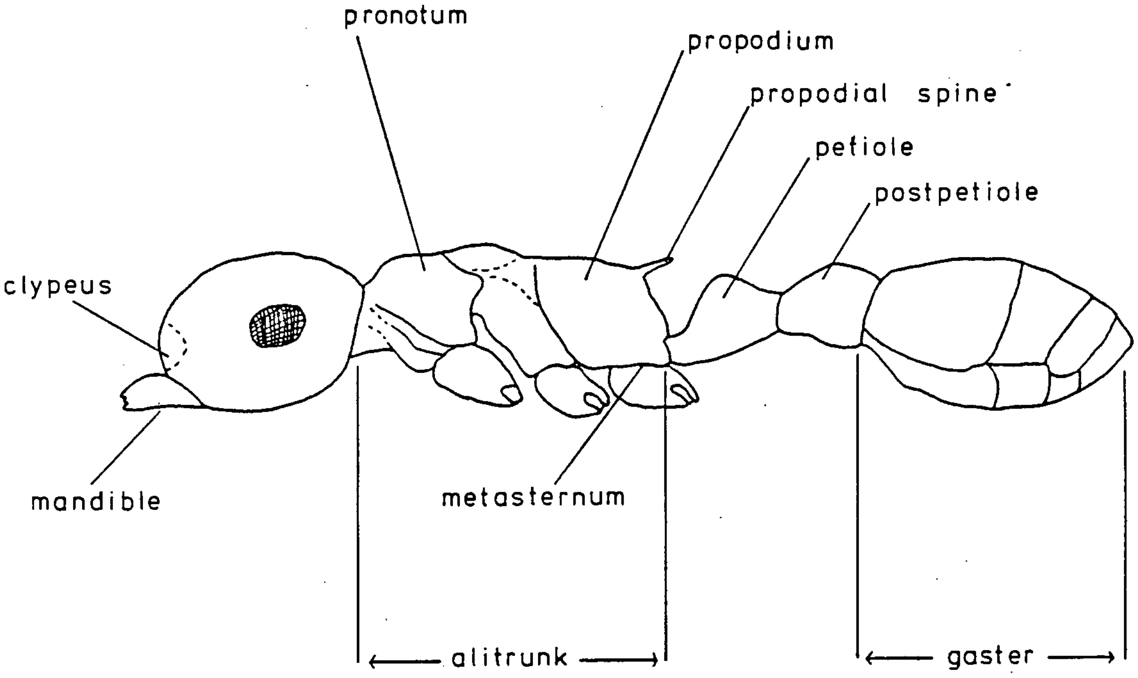

Figure 2.2. Stylized ant showing morphological features used to distinguish the Namib genera.

It is important to note that this key is applicable to central Namib Desert Formicidae only, it has little or no predictive value in other areas.

1. Alitrunk separated from gaster by two reduced segments, the petiole and postpetiole .... 2.

\- Alitrunk separated from gaster by a single reduced segment, the petiole. Sting absent [subfam. Formicinae] .. .. 8.

2. Tibial spurs of hind legs broadly pectinate. Palp formula 6,4. Pretarsal claws equiped with a preapical tooth. Median portion of clypeus posteriorly not deeply inserted between the frontal lobes [subfam. Pseudomyrmecinae]....................... Tetraponera Smith

\- Tibial spurs of hind legs simple or absent, not broadly pectinate. Palp formula less than 6,4. Pretarsal claws simple. Median portion of clypeus posteriorly deeply inserted between the frontal lobes [subfam. Myrmicinae]... .... 3.

3. Postpetiole articulated on dorsal surface of first gastral segment; the gaster in dorsal view roughly heart-shaped and capable of reflexion over the alitrunk. Petiole dorsoventrally flattened and without a node .... Crematogaster Lund

\- Postpetiole articulated on anterior surface of first gastral segment; the gaster in dorsal view not heart-shaped, not capable of reflexion over the alitrunk.

Petiole not dorsoventrally flattened, with a node of some form .... 4.

4. Propodeal spiracle long and narrow, its orifice slit-like. Mesothoracic spiracles opening on dorsum of alitrunk .... <u>Ocymyrmex</u> Emery

\- Propodeal spiracle circular or subcircular, not long and narrow. Mesothoracic spiracles concealed by a pronotal flap on the sides of the alitrunk .... 5.

5. Lateral portions of clypeus raised into a narrow ridge or wall in front of the antennal insertions. Sting terminating in an apical or apicodorsal lamelliform appendage which may be triangular or spatulate.. <u>Tetramorium</u> Mayr

\- Lateral portions of clypeus not raised into a narrow ridge or wall in front of the antennal insertions. Sting simply pointed apically, without a lamelliform appendage .... 6.

6. Palp formula 5,3 or 4,3. Antennal funiculae without a strongly differentiated 3-segmented club. Metasternal process large and powerfully developed ....<u>Messor</u> Forel

\- Palp formula 3,2 or 2,2 or less. Antennal funiculae terminating in a conspicuous 3-segmented club. Metasternal process absent .... 7.

7. Propodeum unarmed. Monomorphic or polymorphic species, the mandibles with 3-4 teeth, the workers never with grossly enlarged head .... <u>Monomorium</u> Mayr

\- Propodeum armed with a pair of spines or teeth. Sharply dimorphic species; soldier with grossly enlarged head, the mandible with 3-4 teeth; worker with normal head and more than 5 teeth on the mandible ... Pheidole Westwood

8. Antennae with 12 segments. Orifice of metapleural glands absent. Antennae inserted well behind the posterior margin of the clypeus .... Camponotus Mayr

- Antennae with 11 segments. Orifice of metapleural glands present and usually traversed by guard-hairs. Antennae inserted close to posterior margin of clypeus .... 9.

9. Propodeum armed with a pair of spines, teeth, or blunt prominences. Petiole usually emarginate, bidentate of bispinose on dorsal margin ....Acantholepis Santschi

- Propodeum unarmed. Petiole without teeth or spines .... Anoplolepis Mayr

2.3.2 Generic notes.

Tetramorium Mayr

The genus has a world-wide distribution with members occupying a diversity of habitats. The majority of species, however, are confined to the Ethiopian zoogeographical area (Bolton, 1980). Eight species have been found in the central Namib Desert. Tetramorium grandinode, T. jordani, T. peringueyi, T. pogonion, T. rufescens and T. solidum belong to the solidum-group. These closely related species are granivorous and are confined to the arid and semi-arid regions of southern Africa (Bolton, 1980). *Tetramorium grandinode*, *T. peringueyi* and *T. solidum* have not previously been recorded in or near the Namib Desert. *Tetramorium sericeiventre*, a member of the *sericeiventre*-group, is the commonest *Tetramorium* in Africa (Bolton, 1980). This species occurs from the Mediterranean to the Cape wherever there is sandy or well drained soil which receives direct insolation. Despite its abundance little is known about its habits. In savannah regions of the Ivory Coast, Levieux (1972) reports that it is predatory on other insects. *Tetramorium* sp. near *caldarium* is a new species that belongs to the *simillimum*-complex (Bolton, pers. comm.). All the *Tetramorium* species are monomorphic.

Monomorium Mayr

This large genus has a world-wide distribution (Arnold, 1916). The African species, including ∼100 sub-Saharan species, are currently being revised (Bolton, in prep.) and consequently it is not possible to give species names or distributions for most species. All members of the genus are monomorphic. Twelve species occur in the central Namib Desert making this the largest genus in this area. Nine of the Namib *Monomorium* species belong to the *salomonis*-group which is the dominant *Monomorium* group throughout savannah to desert regions in Africa (Bolton, pers. comm.). Only *Monomorium* spp. C, D and G belong to other species groups. Of the four species that have been recently examined by a taxonomist, *Monomorium* sp. B and *Monomorium* sp. I are new to science, and have not been collected outside the Namib Desert. *Monomorium viator* is known only from Namibia (Bolton, in prep.), whereas, as the name implies, *M. damarense* has been collected previously in Damaraland, Namibia (Arnold, 1916) but more recent distributional data on this species are not presently available.

Ocymyrmex Emery

The genus is confined to the Ethiopian zoogeographical region in arid to semi-arid habitats of eastern and southern Africa (Bolton, 1981). Three species have been found in the central Namib Desert. *Ocymyrmex velox* has not been previously recorded near or in the Namib Desert although it has been collected in Angola and northern Namibia (Bolton, 1981). Prior to the present study *O. turneri* was known only from one specimen, the holotype, taken in Walvis Bay (Bolton, 1981). In contrast, *O. barbiger* has a much wider distribution, having been collected in numerous regions of Namibia and on the western side of South Africa as far south as Cape Town (Arnold, 1916; Bolton, 1981). Various spectacular features that characterize this genus have been reported previously, such as their rapid, apparently erratic locomotion (Arnold, 1916; Bolton, 1981; Kemp, 1951) and their unusual temporal niche, the ants being active during the heat of the day (Arnold, 1916; Kemp, 1951). According to Prins (1963, 1965) members of this genus are primarily granivorous but sometimes prey on live insects, particularly termites. All are monomorphic.

Crematogaster Lund

This large genus has a world-wide distribution (Arnold, 1920). The taxonomy of the African species is confused and reliable species determinations are not at present possible (Bolton, pers. comm.). Arnold (1920) records that members of this genus are primarily arboreal and feed on honeydew. Three monomorphic species have been found in the central Namib Desert.

Pheidole Westwood

This large genus has a world-wide distribution (Arnold, 1920). Workers are dimorphic, with two discrete castes, minors and majors, based on large size differences. Unfortunately the taxonomy of the African species is confused and previous determinations are untrustworthy (Bolton, pers. comm.), thus the literature containing distributional records is unreliable. Only one species, *P. tenuinodis*, has been recorded in the central Namib Desert. This species appears to have a wide distribution in southern Africa. Arnold (1920) reports that *Pheidole* spp. are omnivorous with some species exhibiting preferences for seeds and/or honeydew.

Messor Forel

This genus inhabits grassland, savannah and arid areas in the Palaearctic, Nearctic, Madagascar and Afrotropical regions. The Palaearctic, including North Africa, is the centre of distribution, with the Afrotropical region, which includes the Namib Desert, having relatively few species (Bolton, 1982). Only one species, *M. denticornis*, has been found in the central Namib Desert. This species has been previously recorded at Luderitz and Spitzkop in the Namib Desert and has a reasonably broad distribution in Namibia, Botswana and the western side of the Cape Province of South Africa. All members of the genus are granivorous (Bolton, 1982). Workers exhibit continuous polymorphism whereby there is a continuous gradation from small to large workers.

Anoplolepis Santschi

This is a very small genus, comprising only four described species, which is confined to southern Africa including Angola and Zimbabwe (Prins, 1982). Two species, *A. steingroeveri* and an unidentified species, occur in the central Namib Desert. *Anoplolepis steingroeveri* is confined to semi-arid and arid regions of southern Africa and has previously been collected in Namibia on a farm, Choaherib (Arnold, 1922), which is located on the eastern edge of the central Namib Desert. Members of this genus are very aggressive and feed predominantly on honeydew (Arnold, 1922; Prins, 1982). *Anoplolepis steingroeveri* workers exhibit continuous polymorphism whereby there is a continuous gradation from small to large individuals. Repletes, a caste with large distensible gasters which can store liquid food in their crops, occur in this species (Arnold, 1922; Prins, 1982). The unidentified *Anoplolepis* species appears to be monomorphic but, owing to the small sample size and a lack of detailed observations, this has not been confirmed.

Acantholepis Mayr

The taxonomy of this genus is confused, even the genus name is preoccupied by a fish (B. Bolton, pers. comm.). According to Arnold (1920) the genus is widespread, occurring in the Palaearctic, Ethiopian and Indo-Malayan regions. Members of the genus are predominantly honeydew feeders and some appear to have a replete caste. Only one monomorphic species has been recorded in the central Namib Desert. In this species the gaster of foraging workers is very distensible, accounting for most of the size variation in workers. It is not known whether sedentary repletes occur in the nest.

Camponotus Mayr

This large genus has a world-wide distribution. Workers exhibit continuous polymorphism whereby there is a continuous gradation from small to large individuals. Four species occur in the central Namib Desert; *C. maculatus*, *C. mystaceus*, *C. fulvopilosus* and *C. detritus*. *Camponotus maculatus* is widely distributed in Africa, occurring in the Sahara Desert (Delye, 1968), and is common in southern Africa (Arnold, 1922). *Camponotus mystaceus* is widespread in southern Africa and has previously been recorded from Rooibank in the central Namib Desert (Arnold, 1922). *Camponotus fulvopilosus* is common in the arid western half of southern Africa and *C. detritus* has been recorded in the central Namib Desert at various locations within the dune field (Arnold, 1924; Curtis, 1983). There is some debate as to whether *C. detritus* is a valid species and whether it is endemic to the dune-fields of the Namib Desert (A.J. Prins, pers. comm.). Electrophoretic studies indicate that *C. detritus* is not distinct from *C. fulvopilosus* (Lighton, unpubl.). Specimens resembling *C. detritus* have recently been collected at Springbok, Cape Province (M. Molteno, pers. comm.) and there is an unsubstantiated report of *C. detritus* having been collected at Matjiesfontein in the Cape Province (A.J. Prins, pers. comm.). *Camponotus maculatus* and *C. mystaceus* are nocturnal (Arnold, 1922) whereas *C. fulvopilosus* and *C. detritus* are diurnal (Arnold, 1924; Curtis, 1983). All four species are predominantly honeydew feeders (Arnold, 1922, 1924; Curtis, 1983).

Tetraponera Smith

This small genus has a widespread distribution in southern Africa (Arnold, 1916). Most members of the genus are arboreal, nesting in hollow twigs or thorns. Only one species, *T. ambigua*, has been recorded in the central Namib Desert. *Tetraponera ambigua* is known to use *Acacia* spp. thorns as a nesting site and has previously been recorded in Botswana (Arnold, 1916). No record of *T. ambigua* occurring in Namibia has apparently been published.

2.3.3 SPECIFIC NOTES

Tetramorium rufescens Stitz

TL 4.0-5.1; dull red, gaster sometimes darker than head and alitrunk. This species is widely distributed in the eastern half of the gravel plains and dune-field (Fig. 2.3). In the dune-field it occurs predominantly on the interdune valleys but has also been seen foraging on dune slopes. On the gravel plains nests are frequently located in small hollows and are fairly conspicuous, comprising up to six entrances of 2-5 mm diameter. Members of this species are predominantly diurnal, individual foraging granivores.

Tetramorium pogonion Bolton

TL 3.8-4.1; blackish-brown. This species has been collected only twice, once in a pitfall trap situated on a sand dune and once by hand on the gravel plains just east of the dune field (Fig. 2.3). No nests have been located. *Tetramorium pogonion* is a diurnal, individual foraging granivore.

Tetramorium solidum Emery

TL 4.1-5.1; dark brown to blackish-brown. This species has been collected at only two sites on the gravel plains (Fig. 2.3) and no nests have been located. This species is a diurnal, individual foraging granivore.

Tetramorium grandinode Santschi

TL 5.0-5.3; bicoloured with deep reddish-brown to blackish-brown head and alitrunk and a dull red gaster. *Tetramorium grandinode* occurs on the gravel plains on the eastern edge of the Namib Desert (Fig. 2.3). Nests are inconspicuous and contain up to four entrances of 3-5 mm diameter. Members of this species are diurnal, individual foraging granivores.

Tetramorium jordani Santschi

TL 5.3-5.8; black to blackish-brown. *Tetramorium jordani* occurs on the eastern half of the dune-field (Fig. 2.4) where it is found predominantly on sand dunes but also occurs on the interdune valleys. Nests are inconspicuous, usually comprising a single entrance of 2-5 mm diameter, situated at the base of perennial grass species such as Stipagrostis lutescens. Members of this species are diurnal, individual foraging granivorous ants.

Tetramorium peringueyi Arnold

TL 4.4-5.7; orange-red to deep red. This species occurs on the gravel plains on the eastern edge of the Namib Desert (Fig. 2.4). No nests have been located. Tetramorium peringueyi is a diurnal, individual foraging granivore.

Tetramorium sericeiventre Emery

TL 3.3-4.4; bicoloured with a dull red head and alitrunk and a black gaster. Tetramorium sericeiventre is widely distributed on the eastern half of the gravel plains and on interdune valleys in the dune field (Fig. 2.4). Nests have a single entrance of 3-5 mm diameter. The conspicuousness of the nests is enhanced by a ring of discarded refuse about the entrance. In contrast to the predatory nature of T. sericeiventre in the Ivory Coast (Levieux, 1972), in the Namib Desert this diurnal, individual foraging species is an omnivore, taking a diversity of food types including arthropod fragments, grass stems, leaves and seeds.

Tetramorium sp. near caldarium (Roger)

TL 2.1-2.4; yellow or light yellowish-brown with the gaster a darker shade than the head and alitrunk. Only a few specimens have been collected in a pitfall trap on the gravel plains (Fig. 2.4). Nothing is known about the habits of this species.

Monomorium viator Santschi

TL 3.5-3.9; bicoloured with dark brown head and gaster, and an orange alitrunk. *Monomorium viator* is widely distributed on the gravel plains and also occurs on interdune valleys (Fig. 2.5). Nests are inconspicuous with one, sometimes two, entrances of 1-2 mm diameter. Members of this species are predominantly nocturnal, individual foraging granivores.

Monomorium sp. B

TL 2.7-3.1; dark brown. *Monomorium* sp. B is widely distributed on the gravel plains (Fig. 2.5). Nests are inconspicuous and have a single entrance of 1-2 mm diameter. Members of this species are diurnal, individual foraging omnivores which take a variety of food types including seeds, vegetative parts of plants (especially grasses), arthropod fragments and honeydew.

Monomorium sp. I

TL 2.7-2.9; bicoloured with pale reddish-brown head and alitrunk and dark brown to black gaster. This is a rare, apparently arboreal species, that has been found on the gravel plains, at the eastern edge of the dune field and at Tsondab vlei (Fig. 2.6). Nests have not been located but are likely to be situated in trees. Workers are diurnally active and have been observed collecting nectar from the extrafloral nectaries on *Moringa ovalifolia* and honeydew from Homoptera on *Acacia* spp..

Monomorium sp. G

TL 1.7-1.9; translucent, pale orange-brown. This small species occurs in the eastern half of the central Namib Desert on the gravel plains (Fig. 2.6). Nothing is known about the habits of this ant. All specimens were taken in pitfall traps, some located at the base of plants, whereas others were over 50 m from the nearest plant. It seems likely therefore that they are not dependent on perennial vegetation or honeydew-exudate foods. In view of their pale, translucent coloration they are probably nocturnal.

Monomorium damarense Forel

TL 2.4-2.6; orange-brown. *Monomorium damarense* was found at only two localities, on the eastern plains of the Namib Desert in an ephemeral water course, and in the Kuiseb River bed at Gobabeb (Fig. 2.6). Nests were located in soft sand at the base of perennial shrubs; on the gravel plains in association with *Boscia foetida* and *Pecheul Loeschia leubnitziae* and in the Kuiseb River in association with *P. leubnitziae*. The ants were diurnally active but their feeding habits are unknown.

Monomorium sp. C

TL 2.2-2.6; dark brown to black. *Monomorium* sp. C is widely distributed on the gravel plains and also occurs on interdune valleys (Fig. 2.7). Nests are inconspicuous with a single entrance approximately 1 mm in diameter. Members of this species are diurnal, individual foraging granivores, taking predominantly *Stipagrostis* spp. seeds.

Monomorium sp. D

TL 1.3-1.5; translucent, pale orange-brown. This minute species has been collected at only one locality, near Ganab on the gravel plains (Fig. 2.7). The ants appeared to nest within perennial clumps of *Stipagrostis* sp.. Members of this species are diurnal, honeydew feeders and were observed tending Homoptera on perennial *Stipagrostis* sp. clumps. Because of its size and habits this is an inconspicuous species likely to be overlooked and may have a much wider distribution in the Namib Desert.

Monomorium sp. K

TL 2.0; pale brown. This species is known from two specimens only, both collected in a pitfall trap situated at the base of *Pecheul Loeschia leubnitziae* on the eastern edge of the gravel plains (Fig. 2.5). Nothing is known about the habits of this ant species.

Monomorium sp. J

TL 2.2; pale brown. This species is known from only three specimens taken in a pitfall trap situated on the slope of a sand dune (Fig. 2.6), and consequently nothing is known about its habits.

Monomorium sp. H

TL 2.0-2.2; medium brown. *Monomorium* sp. H was found at one site on the eastern plains of the Namib Desert (Fig. 2.6). All specimens were collected in pitfall traps situated at the base of *Boscia foetida*. Nothing is known about the habits of this ant species.

Monomorium sp. E

TL 2.3-2.6; dark brown to black. This species is apparently restricted to the eastern half of the Namib Desert gravel plains (Fig. 2.7). Nests have not been located. *Monomorium* sp. E is a diurnal, individual foraging granivore.

Monomorium sp. F

TL 2.9-3.1; dark brown to black. *Monomorium* sp. F is the only Namib ant species that is apparently restricted to the western half of the desert, in the cool fog zone, on the gravel plains (Fig. 2.7). Nests are inconspicuous and have a single entrance of 1-2 mm diameter. Members of this species are diurnal, individual foraging omnivores which take a variety of food types, especially seeds and arthropod fragments.

Ocymyrmex barbiger Emery

TL 6.7-7.2; reddish-brown. *Ocymyrmex barbiger* is widespread on the gravel plains and interdune valleys in the eastern half of the desert, but in the Kuiseb River and on the interdune valleys near the river it penetrates westwards to at least Klipneus. At the eastern edge of the dune-field this species also occurs on the sand dunes (Fig. 2.8). Nests are inconspicuous, normally have one entrance hole 5-10 mm in diameter and in sandy areas, such as the Kuiseb River, are usually situated at the base of some vegetation or in silt beds. *Ocymyrmex barbiger* is a diurnal, individual foraging insectivorous ant, almost exclusively scavenging dead insects and taking particular advantage of heat-stressed victims. These findings are contrary to the views of Prins (1963, 1965) that members of the genus are primarily granivorous.

Ocymyrmex turneri Donisthorpe

TL 5.4-5.8; blackish-brown. Ocymyrmex turneri is widespread on the gravel plains, occurring across the entire width of the Namib Desert (Fig. 2.8). Nests are inconspicuous, with one entrance hole 2-5 mm in diameter. Like O. barbiger, this species is a diurnal, individual foraging insectivore that primarily retrieves dead insects.

Ocymyrmex velox Santschi

TL 10.0-10.7; bicoloured with a red head and brownish-black alitrunk and gaster. This species is restricted to the gravel plains in the east, occurring particularly near inselbergs and in stony ground (Fig. 2.8). Nests are inconspicuous and normally have one entrance hole 5-20 mm in diameter. A semilunar crater, comprising sand and pebbles removed from the nest, occasionally occurs at the nest entrance. Ocymyrmex velox is a diurnal, individual foraging insectivorous species that preys principally on Hodotermes sp. during termite erruptions and scavenges for dead arthropods when termites are not active.

Crematogaster sp. A

TL 3.3-3.8; bicoloured with a red-brown head and alitrunk and a black-brown gaster. This species has only been found in the vicinity of Gobabeb in the Kuiseb River and in one of its tributaries where it occurred on Acacia spp. (Fig. 2.9). Nests have not been located but are almost definitely situated in trees (Arnold, 1920). Members of this species are diurnal, individual foraging honeydew feeders.

Crematogaster sp. B

TL 3.6-3.9; bicoloured with a red head and alitrunk and a black gaster. Crematogaster sp. B occurs on Acacia sp. trees on the gravel plains in the eastern side of the Namib Desert, on Acacia sp. trees in the Kuiseb River and on Stipagrostis grasses on the sand dunes in the eastern dune-field (Fig. 2.9).. In the dune-field nests are located at the base of Stipagrostis spp.. No nests have been located on the gravel plains or Kuiseb River but they are most probably situated in trees (Arnold, 1920). Members of this species are diurnal, individual foraging honeydew feeders.

Crematogaster sp. C

TL 3.6-3.8; red-brown. This species has been found at only two localities, 30 km north of Gobabeb on a Euclea pseudobenus tree and 56 km north-east of Gobabeb on an Acacia erioloba (Fig. 2.9). No nests were located but they were probably situated in the trees. Crematogaster sp. C is a diurnal, individual foraging honeydew feeder.

Pheidole tenuinodis Mayr

TL 2.5-2.6 (minor), 4.5-4.9 (major); medium brown to blackish-brown. *Pheidole tenuinodis* is widely distributed on the gravel plains and also occurs on interdune valleys at Sandwich Harbour and at the eastern edge of the dune-field (Fig. 2.10). Nests are inconspicuous, typically with one, but occasionally up to five, entrances of 3-5 mm diameter. Members of this species are predominantly nocturnal to crepuscular. They are primarily seed eaters but also regularly take honeydew and nectar. Foragers collect food individually but sometimes employ group foraging along trunk-trails leading to specific, localized food sources, such as a nectar-secreting plant, or a plant heavily infested with honeydew-secreting Homoptera.

Messor denticornis Forel

TL 5.5-11.0; black. *Messor denticornis* is widely distributed on the gravel plains, particularly on the eastern half of the Namib Desert, and at Tsondab vlei (Fig. 2.10). Nests are fairly conspicuous, usually comprising a nest disk of 0.5-1.0 m diameter and a system of radiating pathways from which small pebbles have been cleared by the ants. Each nest has one to four entrance holes of 10-30 mm diameter. Colonies are polydomous, containing up to four nests which are often interconnected by surface pathways. In terms of biomass this is the dominant ant species on the eastern plains (see section 4.3) and it is occasionally preyed upon by antbear, *Orycteropus afer*. As a consequence of antbear activity the nest disks frequently contain large holes (approximately 50-70 X 30 X 30 cm). Members of this species are predominantly nocturnal, group foraging granivores. Workers employ individual foraging to collect insect material and seeds when seeds are relatively scarce.

Anoplolepis steingroeveri (Forel)

TL 2.9-8.0; blackish-brown. This species is widely distributed on the gravel plains and also occurs at Tsondab and Mniszeckie vleis in the dune-field (Fig. 2.11). Nests are relatively conspicuous, with a series of entrances of about 5-10 mm diameter which are usually situated at the base of some perennial vegetation or below rock slabs. The conspicuousness of the nests is enhanced by the aggressive habits of these ants which swarm out towards, and sting, any animal large enough to set up vibrations on the surface near their nests. Members of this species are diurnal, individual foraging honeydew and nectar feeders. Their distribution is dependent on perennial vegetation. Nests have been located below or near the following plants: *Salsola tuberculata*, *Arthraerua leubnitziae*, *Welwitschia mirabilis*, *Moringa ovalifolia*, *Calicorema capitata*, *Acacia* spp., *Asclepias buchenaviana* and *Stipagrostis* spp..

Anoplolepis sp.

TL 2.4-3.0; medium brown. This species has been located once only, on the gravel plains in soft sand on the eastern edge of the Namib Desert (Fig. 2.11). Workers were active during the heat of the day but nothing further is known about their habits.

Acantholepis sp.

TL 2.0-3.2; black. This species is widely distributed on the gravel plains and also occurs at Sandwich Harbour (Fig. 2.11). Nests are inconspicuous, normally with one entrance of 1-2 mm diameter, and are situated at the base of some perennial vegetation. Members of this species are diurnal, individual foraging honeydew and nectar feeders. Their distribution is dependent on perennial vegetation and nests have been located below or near the following plants: *S. tuberculata*, *A. leubnitziae*, *W. mirabilis*, *B. foetida*.

Camponotus detritus Emery

TL 7.0-16.0; dorsally bicoloured with dark reddish-brown to black head and alitrunk and predominantly ochre to buff gaster with a few black blotches, ventrally a uniform dark reddish-brown to black. *Camponotus detritus* is widespread on sand dunes across the width of the desert and in the Kuiseb River from approximately 20 km east of Homeb to Walvis Bay

(Fig. 2.12). With the exception of a small population on the west side of Swartbank Mountain, these ants do not occur on the gravel plains or on interdune valleys. Nests are situated at the base of vegetation, usually a clump of perennial grass, and typically contain one entrance hole 10-15 mm in diameter. Colonies are polydomous, containing up to four nests (Curtis, 1983). *Camponotus detritus* is predominantly a diurnal, individual foraging honeydew feeder.

Camponotus fulvopilosus (De Geer)

TL 10.0-16.0; dorsally bicoloured with a dark brown to black head and alitrunk and an ochre to buff gaster, ventrally a uniform dark brown to black. This species is confined to the eastern edge of the gravel plains where it commonly occurs in well vegetated ephemeral water courses (Fig. 2.12). Nests are typically situated below rock slabs and contain one entrance hole of 10-15 mm diameter. Members of this species are predominantly diurnal, individual foraging honeydew feeders which derive their food primarily from Homoptera occurring on *Acacia* trees.

Camponotus maculatus (F.)

TL 7.7-12.0; translucent, pale brown. *Camponotus maculatus* is widely distributed on the gravel plains (Fig. 2.12). The nests of these nocturnal, individual foraging ants have not been located.

Camponotus mystaceus Emery

TL 7.0-15.0; translucent, pale brown but sometimes with dark brown on head and gaster. This species is widely distributed on the gravel plains, occurring across the width of the desert, and occurring on sand dunes on the eastern dune-field (Fig. 2. 12). Nests of this species have not been located. *Camponotus mystaceus* is a nocturnal, individual foraging honeydew feeding species. Workers obtain honeydew from Homoptera occurring on *Stipagrostis* spp. on sand dunes. On the gravel plains workers have been observed taking nectar from *A. leubnitziae* flowers.

Tetraponera ambigua (Emery)

TL 3.8-4.1; orange-brown. This species has been located on one occasion only, on the eastern edge of the Namib Desert (Fig. 2.12), where it was seen foraging on an *Acacia* sp. during the day. Nothing is known about the habits of this species.

2.3.4 General discussion and conclusions

As all habitats were not sampled with equal intensity, interhabitat comparisons could be misleading. The gravel plains were sampled most intensively, and perhaps because of this the majority of ant species were found in this habitat. Of the 36 ant species recorded in the central Namib Desert, 33 were found on the gravel plains. In contrast, only 12 species were found in the dune-field and 9 of these also occurred on the gravel plains. The predominance of ants on the gravel plains may however be genuine and not a reflection of biased sampling, as Bernard (1964) and Delye (1968) noted a similar distribution for Sahara Desert ants. Only three species, *C. detritus*, *T. jordani* and *Monomorium* sp. J, have been recorded in the Namib dune-field alone. Of these three species, the former two were common and conspicuous in the dune-field and their apparent absence on the gravel plains is probably real and not due to inadequate sampling. *Monomorium* sp. J was collected once only in the dune-field and there is thus insufficient evidence to assess whether this is a dune-endemic species or not.

Thirteen of the 36 Namib Desert ant species were strongly associated with perennial vegetation. This dependence on perennial vegetation reflects the ants' requirements for a regular source of honeydew, nectar and/or nesting sites. All of the Formicinae and Pseudomyrmecinae fall into this category, as do the *Crematogaster* species and three *Monomorium* species in the Myrmicinae. The majority of Myrmicinae were not dependent on perennial vegetation, relying primarily on seeds, insects or both for their food. This freedom from perennial vegetation probably explains in part the dominance of the Myrmicinae in the extremely arid, central Namib Desert where perennial vegetation is sparse or absent for much of the region (Robinson, 1978).

Of the 28 Namib Desert ant species for which trophic roles could be assigned with reasonable confidence, 11 were granivorous, 11 were honeydew-nectar feeders, 3 were omnivores and 3 were insectivores. This accords well with data from other deserts of the world where the major trophic categories into which ants fall are seed, honeydew-nectar and insect feeders and omnivores (Chew, 1977; Delye, 1968; Pisarski, 1978; Whitford, 1978a).

Bearing in mind possible differences in the depth of taxonomic knowledge and sampling intensity, the ant fauna of the central Namib Desert is strikingly similar in its overall composition to that of the central Sahara Desert (Table 2.2). In both deserts the same three subfamilies of ants are present with the fauna being dominated by the Myrmicinae, followed by the Formicinae and with the Pseudomyrmecinae very poorly represented. Similarities also exist at the generic level, with the majority of ants in both deserts belonging to the same genera. The importance of the various genera in each desert varies however. Only one species, *C. maculatus*, occurs in both deserts, although once the revisions of *Crematogaster*, *Monomorium* and *Acantholepis* (Bolton, in prep.) are completed, other species common to both deserts may be revealed.

There are some interesting examples of convergence between the ant faunas of the two regions: The role of

Table 2.2. Composition of ant faunas in the central Sahara and central Namib Deserts. Data on Sahara Desert ants are from Delye (1968).

ANT TAXON	NUMBER OF ANT SPECIES	
	NAMIB	SAHARA
MYRMICINAE		
Messor	1	8
Pheidole	1	3
Tetramorium	8	3
Leptothorax	0	7
Monomorium	12	7
Crematogaster	3	5
Cardiocondyla	0	1
Oxyopomyrmex	0	1
Ocymyrmex	3	0
FORMICINAE		
Cataglyphis	0	5
Camponotus	4	9
Acantholepis	1	2
Anoplolepis	2	0
PSEUDOMYRMECINAE		
Tetraponera	1	2
Total	36	53

insectivore is occupied by the myrmicine genus *Ocymyrmex* in the Namib Desert and by the formicine genus *Cataglyphis* in the Sahara Desert (Delye, 1968; Harkness and Wehner, 1977; Schmidt-Hempel, 1983; Wehner *et al.*, 1983; Wehner and Marsh, in prep.). Despite their different phylogenetic origins, members of both genera occupy the same temporal niche during the heat of the day and exhibit similarities in foraging behaviour and speed of locomotion (Wehner and Marsh, in prep.). The myrmicine genera *Leptothorax* and *Tetramorium* are examples of morphological convergence (Bolton, 1980) and probably occupy the same granivorous niche. In this respect it is interesting that *Tetramorium* species are relatively rare in the Sahara Desert, where *Leptothorax* is abundant, whereas, in the Namib Desert, where *Leptothorax* does not occur, *Tetramorium* is common.

Although the Myrmicinae and Formicinae also dominate the ant faunas of deserts in Australia (Briese and Macauley, 1981; Greenslade and Halliday, 1983) and North America (Chew, 1977; Whitford, 1978a), the Dolichoderinae are also prevalent and Dorylinae and Ponerinae subfamilies are present. These differences may reflect different evolutionary histories of the African deserts and these other, more isolated and distant, deserts. They may also reflect differences in aridity, with the more xeric African deserts supporting a relatively simple trophic web excluding the obligatory, predatory doryline and ponerine ants.

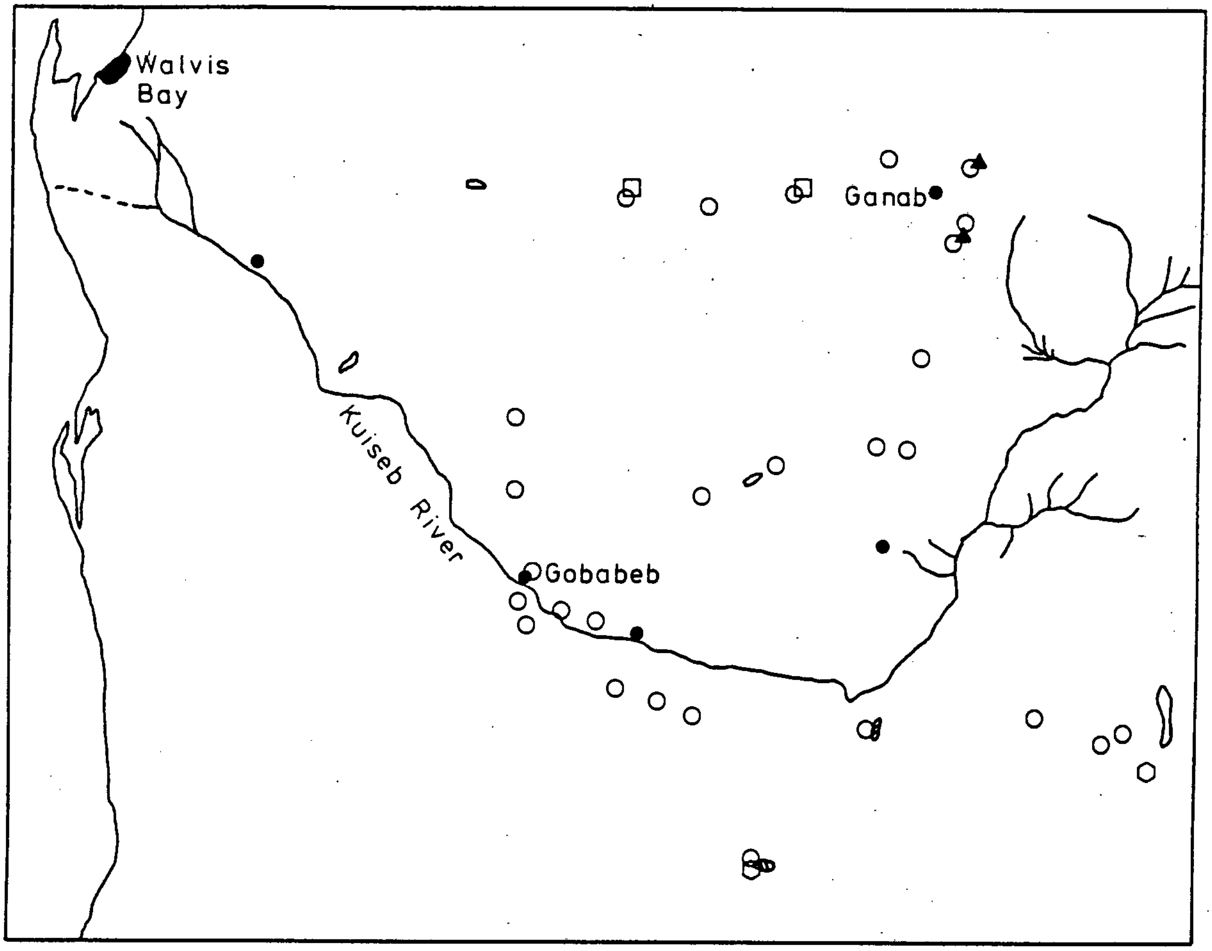

Figure 2.3. Distribution map for Tetramorium rufescens ○, T. grandinode ▲, T. pogonion ⬡ and T. solidum □.

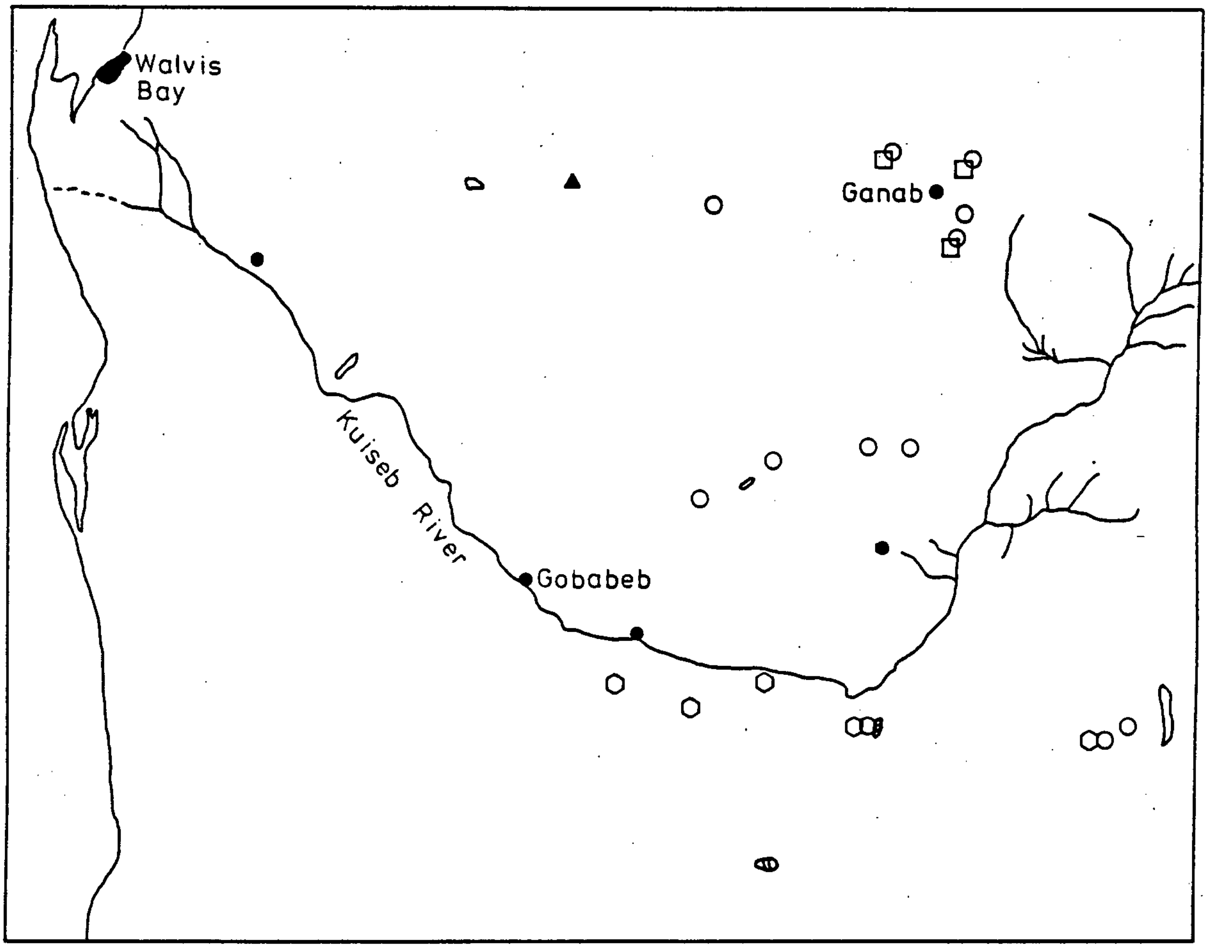

Figure 2.4. Distribution map for *Tetramorium sericeiventre* ○, *Tetramorium* sp. near *caldarium* ▲, *T. jordani* ⬡ and *T. peringueyi* □.

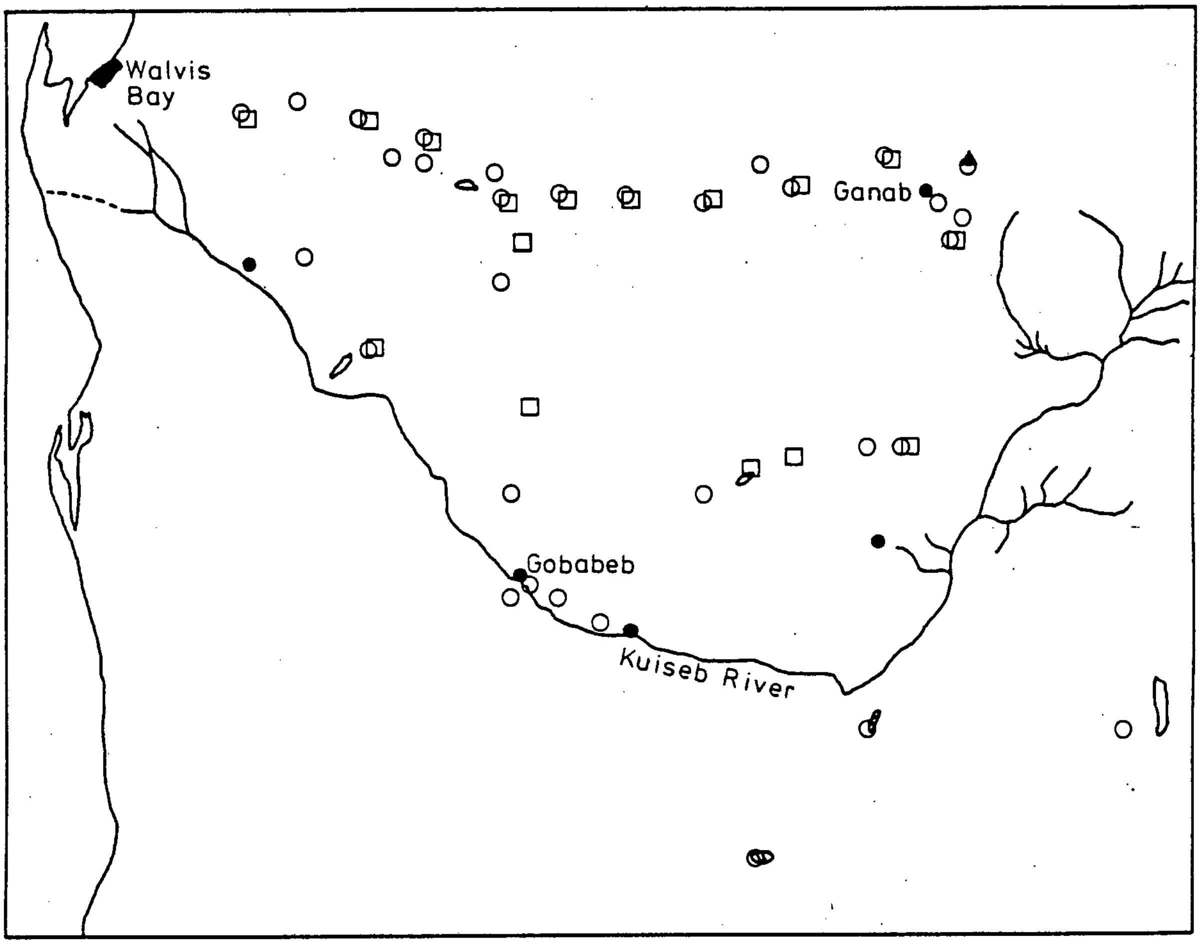

Figure 2.5. Distribution map for Monomorium viator ○, Monomorium sp. K ▲ and Monomorium sp. B □.

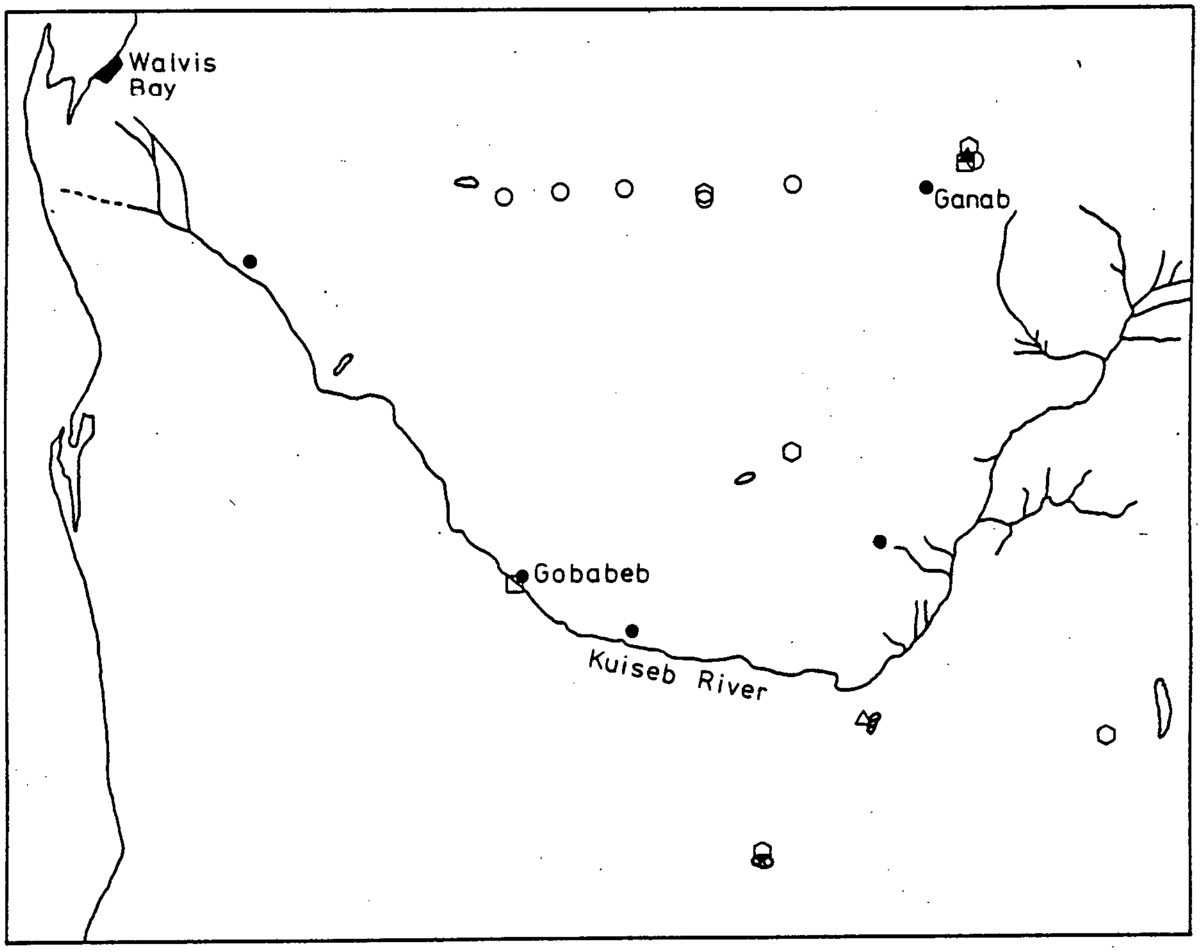

Figure 2.6. Distribution map for Monomorium sp. G ○, Monomorium sp. J △, Monomorium sp. H ▲, Monomorium sp. I and M. damarense □.

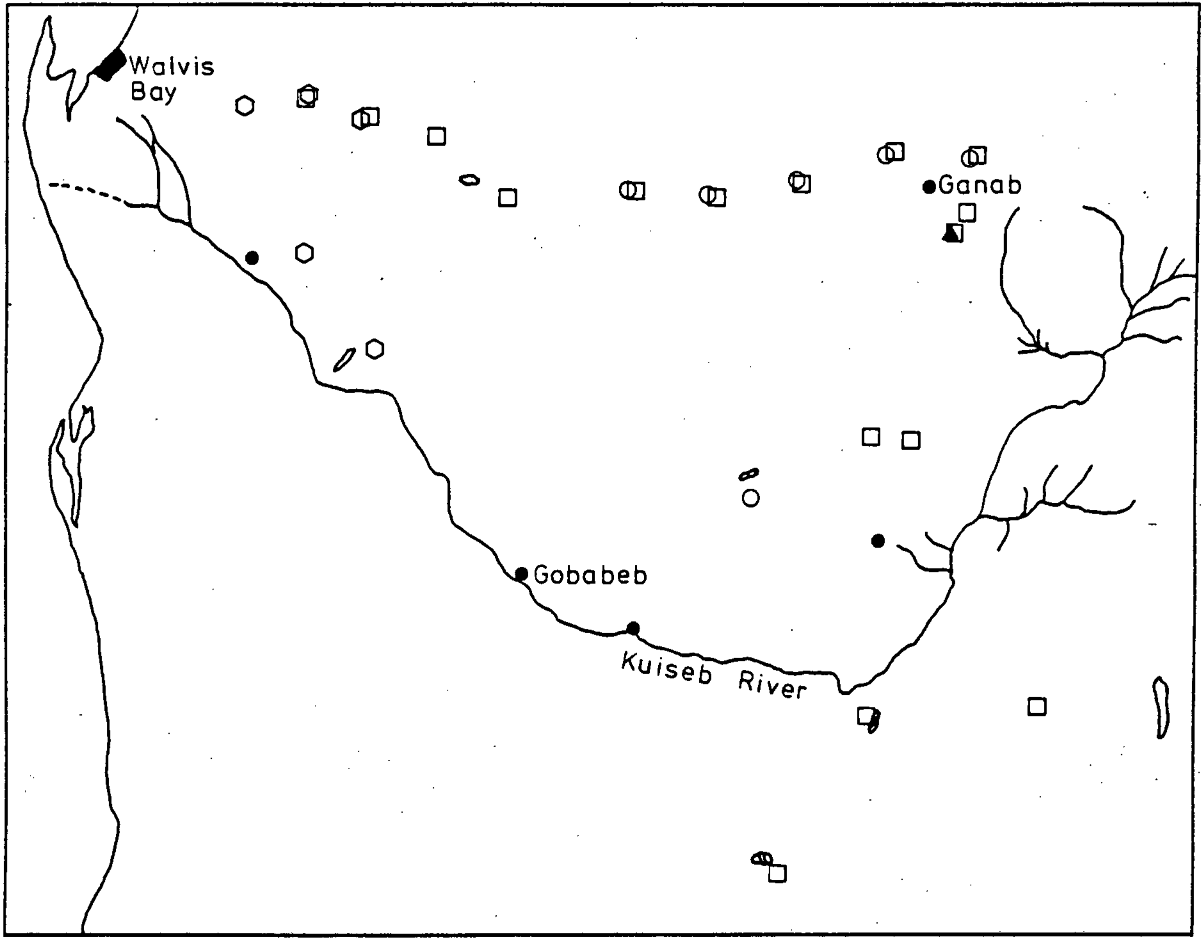

Figure 2.7. Distribution map for Monomorium sp. E ○, Monomorium sp. D ▲, Monomorium sp. F ⬡ and Monomorium sp. C □.

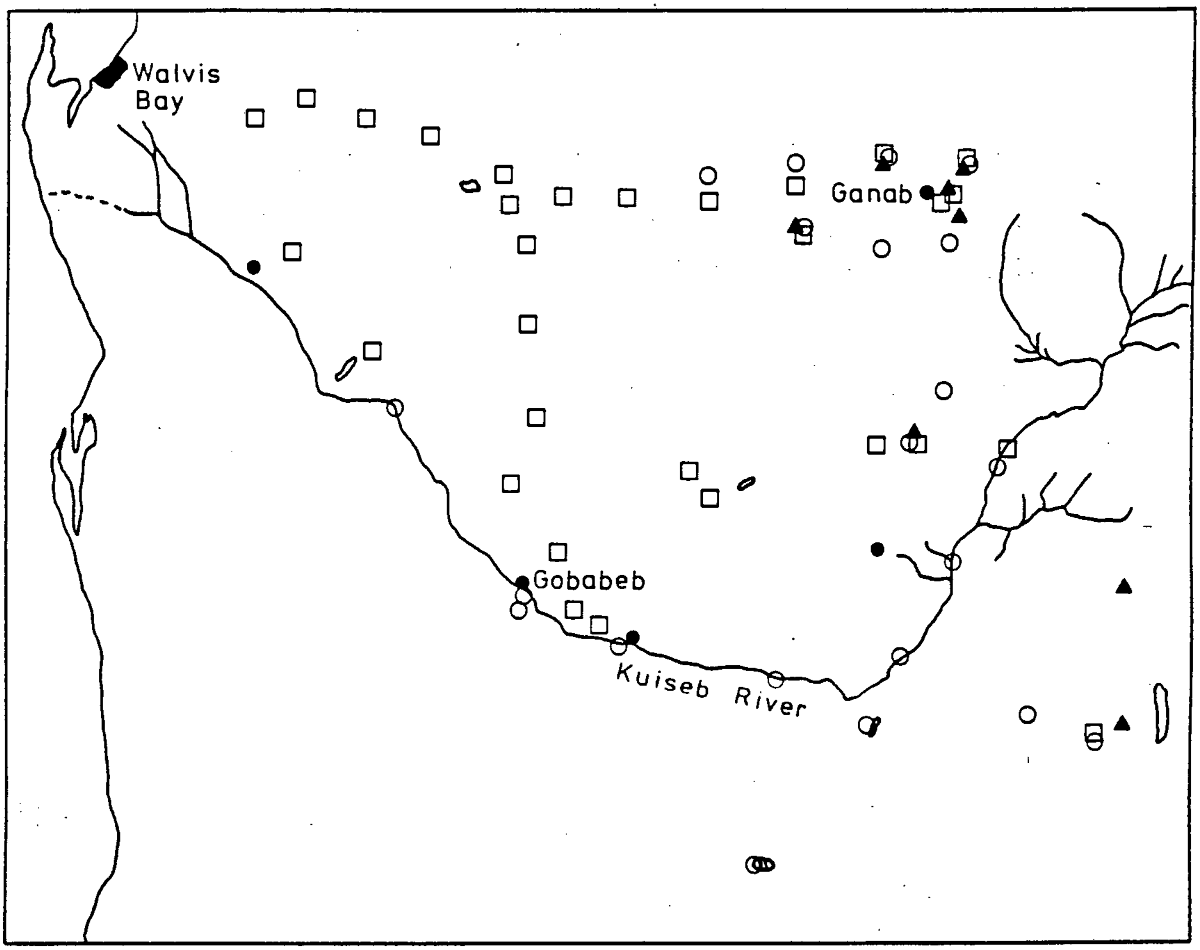

Figure 2.8. Distribution map for Ocymyrmex barbiger ○, O. velox ▲ and O. turneri □.

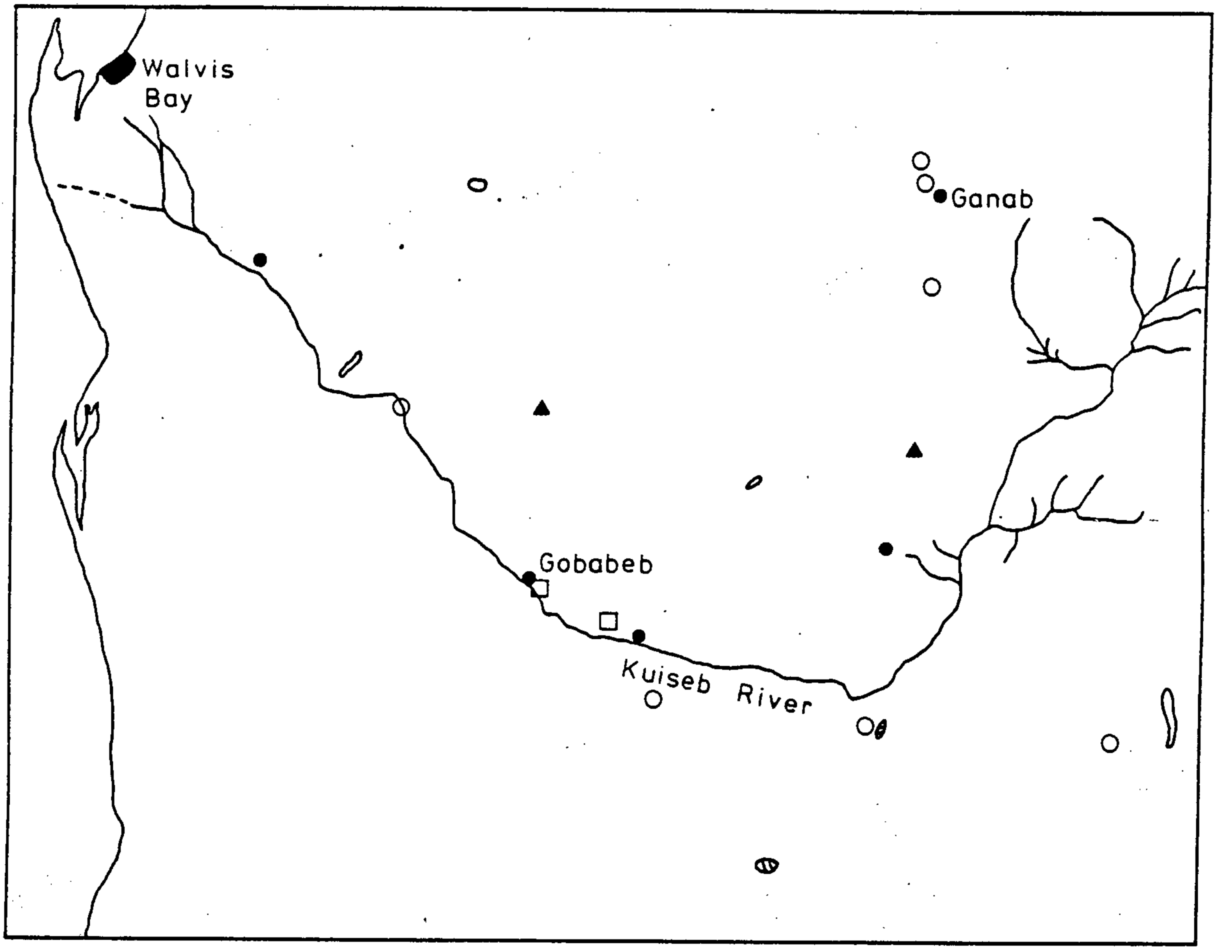

Figure 2.9. Distribution map for <u>Crematogaster</u> sp. B ○, <u>Crematogaster</u> sp. C ▲ and <u>Crematogaster</u> sp. A □.

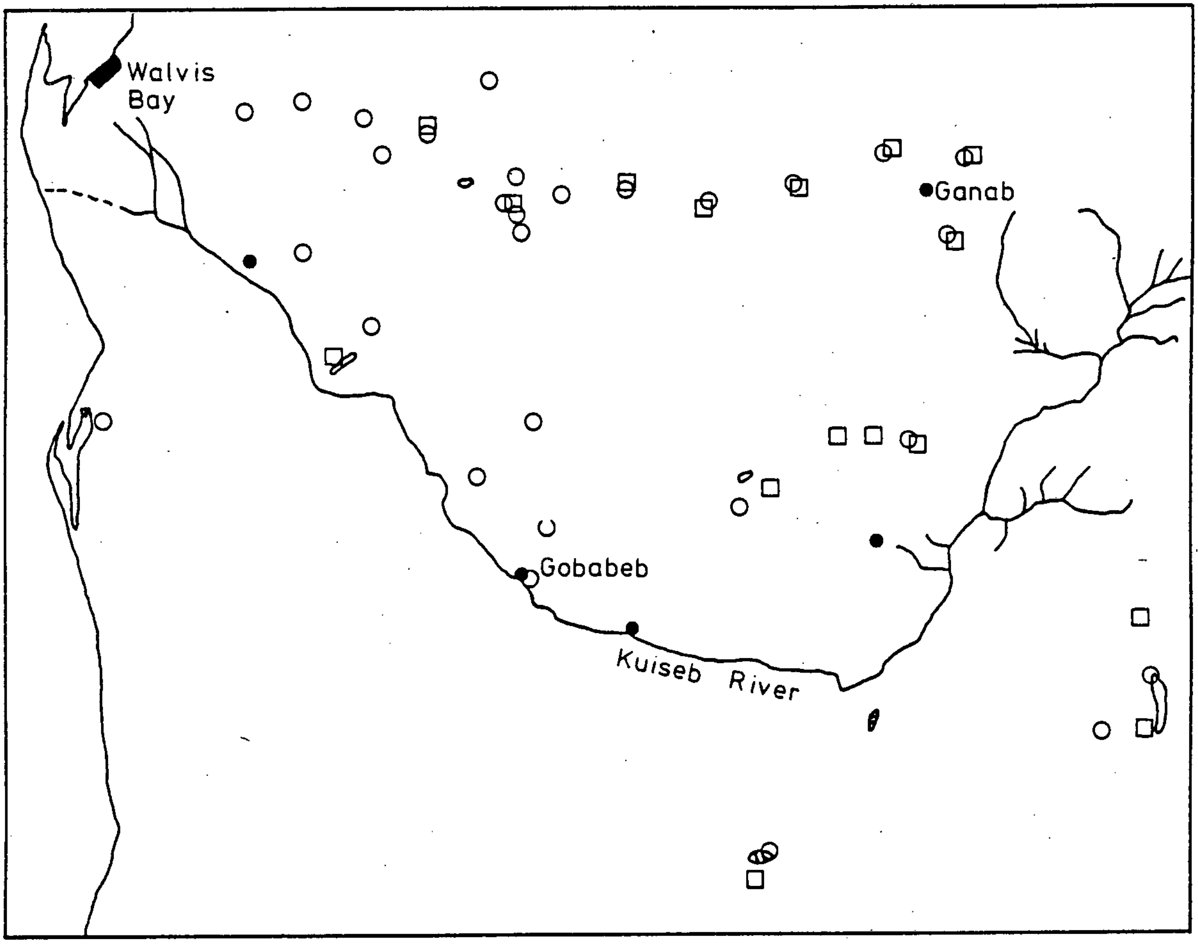

Figure 2.10. Distribution map for *Pheidole tenuinodis* ○ and *Messor denticornis* □.

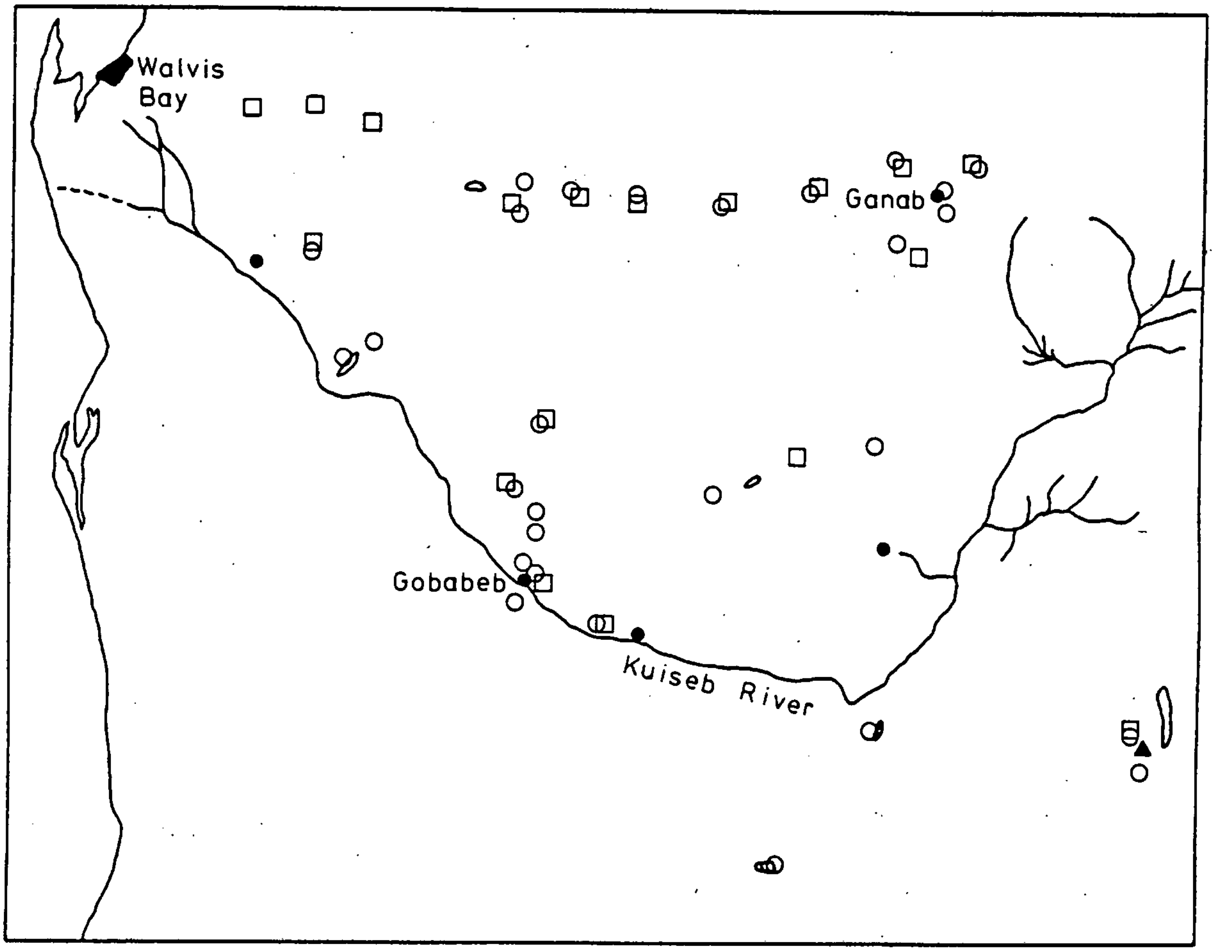

Figure 2.11. Distribution map for Anoplolepis steingroeveri ○, Anoplolepis sp. ▲ and Acantholepis sp. □.

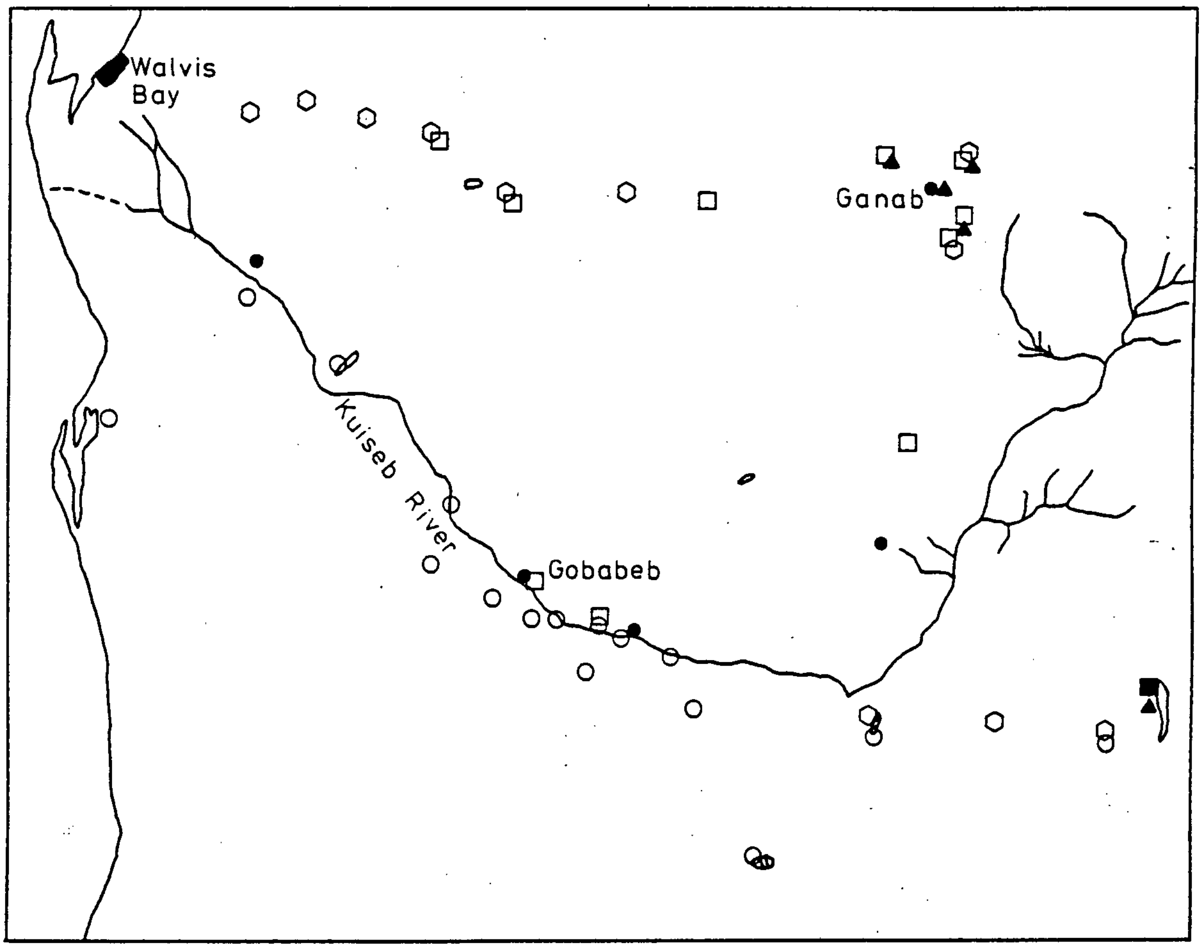

Figure 2.12. Distribution map for *Camponotus detritus* ○, *C. fulvopilosus* ▲, *C. mystaceus* ⬡, *C. maculatus* □ and *Tetraponera ambigua* ■.

SECTION THREE

ANT SPECIES RICHNESS ALONG A CLIMATIC GRADIENT IN THE NAMIB DESERT

3.1 INTRODUCTION

In reviewing desert plant and animal community studies, Pianka (1979) concluded that 'few, if any, generalizations about diversity.....seem possible at present'. For example, in North American deserts the species diversity of granivorous rodents (Brown, 1973) increases with increases in productivity, whereas in the central Namib Desert the diversity of dune-endemic tenebrionid beetles is greatest in the centre of a rainfall gradient (Seely, 1982). Studies on desert ant communities have, however, revealed some consistent trends. Ant species diversity increases with increases in productivity in North American deserts (harvester ants; Davidson, 1977a; harvester ants and insectivores, Bernstein, 1971) and in Australian deserts (all ants; Greenslade & Halliday, 1983). Similar patterns appear to exist for Namib Desert dune ants (Seely, 1982) and the present study is an attempt to establish whether this applies to the ant communities occurring on the gravel plains of the central Namib Desert.

In certain respects the central Namib Desert is ideally suited to investigations of species diversity patterns. Steep gradients of humidity, fog, temperature and rainfall occur across the width of this narrow desert. For example, mean annual rainfall changes from 15 mm to 87 mm in just over 100 km, corresponding to a 1 000 m increase in elevation (Lancaster *et al.*, 1984). Because productivity in deserts is largely dependent on rainfall (Noy-Meir, 1973; Seely, 1978) there is also a steep productivity gradient across the width of the central Namib, although the regular occurrence of fog near the coast (Lancaster *et al.*, 1984) permits the existence of perennial dwarf shrub communities in this otherwise extremely dry zone (Louw & Seely, 1982).

Previous studies have examined patterns of desert ant species diversity over moisture gradients ranging from approximately 80 to 300 mm mean annual precipitation. The steep rainfall gradient of the Namib presents an opportunity to take the analysis into the extremely arid, low productivity end of the moisture/productivity continuum. The present study describes how ant species richness changes across the width of the central Namib on the flat gravel plains and attempts to relate this pattern to the climatic gradient.

3.2 PROCEDURE

On six occasions, between February and April 1984, ants were sampled at intervals of 10 km from 20 km inland of Walvis Bay to the eastern border of the Namib-Naukluft Park, a distance of 100 km (Fig. 3.1). The transect traversed a relatively flat gravel plain from west to east. Over the length of the transect the land sloped gently from an altitude of 150 m to 1000 m. Ants were not collected closer to the coast as this area is in a region of shifting sands and is subject to extensive human disturbance.

Ants were collected in baited pitfall traps. Each pitfall trap comprised a glass test-tube (18 x 150 mm), inserted into the ground so that the rim was flush with the surface, and containing 5 ml ethylene glycol, a slow-evaporating preservative. Bait, in the form of grated cheese and drops of syrup, was scattered about in the vicinity of each trap. The bait was used to increase the probability of ants encountering the traps. Five pitfall traps were inserted at each of the 11 sites along the transect. At each site, the traps were distributed so that all habitat and vegetation types were sampled. For each sampling period, traps were left in position for five consecutive days.

3.3 RESULTS AND DISCUSSION

The levelling off of the accumulative species curves (Fig. 3.2) suggests that most species present at each site were sampled after six sampling periods. Twenty-seven ant species, belonging to two subfamilies and nine genera, were

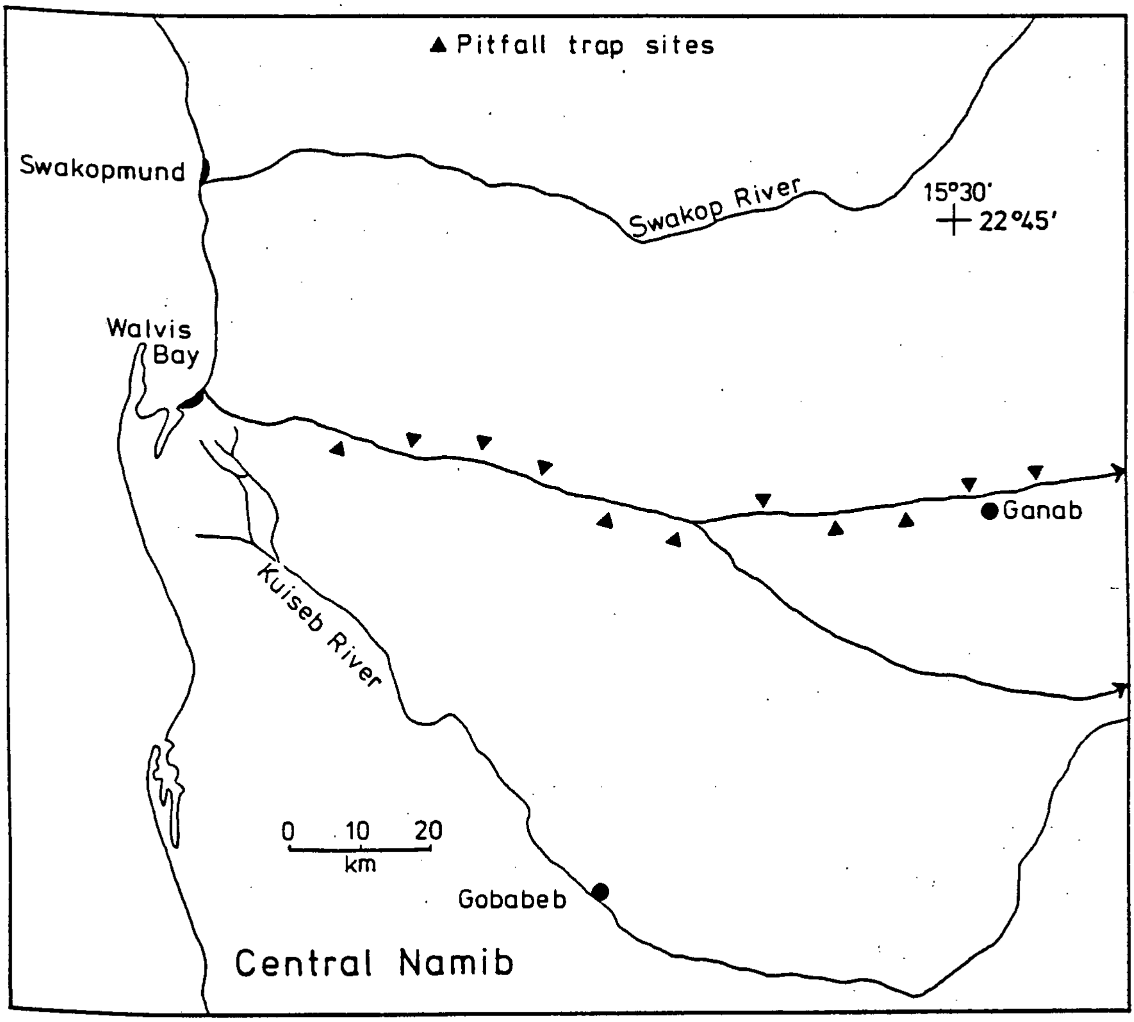

Figure 3.1. Map of the central Namib Desert showing location of pitfall trap sites.

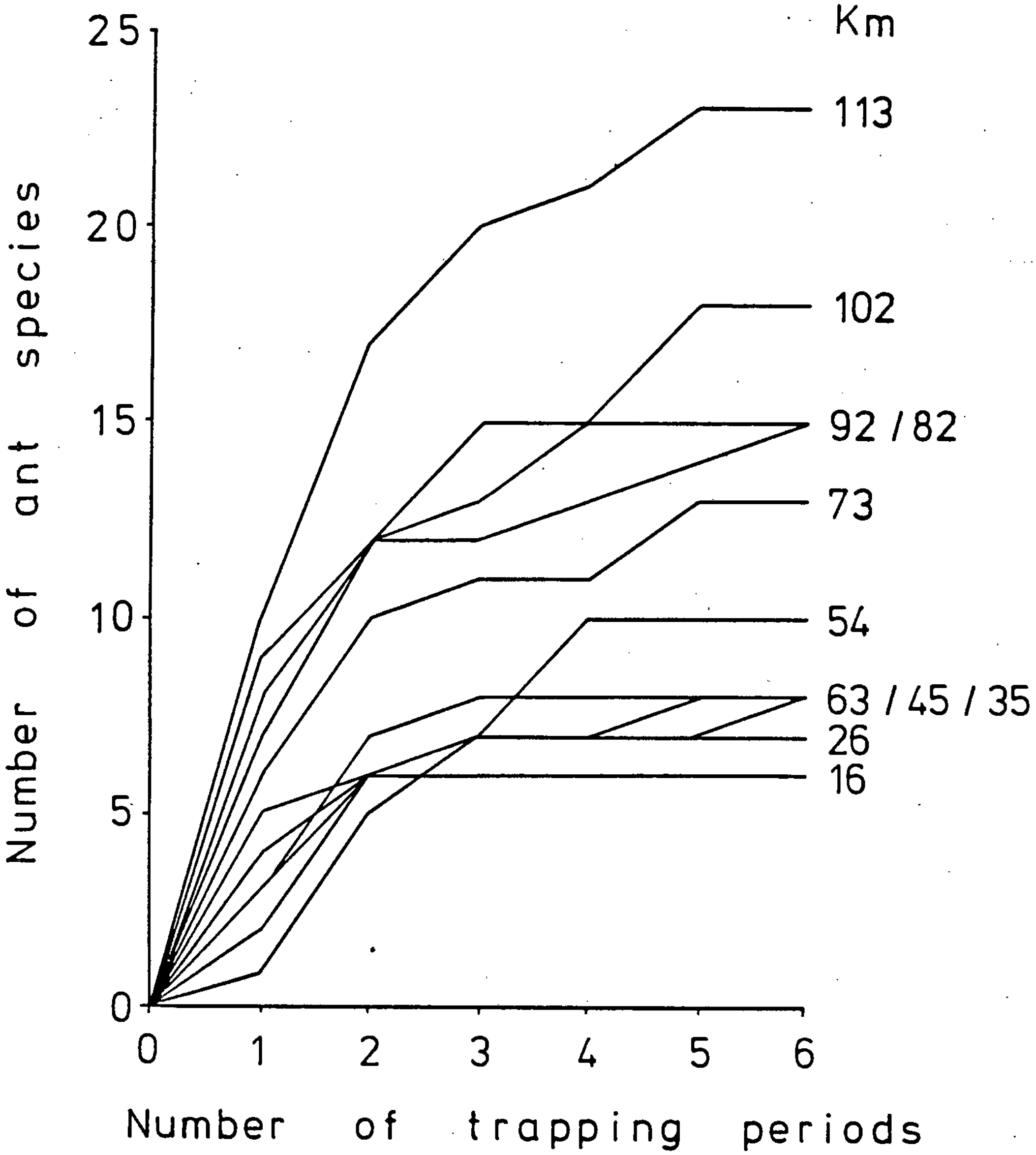

Figure 3.2. Accumulative species curves at 11 pitfall trap sites across the central Namib Desert. Distances from the coast are indicated.

collected across the gradient (Table 3.1). Eighty-one per cent of the ants were myrmicines with 10 species belonging to the genus Monomorium. Crematogaster sp. B is arboreal whereas all the other species nest in the ground and are epigaeic. The Formicinae and Myrmicinae are the largest ant subfamilies, and the dominant ant groups in most terrestrial habitats (Wilson, 1971). Their prevalence becomes more marked in hot and cold deserts as other subfamilies disappear (E.O. Wilson, pers. comm.). For example, in tundra they are the only ant groups present (Gregg, 1972). Similarly, in the central Sahara (Delye, 1968) and Namib (see section 2.3), with the exception of some rare, arboreal Tetraponera belonging to the minor subfamily Pseudomyrmecinae, the Myrmicinae and Formicinae are the only ants present. In the deserts of North America and Australia, however, in addition to the Myrmicinae and Formicinae, the Dolichoderinae are well represented and ponerine and doryline ants are also present (Briese & Macauley, 1981; Chew, 1977; Greenslade & Halliday, 1983; Whitford, 1978a). The absence of the other major ant groups in the Namib and Sahara deserts is not attributable to a lack of time and opportunity to colonize these areas as dolichoderine, ponerine and doryline ants are common in surrounding, more mesic areas (Delye, 1968; Prins et al., 1978). It appears that extreme aridity and low productivity may permit only specialized desert forms to occupy these areas and it is primarily within the Myrmicinae and Formicinae that such ants occur.

Table 3.1. Ant species caught in pitfall traps on the gravel plains.

MYRMICINAE

- *Monomorium viator* Santschi
- *Monomorium damarense* Forel
- *Monomorium* sp. B
- *Monomorium* sp. C
- *Monomorium* sp. E
- *Monomorium* sp. F
- *Monomorium* sp. G
- *Monomorium* sp. H
- *Monomorium* sp. I
- *Monomorium* sp. K
- *Ocymyrmex velox* Santschi
- *Ocymyrmex barbiger* Emery
- *Ocymyrmex turneri* Donisthorpe
- *Crematogaster* sp. B
- *Messor denticornis* Forel
- *Pheidole tenuinodis* Mayr
- *Tetramorium rufescens* Stitz
- *Tetramorium solidum* Emery
- *Tetramorium grandinode* Santschi
- *Tetramorium peringueyi* Arnold
- *Tetramorium sericeiventre* Emery
- *Tetramorium* sp. near *caldarium* (Roger)

FORMICINAE

- *Camponotus maculatus* (F.)
- *Camponotus fulvopilosus* (De Geer)
- *Camponotus mystaceus* Emery
- *Acantholepis* sp.
- *Anoplolepis steingroeveri* (Forel)

Deserts are characterized by low, erratic rainfall which causes primary production to come in short, infrequent pulses (Noy-Meir, 1979/80). Ants in extreme deserts have to contend with long periods of food scarcity and it is significant that it is in the Formicinae and Myrmicinae, in particular, that ants specializing at food storage occur. Many desert myrmicines, and some formicines, are seed harvesters; e.g. Australia: *Meranoplus*, *Pheidole*, *Chelaner*, *Tetramorium* (Briese & Macauley, 1981); North America: *Novomessor*, *Pogonomyrmex*, *Pheidole* (Davidson, 1977a); Sahara: *Messor*, *Pheidole*, *Monomorium* (Delye, 1968); Namib: *Messor*, *Pheidole*, *Monomorium*, *Tetramorium* (present study). Certain formicines have developed an inactive 'replete' caste which have very distensible crops in which liquid foods are stored; e.g. Australia: *Melophorus* (Pisarski, 1978); North America: *Myrmecocystus* (Wheeler, 1910); Sahara: *Camponotus* (Delye 1968); Namib: *Anoplolepis* (Prins, 1982). Only one dolichoderine, *Leptomyrmex* from Australia, is known to store liquid food (Wilson, 1971). Although most ants are opportunistic feeders and in a broad sense omnivorous (Carroll & Janzen, 1973; Stradling, 1978) it is possible to assign them to trophic groups based on the food that they most commonly utilize. Using this criterion most desert Dolichoderinae are opportunistic omnivores and the dorylines and ponerines are obligatory predatory insectivores (Briese & Macauley, 1981; Chew, 1977; Greenslade & Halliday, 1983; Whitford, 1978a). All three groups probably require a regular supply of food, conditions which are more likely to occur in the

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relatively mesic deserts of North America and Australia than in the extremely arid deserts of Africa.

The majority of ants in the deserts of North America (Chew, 1977; Whitford, 1978a), Australia (Pisarski, 1978) and North Africa (Delye, 1968) are seed, honeydew-nectar or insect feeders. In the Namib Desert the ants belong to four major trophic groups: granivores, honeydew-nectar feeders, insectivores and omnivores (Table 3.2). Data on trophic roles come from detailed studies of *O. velox*, *O. barbiger*, *M. denticornis*, *P. tenuinodis*, *T. rufescens*, *T. sericeiventre*, *M. viator*, *Monomorium* sp. B and *Monomorium* sp. C (see sections 4.3 & 8.3) from the taxonomic literature (Arnold, 1917, 1920, 1922, 1924; Bolton, 1980, 1981; Prins, 1982) and from chance observations while collecting the other species. In the Namib Desert most ants are granivorous or honeydew-nectar feeders. All granivores belong to the Myrmicinae. The three *Ocymyrmex* species are insectivorous and primarily scavengers and *T. sericeiventre*, *Monomorium* sp. F and *Monomorium* sp. B have been assigned to the omnivore category as they regularly retrieve a variety of food including arthropod fragments, grass stems and leaves, seeds and honeydew-nectar. *Pheidole tenuinodis* is primarily a harvester ant but regularly supplements its diet with honeydew and nectar. All the formicine species, *Monomorium* sp. I and *Crematogaster* sp. B are predominantly honeydew-nectar feeders. As a consequence their distribution is closely tied to that of the perennial vegetation.

Table 3.2. Distribution of ant species across the central Namib Desert gravel plains.*

SPECIES	TROPHIC GROUP	DISTANCE FROM THE COAST (km) 16	26	35	45	54	63	73	82	92	102	113
Acantholepis sp.	H	X	X	X		X	X	X	X	X	X	X
C. mystaceus	H	X	X	X	X	X		X				X
A. steingroeveri	H					X	X	X	X	X	X	X
C. maculatus	H				X	X			X		X	X
C. fulvopilosus	H										X	X
Crematogaster sp. B	H										X	
Monomorium sp. I	H								X			X
P. tenuinodis	H/G	X	X	X	X	X	X	X	X	X	X	X
M. viator	G	X	X	X	X	X	X	X	X	X	X	X
Monomorium sp. C	G		X	X	X	X		X	X	X	X	X
M. denticornis	G				X	X		X	X	X	X	X
Monomorium sp. E	G							X	X	X	X	X
T. rufescens	G							X	X	X	X	X
T. solidum	G							X		X		
T. peringueyi	G										X	X
T. grandinode	G											X
O. turneri	I		X	X	X	X	X	X	X	X	X	X
O. barbiger	I								X	X	X	X
O. velox	I										X	X
Monomorium sp. B	O	X		X	X	X	X	X	X	X	X	
Monomorium sp. F	O	X	X	X								
T. sericeiventre	O								X		X	X
Monomorium sp. G	?					X	X	X	X	X		X
M. damarense	?											X
Monomorium sp. H	?											X
Monomorium sp. K	?											X
Tetramorium sp. near *caldarium*	?						X					

* The presence of each species is indicated by X. The trophic group of each species is indicated where possible; H = honeydew-nectar feeder, G = granivore, I = insectivore, O = omnivore.

Mean annual rainfall at each sampling site was derived by extrapolation from data in Lancaster et al. (1984). Species richness was strongly correlated with mean annual rainfall (Fig 3.3; $y = 3.84 + 0.20x$, $r^2 = 0.94$, $p < 0.001$). Thus, as in North American deserts (Bernstein, 1971; Davidson, 1977a) and Australian deserts (Greenslade & Halliday, 1983) ant species diversity is positively related to productivity. It remains uncertain, however, if there is a causal relationship between productivity per se and diversity of desert ants. The structural complexity of the vegetation, and the diversity of plants, seeds and insects, invariably increase with productivity and any one, or a combination, of these factors may promote species packing.

All Namib Desert species for which adequate information exists (i.e. with the exception of the genera Monomorium, Acantholepis and Crematogaster) occur elsewhere in southern Africa, most being confined to the semi-arid to arid western half of the subcontinent (Arnold, 1917, 1920, 1922, 1924; Bolton, 1980, 1981; Prins, 1982). Thus none of the relatively well researched species is restricted to the Namib Desert. A possible exception to this is the dune species Camponotus detritus, although recent collections suggest that it may occur elsewhere (M. Molteno and A.J. Prins, pers. comms.) and that genetically it is indistinguishable from the widespread C. fulvopilosus (Lighton, unpubl.). Most ant species occurred at

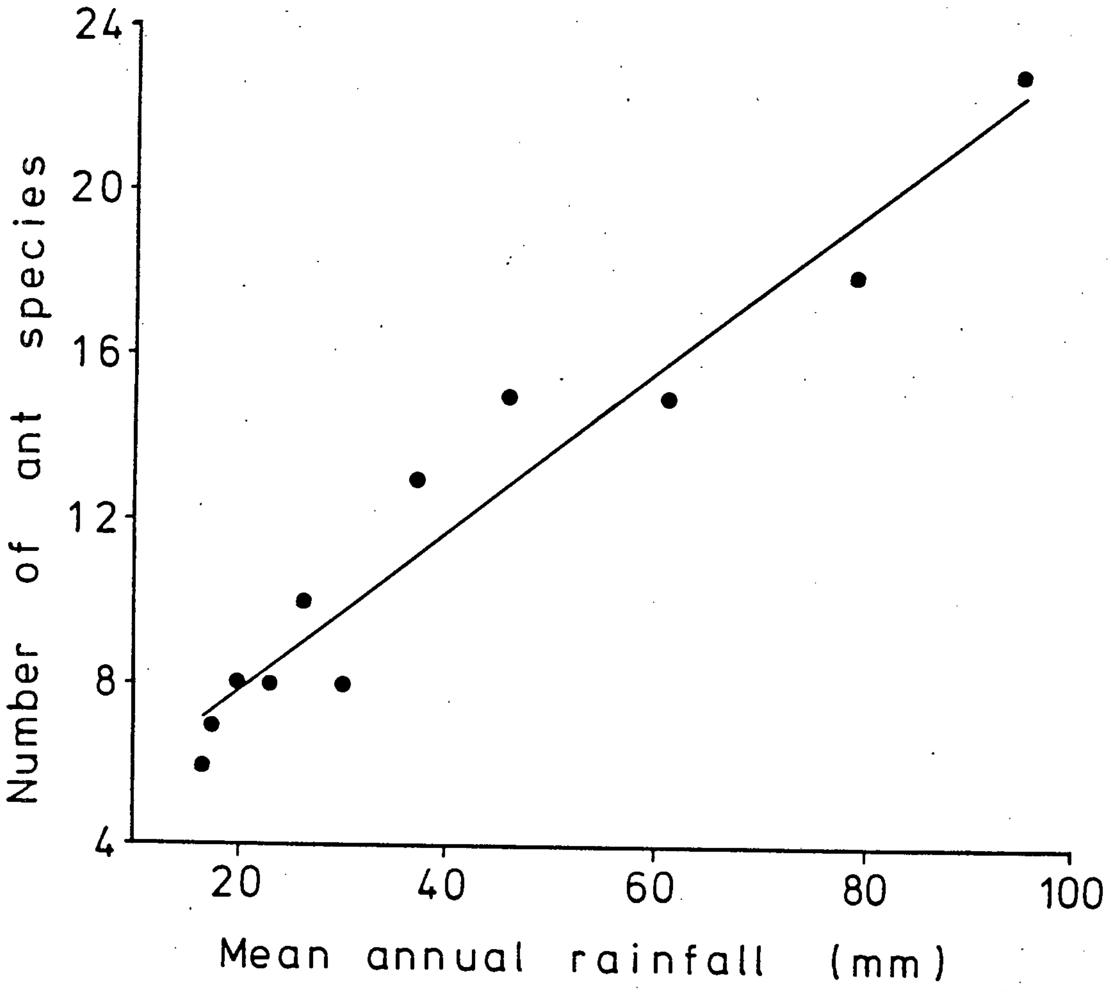

Figure 3.3. Relationship between mean annual rainfall and ant species richness. $y = 3.84 + 0.20x$, $r^2 = 0.94$.

the eastern, more productive end of the transect, and penetrated towards the coast to different extents (Table 3.2). Only one species, *Monomorium* sp. F, was restricted to the coastal fog zone. The distribution of this species coincides with that of the perennial dwarf shrub, *Arthraerua leubnitziae* (Robinson, 1978). Beyond 40 km inland the density of *A. leubnitziae* declines rapidly (Yeaton, unpubl.) and *Monomorium* sp. F does not occur in these areas. The coincidental distribution of the dwarf shrubs and the ants suggests that one or both of these organisms may be dependent on the other. Observations, however, revealed that the ants frequently nest more than 500 m from the nearest shrubs and they were never encountered on the plants. In contrast, *Acantholepis* sp., *P.tenuinodis* and *C. mystaceus* utilized the nectar produced by the flowers of *A. leubnitziae*. It thus appears more likely that *A. leubnitziae* and *Monomorium* sp. F have similar requirements which are met in the coastal region and not further inland. Fog is most probably the common factor upon which the plant and the ant are dependent.

SECTION FOUR

FORAGER ABUNDANCE AND DIETARY RELATIONSHIPS IN A NAMIB DESERT ANT COMMUNITY

4.1.1 INTRODUCTION

Ants are major components of desert ecosystems (Crawford, 1981; Pisarski, 1978) yet there are few studies which have satisfactorily determined the relative abundances of species within any given desert community. Various techniques have been used for obtaining data on relative abundances but all rest on untested assumptions or disregard potentially important biases. Measures based on colony density (Bernstein, 1979; Briese & Macauley, 1977; Whitford, 1978a), for example, invariably lack details on colony size. Counting ants visiting baits (Chew, 1977; Davidson, 1977a; Morton, 1982) assumes that the bait is equally attractive to all species and introduces other potential sources of variation related to providing an unnaturally concentrated food source such as interference interactions and different foraging modes. Pitfall trapping (Greenslade & Halliday, 1983) assumes equal capture probabilities for all species. Periodic hand collections (Greenslade & Halliday, 1983) assume that collections coincide with similar activity phases of all species despite well documented interspecific differences in diel activity patterns that occur in desert ant communities (Bernstein, 1974; Briese &

Macauley, 1980; Whitford & Ettershank, 1975; Whitford et al., 1981). Furthermore, the structure of desert ant communities cannot be accurately assessed at one point in time (Chew, 1977; Whitford, 1978a) and therefore the value of some studies (eg Davidson, 1977a; Morton, 1982) may be reduced.

With these limitations in mind, an attempt was made to quantify the relative abundances of ant species in a Namib Desert community. A study of the efficacy of pitfall trapping indicated that this technique would not provide reliable, biologically meaningful data on the structure of this community (Marsh, 1984). Similarly, quantitative colony excavations were not feasible owing to edaphic factors. Finally, a study of diel activity (see section 5.3.2) revealed substantial interspecific differences in activity patterns with some species having very short periods when surface activity occurred. To overcome these difficulties, a technique involving continuous censusing of surface active foragers for a minimum of 24 consecutive hours was devised. This section reports the results of such a study over a 17 month period. The trophic relationships of the most common species in the community are also documented. The following specific questions were posed: How robust is the structure of the forager community? How stable are the dietary relationships between species at any given moment in time and within a species through time?

4.1.2 STUDY SITE

The study site was situated on the gravel plains of the central Namib Desert near Ganab (28°08'S; 15°37'E). The study was conducted within a 16 ha plot situated centrally on an apparently uniform, flat 100 ha plain (Fig. 4.1). For most of the study there was no photosynthetically active vegetation in the habitat, the only indication of plant life being scattered clumps of grass stubble.

Two rainfall events occurred during the study period. In 1982, 97.2 mm fell in the area, the majority of it during March and April. This event resulted in a flush of plant growth and production of seed. The majority of plant species were grasses (see section 6.1.2). No effective rain fell in 1983 and 15.8 mm fell during the first half of 1984, mostly in March. This event also resulted in plant growth and seed set. Perennial and annual grasses grew and set seed in 1982, however, only perennial grasses responded in 1984. The amount of vegetation was visibly less in 1984 and the numerical density of seeds of some of the dominant grass species was substantially lower (see section 6.3.3).

4.2 PROCEDURE

The presence of ant species in a 16 ha plot was determined using a variety of techniques. Ants were sampled at bait

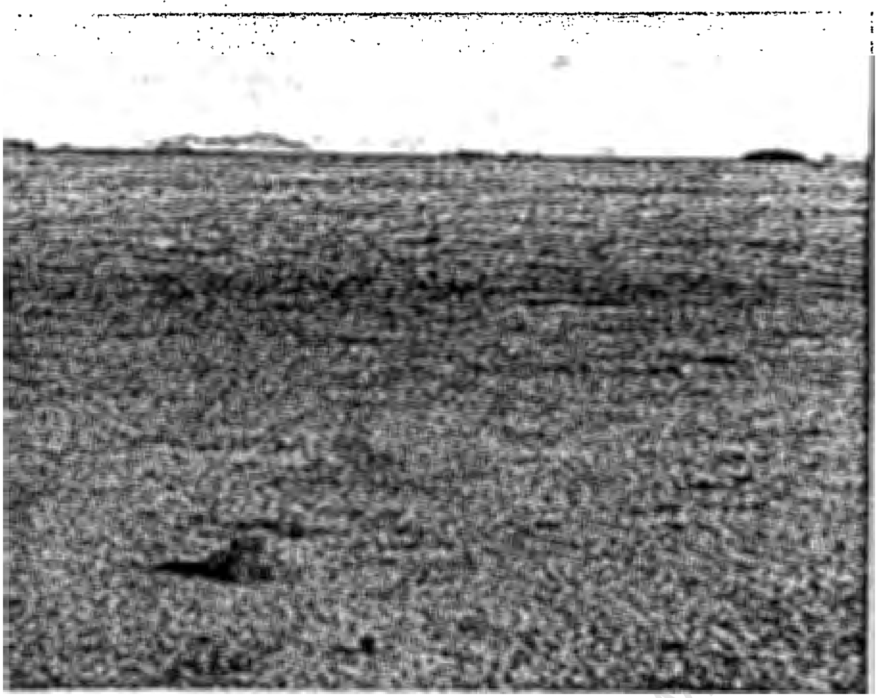

Figure 4.1. The study site in January 1984 showing small clusters of grass stubble.

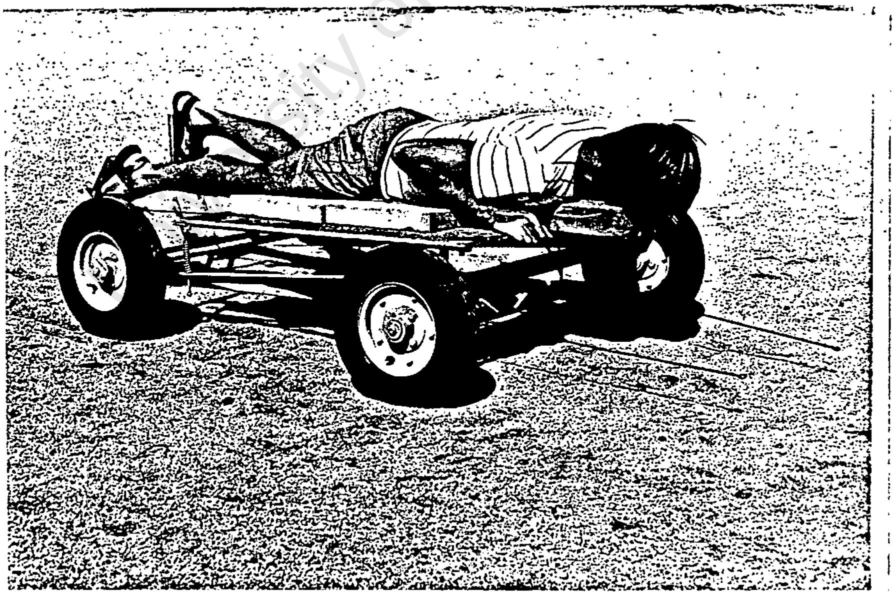

Figure 4.2. Vehicle used for censusing foraging ants. Note the two antennae demarcating a 50 cm wide transect.

points using cheese, seed and sugar-water as baits, in pitfall traps using ethylene glycol as a preservative and during visual censuses.

Monthly estimates of ant abundance were obtained during visual censuses of surface active foragers. Each census was conducted for 24 or 48 consecutive hours. Observers lay face-down on a pedal-powered vehicle (Fig. 4.2) and collected all ants that were encountered between two antennae attached 50 cm apart to the front of the vehicle. Transects were randomly orientated within the plot and the length of each 24 h transect was measured on an odometer. The initial departure point and direction were selected using a set of randomly generated grid references and azimuth directions. Observers maintained a straight course until they arrived at the plot boundary at which point the transect orientation was changed to another randomly generated azimuth direction that led back into the plot. A fluorescent lamp was used for nocturnal observations. Censuses were conducted for 17 consecutive months between January 1983 and May 1984 inclusive. For each month the census data were expressed as the number of ants ha^{-1} that were encountered in a 24 h period. The biomass of foraging ants ha^{-1} 24 h^{-1} was determined for each species by multiplying the numerical density data by the mean dry mass of foragers of each species. For polymorphic species, 100 foragers were collected at random, dried at 60°C for 24 h and weighed. For monomorphic species 20 individuals were dried and weighed. The relative importance of each species was expressed in terms of numerical abundance and biomass. Kendall's coefficient of concordance (Siegel, 1956) was used to test the degree of association between the 17 sets of species importance data.

Nest density was estimated by locating and marking all nests of all species occurring within five 1600 m^2 plots distributed randomly within the general study area (an apparently uniform region of ~100 ha). Ants were lured to a grid of baits, each bait point spaced 5 m apart, and successful foragers were followed to their nests. Owing to the high density of Monomorium sp. C nests, and the difficulty in locating them, a 100 m^2 subsample of each 1600 m^2 plot was searched intensively using bait points spaced at 2 m intervals.

Food items were collected from foragers returning to their nests in January and August 1982 and May 1984. The three sample periods were selected because ants were moderately active and assistance was available during these periods, thus ensuring that forage samples could be collected for all species within a one week period. Forage was taken from the eight most common species only. Other species could not be sampled intensively because, although foragers were occasionally found, no nests were located and forage sample sizes were inadequate for comparative analyses. A minimum of four nests per species per collecting period was sampled. The food items were placed into one of four categories; grass seed, dicotyledon seed, non-seed plant material and arthropod.

Niche breadths were calculated using the inverse of Simpson's (1949) diversity measure: $B = 1/\sum p_i^2$ where p_i is the proportion of the i^{th}food category in the sample. For these calculations three food categories were used; seed, non-seed plant matter and arthropod. Calculated this way, niche breadth can range from one to three. Niche overlap between any two samples was calculated using Pianka's (1973) measure of similarity: $O = \dfrac{\sum p_i \; q_i}{\sqrt{\sum p_i^2 \sum q_i^2}}$ where p_i is the proportion of the i^{th} food item in one sample and q_i is the proportion of the i^{th} food category in the second sample. Values of niche overlap range from zero to one. Kendall's coefficient of concordance (w) was calculated to test for the degree of association in rank order of species pair overlap values between the three samples.

The volume of each item of forage was estimated using the technique of Chew & De Vita (1980): the shape of the object was determined, most objects conforming to one, or a combination of two, of the following shapes: cylinder, truncated cone, sphere, triangular solid, rectangular solid. Critical dimensions of each object were then measured to 0.1 mm under a stereoscopic microscope and the volume calculated using standard geometric formulae. A Mann-Whitney U-test was used to detect interspecific differences in food particle size. Dry body mass was regressed against food particle volume to determine whether there was any correlation between body size and food particle size. Species were ranked according to mean size of food particle for each of the three sample periods and Kendall's coefficient of concordance (w) was calculated to test for the degree of association in species rank order.

4.3 RESULTS

Thirteen ant species, the majority Myrmicines, were collected in the study area (Table 4.1). There was considerable interspecific variation in body size. *Messor denticornis* and the two *Camponotus* species exhibited continuous size polymorphism, *Pheidole tenuinodis* was dimorphic with minor (TL 2.5-2.6 mm) and major workers (TL 4.5-4.9 mm) and the remaining species were monomorphic. *Monomorium* sp. D was found on one occasion only, was restricted to a relatively large clump of grass stubble and was apparently not epigaeic. This species was not found during the regular monthly censuses. All the other species were epigaeic and were readily located during censuses. Eleven of these species were discovered before the census study began using a combination of bait and pitfall traps, however *Tetramorium peringueyi* was discovered only during the census. The accumulative species curve (Fig. 4.3) reached a plateau after eight 24 h censuses and remained constant for the remainder of the study period suggesting that all species occurring in the study plot were sampled.

Table 4.1. Sizes of ants occurring on the study plot.

SPECIES	TOTAL LENGTH (mm)	DRY MASS (mg)	
	RANGE	X̄	± SD
MYRMICINAE			
Messor denticornis	5.5 - 11.0	2.96	2.30
Pheidole tenuinodis	2.5 - 4.9	0.11	0.03
Ocymyrmex barbiger	6.7 - 7.2	1.44	0.16
Tetramorium sericeiventre	3.3 - 4.4	0.32	0.08
Tetramorium rufescens	4.0 - 5.1	0.72	0.11
Tetramorium grandinode	5.0 - 5.3	0.80	0.10
Tetramorium peringueyi	4.4 - 5.7	0.90	0.12
Monomorium viator	3.5 - 3.9	0.22	0.10
Monomorium sp. B	2.7 - 3.1	0.11	0.05
Monomorium sp. C	2.2 - 2.6	0.04	0.02
Monomorium sp. D	1.3 - 1.5	no data	
FORMICINAE			
Camponotus maculatus	7.7 - 12.0	2.80	1.60
Camponotus mystaceus	7.0 - 15.0	2.00	1.00

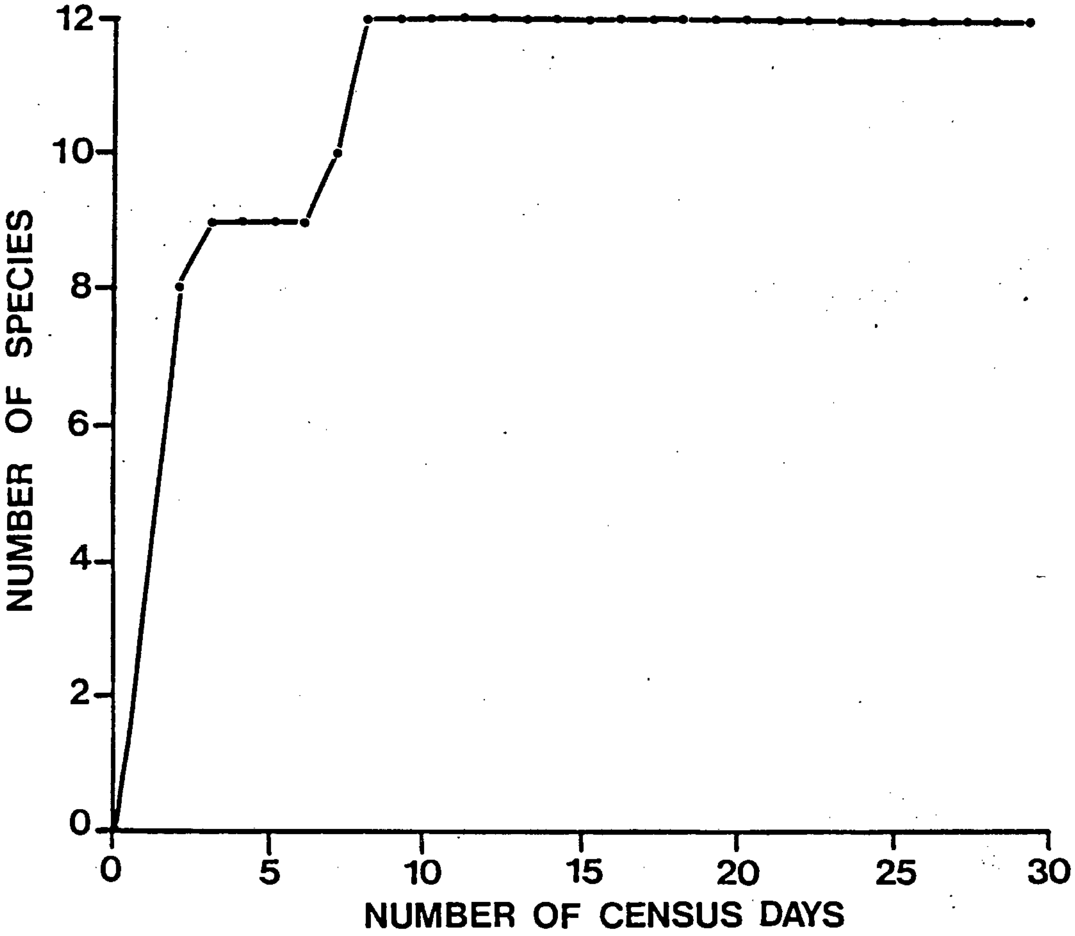

Figure 4.3. The relationship between cumulative species and cumulative census periods.

The numerical density of foragers of all species fluctuated markedly during the study period (Fig. 4.4). Forager density peaked in April in 1983 and 1984 and was very low between July 1983 and February 1984. The 1984 peak in forager density was considerably lower than that of 1983 and only spanned two months, March and April. In contrast, forager density remained high for at least five months in 1983, January to May, and a trial-run census in December 1982 also revealed high densities of foragers. All species exhibited high coefficients of variation in numerical density through time (Table 4.2) indicating that no particular species, or subset of species, was responsible for the community-wide changes in ant forager abundance. The majority of foragers were nocturnal in summer (December to April/May) and diurnal in winter (Fig. 4.5).

The rank order of species depended on whether species importance was based on numerical density or biomass per unit area (Table 4.3). For both criteria the top three species were M. denticornis, T. rufescens and M. viator, although the order within this group depended on the criterion used. These three species comprised 81.0 % of the total forager community in terms of numerical density and 94.7 % in terms of biomass. Rank order of species within the community varied from month to month but overall patterns were fairly stable. Kendall's coefficient of concordance was highly significant using

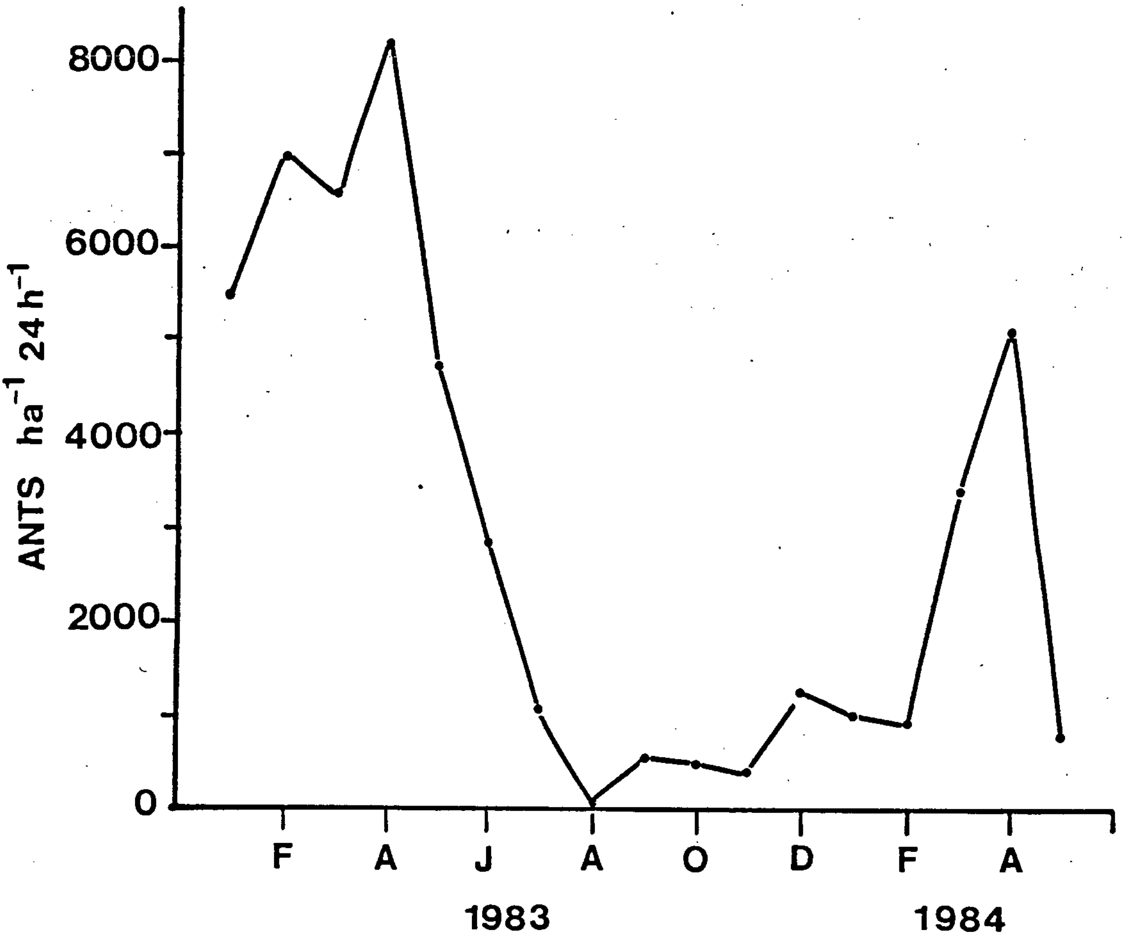

Figure 4.4. Numerical density of foraging ants (# ha^{-1} 24 h^{-1}) during 1983 and early 1984.

Table 4.2. Coefficients of variation in ant density during the study period.

SPECIES	CV (%)
Messor denticornis	117.8
Pheidole tenuinodis	113.7
Ocymyrmex barbiger	119.5
Tetramorium sericeiventre	120.7
Tetramorium rufescens	103.4
Tetramorium grandinode	238.2
Tetramorium peringueyi	86.5
Monomorium viator	112.2
Monomorium sp. B	95.4
Monomorium sp. C	96.3
Camponotus maculatus	208.0
Camponotus mystaceus	111.3

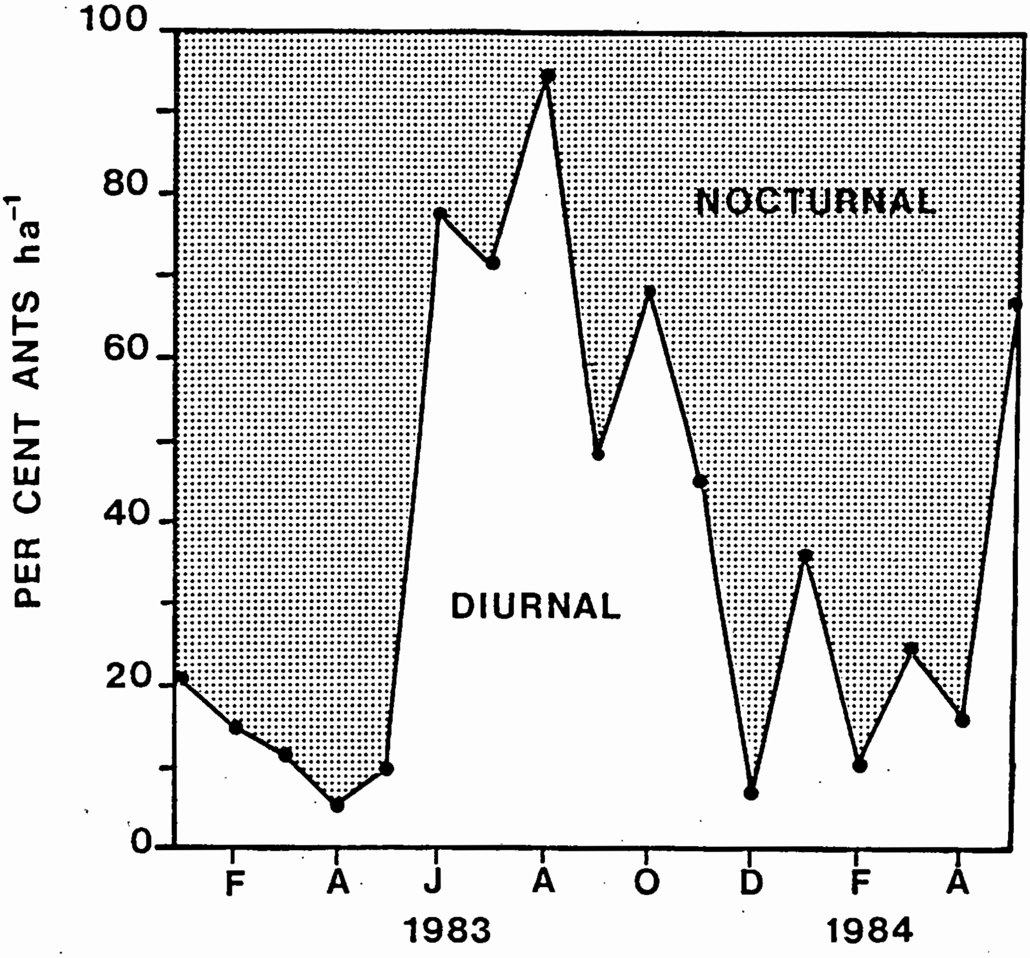

Figure 4.5. The proportion of foraging ants (% of numerical density 24 h^{-1}) that were diurnally and nocturnally active over a 17 month period.

Table 4.3. Rank sequence of ant species based on numerical density and biomass. Data are expressed as numbers and mass (mg) of ants per hectare per day as well as per cent of the total numbers or biomass of the community. The data are from 17 pooled monthly censuses. Where species had identical densities or biomass their rank position was decided using the data extended to three decimal places.

RANK	NUMERICAL DENSITY			BIOMASS		
	SPECIES	# ha^{-1}	%	SPECIES	mg ha^{-1}	%
1	*T. rufescens*	1096	41.52	*M. denticornis*	1438	57.95
2	*M. viator*	555	21.03	*T. rufescens*	789	31.80
3	*M. denticornis*	486	18.41	*M. viator*	122	4.92
4	*P. tenuinodis*	265	10.04	*C. maculatus*	46	1.85
5	*Monomorium* sp. C	88	3.33	*P. tenuinodis*	33	1.33
6	*T. sericeiventre*	71	2.69	*T. sericeiventre*	23	0.93
7	*Monomorium* sp. B	41	1.55	*T. grandinode*	13	0.52
8	*C. maculatus*	16	0.61	*Monomorium* sp. B	5	0.20
9	*T. grandinode*	16	0.61	*O. barbiger*	4	0.16
10	*O. barbiger*	3	0.11	*C. mystaceus*	4	0.16
11	*C. mystaceus*	2	0.08	*Monomorium* sp. C	4	0.16
12	*T. peringueyi*	0.5	0.01	*T. peringueyi*	0.5	0.02

numerical density data ($w = 0.79$, $p < 0.001$) and biomass data ($w = 0.64$, $p < 0.001$), indicating that the relative ranking of species within the community was stable through time.

Nest densities of seven of the common ant species varied considerably from 4.4 ha^{-1} (M. denticornis) to 525 ha^{-1} (Monomorium sp. C) (Table 4.4). For most species there was considerable variation in nest density between 1600 m^2 plots as indicated by the large standard deviations obtained. A significant negative correlation between Ln mean body mass and Ln mean nest density ($Y = 1.08 - 0.97X$, $r = 0.95$, $p < 0.01$) was also apparent, suggesting that smaller species tended to have higher nest densities.

The diets of eight common ant species on three widely-spaced occasions varied within and between species (Fig. 4.6). Tetramorium sericeiventre was the only species that had a reasonably consistent diet over all samples. Intraspecific variability in diet made it difficult to assign species to a definite trophic group. In a broad sense all the species were omnivorous. Messor denticornis, T. rufescens, Monomorium sp. C, M. viator and P. tenuinodis occasionally harvested and stored large quantities of seed and are probably best regarded as granivores. Ocymyrmex barbiger predominantly took arthropod carrion during the one sample period when the ants were sufficiently active to collect their forage. As this species consistently took arthropod carrion in a more detailed

Table 4.4. Nest densities of seven common ant species. (N) refers to the number of plots sampled *.

SPECIES	NESTS ha^{-1}		N
	$\bar{X}$	SD	
Monomorium sp. C	525.0	340.0	5
_P._ _tenuinodis_	101.5	82.2	5
Monomorium sp. B	46.9	12.0	5
_T._ _sericeiventre_	43.8	22.8	5
_M._ _viator_	35.9	7.9	5
_T._ _rufescens_ **	22.5	9.4	5
_M._ _denticornis_ **	4.4	0.9	10

* 100 m^2 plots for _Monomorium_ sp. C., 2000 m^2 walking transects for _M._ _denticornis_ and 1600 m^2 plots for the other species.

** data from section 6.3.2.

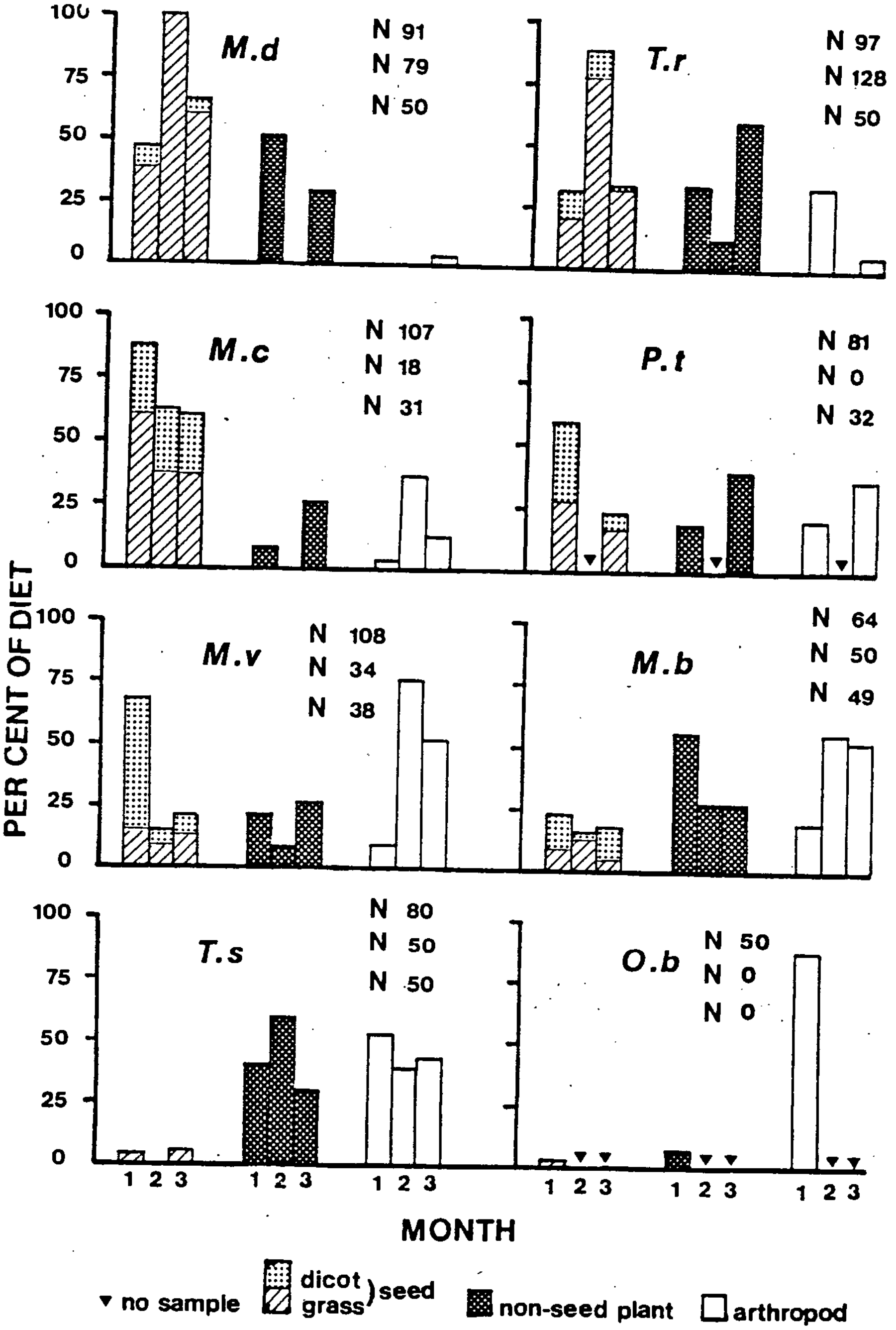

Figure 4.6. Proportion of three food categories in the diets of eight common ant species. January 1982 = 1, August 1982 = 2, May 1984 = 3. Sample sizes refer to January = N1, August = N2 and May = N3. M.d = Messor denticornis, T.r = Tetramorium rufescens, M.c = Monomorium sp. C, P.t = Pheidole tenuinodis, M.v = Monomorium viator, M.b = Monomorium sp. B, T.s = Tetramorium sericeiventre, O.b = Ocymyrmex barbiger.

study in the Kuiseb River bed (see section 8.3) it can, with reasonable confidence, be regarded as an arthropod scavenger. The remaining two species, *Monomorium* sp. B and *T. sericeiventre*, regularly took a diversity of food items, never large quantities of seed, and are best assigned to an omnivore category. The proportion of grass seed relative to dicotyledon seed also varied between samples in most species. Incidental observations on the remaining four species, at the study area and elsewhere in the central Namib Desert, revealed that the two *Camponotus* species were predominantly honeydew feeders and the two *Tetramorium* species were predominantly granivorous.

Bearing in mind that dietary niche breadth can range from one to three, intraspecific variability in diet diversity was considerable (Table 4.5). Of the six species for which three samples were collected, only *Monomorium* sp. B and *T. sericeiventre* had relatively constant niche breadths through time as indicated by the low coefficients of variation obtained. The lowest niche breadth was that of *M. denticornis* in the August sample when this species took seeds exclusively, primarily grass seed. The highest niche breadth was that of *T. rufescens* in the January sample when this species took approximately equal proportions of the three food categories (Fig. 4.6).

Intraspecific variability in diet is reflected in between sample dietary niche overlap values (Table 4.6). The only

Table 4.5. Dietary niche breadths and coefficients of variation (CV) in niche breadth of eight common ant species.

SPECIES	JAN 1982	AUG 1982	MAY 1984	CV (%)
	MONTH			
M. denticornis	1.99	1.00	1.90	33.7
T. rufescens	3.00	1.28	2.09	40.6
T. sericeiventre	2.16	1.92	2.24	8.1
P. tenuinodis	2.30	-	2.86	15.5
M. viator	1.94	1.63	2.56	23.0
Monomorium sp. B	2.43	2.39	2.51	2.5
Monomorium sp. C	1.28	1.88	2.23	26.7
O. barbiger	1.28	-	-	-

Table 4.6. Between sample similarity of diet for seven common ant species. See text for explanation of similarity index.

SPECIES	SAMPLE COMPARISONS		
	Jan x Aug	Jan x May	Aug x May
M. denticornis	0.59	0.89	0.89
T. rufescens	0.49	0.79	0.60
M. viator	0.31	0.48	0.94
T. sericeiventre	0.94	0.98	0.99
Monomorium sp. B	0.72	0.75	0.97
Monomorium sp. C	0.79	0.89	0.80
P. tenuinodis	-	0.77	-

species that exhibited high similarity in diet through time was *T. sericeiventre*, thus confirming the impression obtained from inspection of Fig. 4.6. Dissimilarities in diet were quite marked, the extreme being *M. viator* in which the diets in January and August showed an overlap of 0.31 only. Over all species and samples, dietary niche overlap averaged 0.62 (N = 64, SD = 0.26). However, as a consequence of intraspecific variability in diet, interspecific similarities varied considerably through time for all species pairs (Table 4.7). The greatest change in dietary similarity was that between the two *Tetramorium* species which had high similarity in January (O = 0.92) and high dissimilarity in August (O = 0.13). Interspecific overlap values ranged from complete dissimilarity (*M. denticornis* x *T. sericeiventre* in August) to almost complete similarity (*M. viator* x *Monomorium* sp. B in May). There was no concordance between overlap values over the three sample periods ($w = 0.49$, $p > 0.1$) indicating that shifts in dietary overlap were random with no tendency for changes to be directional between any two sample periods.

There was considerable intra- and interspecific variation in the size of food particles taken (Table 4.8). Using data from all samples most species took statistically distinct food particle sizes ($p < 0.05$, Mann-Whitney U-test) although the large standard deviations reveal considerable overlap between species. The only species pairs that were not statistically different in food particle size utilization were *M. denticornis*

Table 4.7. Interspecific dietary niche overlap values for three widely spaced occasions.

SPECIES PAIR	MONTH		
	JAN	AUG	MAY
M. denticornis x *T. rufescens*	0.76	0.98	0.82
M. denticornis x *T. sericeiventre*	0.53	0	0.45
M. denticornis x *P. tenuinodis*	0.71	-	0.62
M. denticornis x *M. viator*	0.56	0.12	0.45
M. denticornis x *Monomorium* sp. B	0.84	0.22	0.34
M. denticornis x *Monomorium* sp. C	0.68	0.65	0.90
M. denticornis x *O. barbiger*	0.10	-	-
T. rufescens x *T. sericeiventre*	0.92	0.13	0.76
T. rufescens x *P. tenuinodis*	0.85	-	0.81
T. rufescens x *M. viator*	0.64	0.14	0.56
T. rufescens x *Monomorium* sp. B	0.89	0.29	0.51
T. rufescens x *Monomorium* sp. C	0.54	0.69	0.81
T. rufescens x *O. barbiger*	0.71	-	-
T. sericeiventre x *P. tenuinodis*	0.60	-	0.97
T. sericeiventre x *M. viator*	0.38	0.64	0.91
T. sericeiventre x *Monomorium* sp. B	0.82	0.85	0.91
T. sericeiventre x *Monomorium* sp. C	0.19	0.36	0.61
T. sericeiventre x *O. barbiger*	0.84	-	-
P. tenuinodis x *M. viator*	0.90	-	0.94
P. tenuinodis x *Monomorium* sp. B	0.71	-	0.92
P. tenuinodis x *Monomorium* sp C	0.82	-	0.77
P. tenuinodis x *O. barbiger*	0.47	-	-
M. viator x *Monomorium* sp B	0.63	0.94	0.98
M. viator x *Monomorium* sp. C	0.65	0.74	0.65
M. viator x *O. barbiger*	0.21	-	-
Monomorium sp B x *Monomorium* sp C	0.36	0.71	0.60
Monomorium sp B x *O. barbiger*	0.41	-	-
Monomorium sp. C x *O. barbiger*	0.11	-	-

Table 4.8. Estimated volumes (mm^3) of individual food particles collected by the eight most common ant species.

SPECIES	SAMPLE	MEAN	SD	MIN	MAX	N
M. denticornis	Jan	12.13	24.04	0.05	135.59	91
	Aug	0.28	0.04	0.17	0.44	97
	May	2.98	7.77	0.08	35.49	49
	All	8.93	20.35	0.05	135.59	237
T. rufescens	Jan	1.30	2.11	0.01	14.48	96
	Aug	0.46	0.76	0.03	4.99	128
	May	1.25	3.36	0.02	16.78	50
	All	1.28	2.59	0.01	16.78	274
T. sericeiventre	Jan	1.16	1.98	0.01	9.65	80
	Aug	2.98	4.37	0.06	21.74	50
	May	1.19	1.70	0.08	7.53	50
	All	1.68	2.90	0.01	21.74	180
P. tenuinodis	Jan	0.77	1.05	0.01	7.04	81
	May	0.59	0.88	0.01	3.62	32
	All	0.72	1.01	0.01	7.04	113
M. viator	Jan	0.48	0.53	0.002	3.77	108
	Aug	0.24	0.26	0.01	1.08	34
	May	0.26	0.27	0.01	3.40	38
	All	0.39	0.51	0.002	3.77	180
Monomorium sp. B	Jan	0.86	2.54	0.004	15.91	64
	Aug	0.30	0.64	0.003	3.06	48
	May	0.28	0.57	0.01	2.82	49
	All	0.52	1.69	0.003	15.91	161
Monomorium sp. C	Jan	0.39	0.31	0.002	1.32	107
	Aug	0.15	0.12	0.03	0.63	18
	May	0.32	0.49	0.01	2.27	31
	All	0.36	0.36	0.002	2.27	156
O. barbiger	Jan	4.77	5.67	0.06	28.96	50

x *O. barbiger* ($p > 0.10$), *T. rufescens* x *P. tenuinodis* ($p > 0.10$) and *M. viator* x *Monomorium* sp. C ($p > 0.10$). Despite this, however, no consistent relationship between body length and mean food particle size was apparent. Considering all samples there was a positive relationship between body size and food particle size ($Y = -4.14 + 1.43X$, $r = 0.95$, $p < 0.01$). In the January and May samples similar relationships existed (January: $Y = -6.11 + 2.01X$, $r = 0.95$, $p < 0.01$; May: $Y = -1.06 + 0.49X$, $r = 0.96$, $p < 0.01$), whereas in August there was no relationship ($Y = 0.90 - 0.04X$, $r = 0.10$, $p > 0.05$). This indicates temporal variation in the ant size/food particle size relationship. Furthermore, there was no concordance through time between the relationship of species sequence to food particle size ($w = 0.61$, $p > 0.05$). This indicates that species do not occupy the same relative position to one another in terms of the food particles utilized. For example, *Monomorium* sp. C did not consistently take smaller items than its two congeners. It did in two samples but it took larger items in one sampling period.

4.4 DISCUSSION

From the results it is clear that a single survey of the community would not have provided a true picture of its structure. First, on the average only 70 % of the species known to occur in the community were sampled in any one census. No single census sampled all species and only 2 of 17 censuses included 11 of the 12 species. Secondly, although community structure was reasonably robust through time, rank order was not the same at each census, not even for the three most abundant species. Thus in order to describe the structure of this community reasonably well several censuses were necessary. This conclusion supports those of Chew (1977) and Whitford (1978a) on North American desert ant communities and that of Wiens (1981) for terrestrial vertebrates in general and North American bird communities in particular.

Food availability has a marked effect on the activity levels of foraging ants in arid environments (Bernstein, 1974; Briese & Macauley, 1980; Whitford & Ettershank, 1975; Whitford *et al*., 1980; Whitford *et al*., 1981). In the present study, fluctuations in forager abundance were primarily attributable to variations in food availability. Two pulses of primary production, separated by a long period of food scarcity, occurred during the present study. The availability of forage for *M. denticornis* and *T. rufescens* peaked in November 1982 and a smaller pulse occurred in April 1984 (see section 6.3.3). It seems reasonable to deduce that similar patterns of food availability occurred for all ant species in the community, particularly for those species that utilized seeds. Thus the second, and smaller, peak in forager abundance coincided with the 1984 pulse of food, whereas the first peak in forager abundance occurred five months after the major pulse of food. The continued increase in forager abundance despite a progressive decrease in food availability during early 1983 has been interpreted as evidence that food was superabundant during this period (see section 6.4). The decoupling of forager abundance and food abundance could be due to climatic factors and/or the lag time from food collection to production of workers.

Seasonal shifts in diel activity patterns have been noted for numerous desert ant species (Gamboa, 1976; Whitford, 1978a; Whitford & Ettershank, 1975; Whitford *et al.*, 1976) and these are normally thought to be in response to shifts in climatic conditions, especially temperature. In the present study, the shift from predominantly nocturnal to predominantly diurnal activity during the winter period reflects in part diel activity shifts by certain species such as *T. rufescens* and *P. tenuinodis* that have been documented elsewhere (see section 5.3.2). These shifts are related to changes in the thermal environment. Overall activity levels were also depressed during winter because of food scarcity and in certain censuses some of the usually dominant harvester species, including the nocturnal *M. denticornis* and *M. viator*, were almost completely inactive whereas the diurnal non-harvester species remained active. In August 1983, for example, *T. sericeiventre* was the dominant species numerically and in biomass while *M. denticornis* and *M. viator* did not occur in the transect.

Granivorous ants are typically the dominant (Briese, 1982;

Chew, 1977) or codominant (Whitford, 1978a) trophic group in desert ant communities. In the present study, harvester ants were dominant in terms of species richness and in terms of forager numerical density and biomass. Seven of 12 species were harvester ants, 94.7 % of all foragers encountered were harvesters making up 96.7 % of the total forager biomass. The overwhelming dominance of harvester ants is to be expected because they are predominantly primary consumers that rely on a relatively dependable and nutritious food resource which can be stored for extensive periods (Brown et al., 1979; Carroll & Janzen, 1973). The relative scarcity of other trophic groups is attributable to the absence of perennially green vegetation and to the fact that they are predominantly secondary consumers.

The large fluctuations in dietary niche breadth and overlap that were exhibited by most of the ants in the present study are indicative of opportunism. Only the omnivorous species, which had broad generalized diets, did not show this dietary variation. Flexible feeding habits have been reported for many desert ant species (Briese & Macauley, 1981; Whitford, 1978b). Trophic flexibility facilitates coping with the vagaries of a variable environment where the food supply is unpredictable in time and space. Furthermore, although food resources are partitioned according to size in certain North American desert ant communities, with large species taking large food items and vice versa (Chew & De Vita, 1980;

Davidson, 1977a), this relationship is not clear in the Namib Desert community nor in a desert ant community in Australia (Morton, 1982). These results support the conclusion of Briese & Macauley (1981) that interspecific competition for food is unlikely to be of major importance to ants inhabiting unpredictable arid environments.

The present study clearly indicates the inadequacy of using relative nest densities as a measure of species importance. The species with the highest nest density was one of the least common species and the species with the lowest recorded nest density was one of the most dominant. The continuous census technique, however, proved to be a reliable way of obtaining data on relative and absolute abundance of epigaeic ants. It has several limitations, however. Firstly it is only suited to relatively flat habitats with sparse, low vegetation, otherwise vision would be obscured and movement impeded. Secondly it is labour intensive requiring a minimum of four people to do a 24 h census. Thirdly it provides data on foragers only. Depending on the focus of interest this third feature is not necessarily a negative one. If the relative importance of the ant species in terms of consumption, i.e. in terms of their impact on the resource base of an ecosystem, is of principal concern, then the data collected may be superior to data on the entire ant fauna which would also include non-foraging, subterranean individuals.

SECTION FIVE

ACTIVITY PATTERNS WITHIN A NAMIB DESERT ANT COMMUNITY

5.1 INTRODUCTION

Numerous studies have shown that the activity of ants is partially determined by temperature and/or humidity (Bernstein, 1974; Briese & Macauley, 1980; De Bruyn & De Bruyn, 1972; Gamboa, 1976; Greenaway, 1981; Sanders, 1972; Sheata & Kaschef, 1971; Whitford & Ettershank, 1975; Whitford et al., 1981). Soil surface temperature and humidity of desert environments are subject to large diel and seasonal fluctuations (Oke, 1978) and epigaeic desert ants are therefore liable to encounter a wide range of thermal conditions in a 24 h period.

Preliminary observations indicated that within a community of Namib Desert ants there were interspecific differences in activity patterns over a diel cycle. If thermal conditions are an important determinant of activity patterns it seemed reasonable to expect some correspondence between interspecific differences in physiological thermal tolerances and activity periods. Likewise seasonal changes in the thermal environment should cause shifts in activity patterns. Seasonal shifts in ant activity patterns have been documented in North American deserts (Gamboa, 1976; Whitford & Ettershank, 1975; Whitford et al., 1981) and in a semi-arid region of Australia

(Briese & Macauley, 1980) while a reasonable correspondence between Critical Thermal Maxima and Minima and activity has been shown for some Chihuahuan Desert ant species (Whitford & Ettershank, 1975; Kay & Whitford, 1978). Other factors may prevent an ant species from using the entire activity period for which it is physiologically adapted. For example, Whitford *et al*. (1981) suggest that, in the Chihuahuan Desert , certain *Pheidole* species do not exploit the entire temporal niche potentially available to them, in order to reduce competitive interactions with *Pogonomyrmex* species. Similarly a shift in summer from diurnal to nocturnal activity in *Pognomyrmex rugosus* has been interpreted as a response to predation by diurnal lizards or competition with the ant *Veromessor pergandei* (Mehlop & Scott, 1983).

The present study focuses upon patterns of activity within a Namib Desert gravel plain ant community in relation to season, rainfall and temperature tolerance. Ecological studies of ants in southern African deserts lag far behind those for most other deserts and this is the first study of this nature on a Namib Desert ant community.

5.2 PROCEDURE

The field work for this study was conducted on the gravel plains near Ganab (28°08'S; 15°37'E) on the eastern edge of the Namib Desert. The habitat is a uniform flat plain that supports a grassland community if sufficient rain has fallen (~20mm) but was devoid of photosynthetically active vegetation during the investigation. The only visible vegetation comprised widely scattered, 2-10 cm high grass stubble. Thirteen ant species occur sympatrically in this region but only eight, all myrmicines, were sufficiently abundant to provide adequate data for analyses. All of the species studied live in subterranean nests and are epigaeic foragers.

5.2.1 Activity patterns

Activity patterns were studied in May (winter) and late November-early December (summer) 1982. Three nests of each species were studied. Each nest was observed at regular intervals over a period of 24 h. Twelve nests were observed simultaneously each day and the entire study of 24 nests took two consecutive days each season. In summer each nest was observed continuously for 10 min every hour from 05h00 to 21h00 solar time and thereafter 10 min observations were made at two hourly intervals until 05h00. In winter 10 min observations were made every hour from 07h00 to 21h00 and every two hours thereafter until 07h00. Ocymyrmex barbiger nests were observed for 15 min at each observation period because of low levels of activity. All ants emerging from and returning to the nest entrance were counted. The nests of Messor denticornis and Tetramorium rufescens have multiple entrances and a nest entrance with a high level of activity was selected and observed throughout the 24h period.

Immediately after every 10-15 min observation period the following climatic measurements were recorded: wind speed using a mechanical totalizing anemometer; wet and dry bulb temperatures using a sling psychrometer; soil surface temperature and air temperatures at 1 mm, 3 mm and 5 mm elevation above the soil surface. All temperatures were measured using copper-constantan thermocouples and displayed on a digital recorder (Bailey Instruments, Model BAT-12). Air temperatures were unshaded, black body temperatures and were measured using thermocouples built up with epoxy resin to approximate ant size and painted matt-black. Black body temperatures were used to obtain an approximation of the body temperatures that surface-active ants were likely to experience. The degree of cloud cover was visually estimated.

One day after the summer observations ended 1.3 mm of rain fell on the study site and activity counts were repeated for two nests per species one day after the rainfall event.

5.2.2 Thermal limits

Ants were collected in the field and transported to the laboratory where their Critical Thermal Maxima and Minima were determined within 12 h of capture. Ants were placed individually in 250 ml Erlenmeyer flasks, containing a 2 mm layer of desert sand, and the ambient temperature in the flask at ant height was raised or lowered 1 °C min^{-1}. Temperatures were measured using copper-constantan thermocouples and a digital thermometer. Temperatures were raised by surrounding the flask with water above a heating element. Temperatures were lowered by suspending the flask above a freezer unit. The critical thermal limits were considered to have been reached when the ants were incapable of locomotion. Each individual was used once only, either for a Critical Thermal Maximum or a Critical Thermal Minimum determination.

5.2.3 Behavioural interactions

Incidental observations revealed that the various species reacted aggressively towards each other during field encounters and this suggested that there may be an advantage in having different activity periods so as to minimize interspecific encounters. To obtain an indication of the probability of aggressive or avoidance responses occurring during encounters the two most abundant species, M. denticornis and T. rufescens, were studied in the laboratory. For each test an individual of each species was placed into an 18 cm diameter arena, maintained at room temperature (22 - 25 °C) and the response of each ant noted when they initially encountered one another. A total of 104 encounters, involving 208 individuals, were observed.

5.3 RESULTS

5.3.1 Micro-climate

A summary of the micro-climatic conditions that prevailed on the five days during which ant activity was monitored is presented in Table 5.1. Minimum and maximum surface temperatures were lower in winter than in summer except on the day after rainfall when cloud cover prevented direct insolation and therefore reduced surface heating substantially. The higher minimum surface temperature on 30 November, relative to 29 November, is attributable to the 4 h of cloud cover which occurred at night retarding reradiation. Thermal conditions and vapour pressure deficits were similar for the two days in winter. Similarly, summer daytime thermal and humidity conditions varied little over the period of observation. The principal differences between summer and winter concerned day length and wind. There were 3 h more daylight in summer than in winter and there was substantially more wind during the summer period (Table 5.1). The principal differences between the pre-rain summer and post-rain summer periods were a reduction in maximum surface temperature and maximum vapour pressure deficits after rain, both attributable to an increase in cloud cover and evaporative cooling of the damp surface.

5.3.2 Activity patterns

Table 5.1. Summary of climatic conditions on activity monitoring days. T_s = surface temperature (°C), VPD = vapour pressure deficit (kPa). The number of hours that mean wind speed exceeded 6 m s is given in parenthesis after the one hour maximum wind speed. Sun = hours of sunshine, d = direct sunshine, id = indirect sunshine, the number of hours with cloud are given in parenthesis.

Date (1982)	T_s Min	T_s Max	VPD Min	VPD Max	Wind Mean ($km\ h^{-1}$)	Wind Max ($m\ s^{-1}$)	>6 ms (h)	Sun (h)	Cloud cover (%)
18 May	7.1	40.6	1.2	3.9	3.6	2.7	(0)	10.5 d	0
19 May	6.4	44.2	1.0	4.1	4.3	3.6	(0)	10.5 d	50 (5h)
29 Nov	14.6	52.6	0.6	3.5	9.8	7.2	(2)	13.5 d	0
30 Nov	19.8	53.9	1.0	3.4	11.3	8.8	(3)	13.5 d	90 (4h)
2 Dec	18.8	37.0	0.6	2.2	13.4	6.7	(2)	13.5 id	100 (24h

The activity patterns of the eight ant species, together with pertinent micro-climatic conditions during winter and pre-rain summer are shown in Fig. 5.1. Except for *O. barbiger*, winter and summer patterns were different within each species, with a marked trend towards increased diurnalism in winter. *Messor denticornis*, *Monomorium viator* and *O. barbiger* exhibited unimodal activity patterns in both seasons with the former two species being primarily nocturnal and the latter strictly diurnal with activity confined to the hottest period of the day. *Tetramorium sericeiventre* exhibited bimodal activity in summer and unimodal activity in winter. The other four species exhibited bimodal activity patterns. *Pheidole tenuinodis* was inactive during the middle of the day. The inactive period was substantially shorter in winter. The other bimodal, diurnal species remained active throughout the day in winter, although activity was reduced during the hottest period of the day. In contrast, in summer these species had a period of total inactivity in the middle of the day. *Pheidole tenuinodis* was primarily nocturnal in summer and crepuscular to diurnal in winter. *Monomorium* sp. C, *Monomorium* sp. B, *Tetramorium rufescens* and *T. sericeiventre* were primarily crepuscular to diurnal in summer and almost exclusively diurnal in winter.

Pianka's (1973) measure of resource overlap was used to quantify similarities in activity patterns between species:

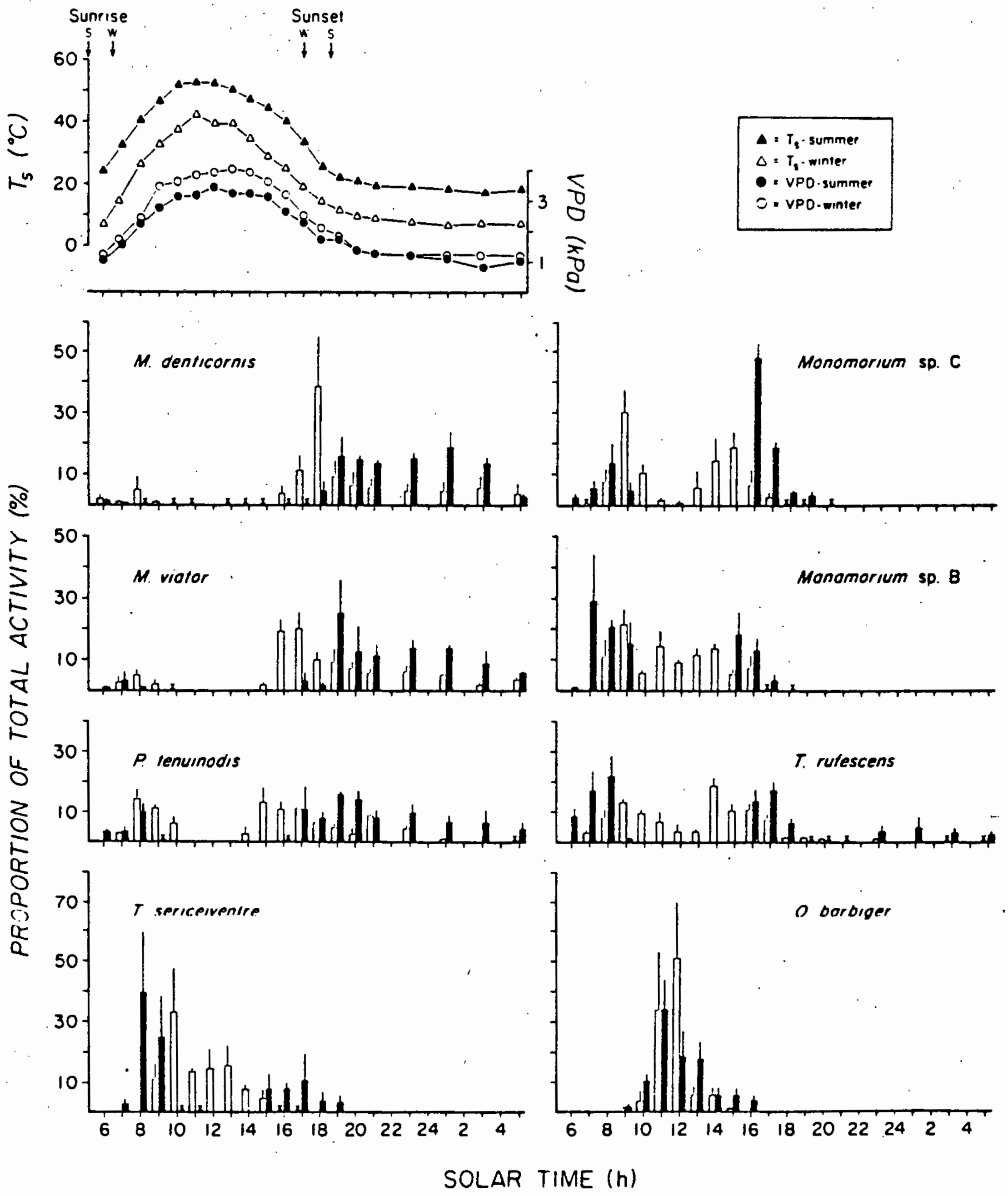

Figure 5.1. Activity patterns of ants in winter (white bars) and pre-rain summer (black bars). The data have been expressed as percentages of the total number of exits and entrances that occurred in a 24 h period. Bar length represents the mean and vertical line length one standard error of three nests. Values less than 1 % are represented by an "x". The sand surface temperatures (T_s) and vapour pressure deficits (VPD) indicated represent hourly means over the 48 h observation period. Note that M. denticornis refers to the genus Messor whereas M. viator refers to the genus Monomorium.

$O_{ij} = \frac{\sum p_{ia} \; p_{ja}}{\sqrt{\sum p_{ia}^2 \sum p_{ja}^2}}$, where P and P are the proportions of the a^{th} time period used by the i^{th} and j^{th} species respectively. Resource overlap, O, can range in value from zero for no overlap to unity for identical resource use. The overlap values for the winter and pre-rain summer periods are presented as a symmetrical matrix in Table 5.2. Of the 28 species pair combinations, 19 showed a decrease in similarity of activity pattern in summer relative to winter and only two species pairs, *P. tenuinodis*-*M. denticornis* and *P. tenuinodis*-*M. viator*, showed marked increases in similarity of activity pattern in summer relative to winter. The binomial probability of obtaining 19 shifts in one direction from 28 independent trials is 0.026, thus this trend is unlikely to be due to chance. *Ocymyrmex barbiger* had very low overlap values with all species in summer but reasonably high values in winter with respect to three other diurnal species; *T. rufecens*, *T. sericeiventre* and *Monomorium* sp. B. The two primarily nocturnal species, *M. denticornis* and *M. viator*, had very high overlap values in both seasons. Both these species had low overlaps with all other species with the exception of *P. tenuinodis*. The shift of *P. tenuinodis* from crepuscular-diurnal in winter to primarily nocturnal in summer is reflected in the summer increases in overlap values with *M. denticornis* and *M. viator*. Concomitantly the activity shift by *P. tenuinodis* resulted in marked reductions in summer overlap values with *T. rufescens*, *Monomorium* sp. B and *Monomorium* sp. C. *Tetramorium rufescens* exhibited moderately

Table 5.2. Temporal niche overlap values for the eight ant species for winter and pre-rain summer. Summer overlap values are on the upper right and winter values on the lower left of the matrix.

SUMMER

	MD	TR	TS	MV	MB	MC	PT	OB
MD	--	.19	.04	.94	.02	.04	.82	0
TR	.19	--	.67	.22	.72	.69	.54	.03
TS	.02	.60	--	.08	.70	.47	.38	.05
MV	.97	.45	.03	--	.07	.09	.87	0
MB	.07	.85	.67	.21	--	.49	.25	.08
MC	.08	.85	.54	.23	.82	--	.27	.07
PT	.47	.74	.30	.73	.60	.70	--	0
OB	0	.30	.55	0	.50	.10	.02	--

WINTER

MD = *M. denticornis*, TR = *T. rufescens*, TS = *T. sericeiventre*
MV = *M. viator*, MB = *Monomorium* sp. B, MC = *Monomorium* sp. C,
PT = *P. tenuinodis*, OB = *O. barbiger*.

high overlap values with *P. tenuinodis* and the three *Monomorium* species and all showed a marked reduction in overlap from winter to summer.

The total number of exits and entrances that occurred in 24 h was computed for each nest by interpolation. A two-way analysis of variance (Sokal and Rohlf, 1981) revealed significant interspecific differences in total daily activity and activity duration ($p < 0.001$) but no significant differences between winter and pre-rain summer (Table 5.3). However, in summer there were significant differences in total daily activity ($p < 0.005$) and activity duration ($p < 0.001$) before and after rain (Table 5.3). For most species total daily activity and activity duration increased after rainfall (Table 5.4). *Ocymyrmex barbiger* showed a decrease in activity duration and conflicting patterns of change in total daily activity after rain.

To determine the relationships between ant activity, surface temperature and vapour pressure deficit, the response curves of activity versus surface temperature and activity versus vapour pressure deficit for each species were linearized using a parabolic transformation (Forsythe and Loucks, 1972) and the data analysed using multiple linear regressions. The relative importance of these physical variables as determinants of ant activity are represented by the standard partial regression coefficients in Table 5.5. The ratios of

Table 5.3. Critical values of two way analysis of variance tests on total daily activity and duration between seasons (winter versus pre-rain summer) and between pre-rainfall and post-rainfall summer periods.

	TOTAL DAILY ACTIVITY			ACTIVITY DURATION		
	F	DF	P	F	DF	P
SEASON						
Between species	12.268	7 , 32	<.001	23.450	7 , 32	<.001
Between seasons	2.011	1 , 32	NS	0.812	1 , 32	NS
Species X season	4.277	7 , 32	<.005	0.885	7 , 32	NS
RAINFALL						
Between species	4.517	7 , 16	<.01	50.541	7 , 16	<.001
Between pre and post-rain groups	12.138	1 , 16	<.005	40.147	1 , 16	<.001
Species X rain	2.891	7 , 16	<.05	5.199	7 , 16	<.005

Table 5.4. Comparison of daily surface activity before and after rainfall in summer.

Species	Nest	Number of ants per nest per day		Duration of activity (hours)	
		Pre-rain	Post-rain	Pre-rain	Post-rain
M. denticornis	1	31 278	74 178	16	24
	2	37 229	52 455	15	19
T. rufescens	1	6 696	62 205	17	24
	2	10 886	205 860	18	24
T. sericeiventre	1	504	8 580	5	10
	2	4 776	29 610	6	10
P. tenuinodis	1	4 185	20 295	18	24
	2	2 964	10 605	16	22
M. viator	1	6 111	77 100	13	22
	2	21 936	120 540	16	24
Monomorium sp. B	1	756	1 065	7	9
	2	570	1 320	5	11
Monomorium sp. C	1	810	2 355	7	12
	2	1 014	1 650	9	6
O. barbiger	1	376	152	6	1
	2	104	327	7	3

the standard partial regression coefficients suggest that, in general, surface temperature influenced activity more than vapour pressure deficit. The adjusted R^2 values imply, however, that a substantial amount of the variation in activity is not explained by these two physical variables. Although the adjusted R^2 values were moderately low for most species (0.049 - 0.585), nine of them are significant ($p < 0.05$) and most of the remainder are close to significance. A Fisher's combined probability test (Sokal and Rohlf, 1981) reveals that the overall relationship between surface temperature, vapour pressure deficit and activity is significant (χ = 120.9854; df 32; $p < 0.05$).

Table 5.6 lists minimum and maximum black body temperatures tolerated by the various species in the field during the three sampling periods, and the range of temperatures at which nests were maximally active. All species were active over a wide thermal range with the predominantly nocturnal and facultative species operating over the widest range of temperatures. Despite the range of temperatures over which activity occurred, all nests, irrespective of season, were maximally active over a fairly narrow range of temperatures. Maximal activity is defined as the greatest number of ants emerging and returning to the nest in a 10 or 15 min observation period. In those species that were most active during relatively cool conditions 'preferred' temperatures were situated approximately midway between the minimum and

Table 5.5. Relative importance, as measured by standard partial regression coefficients (c), of soil surface temperature T_s (°C) and vapour pressure deficit (kPa) as determinants of ant activity.

Species	Season	$T_s (c_s)$	VPD(c_v)	Ratio (c_s/c_v)	Adjusted R^2	P	N
M. denticornis	Summer	-0.431	-0.113	3.8:1	.209	<.05	33
	Winter	-0.095	-0.296	1:3.1	.083	<.10	34
M. viator	Summer	-0.306	-0.097	3.2:1	.049	<.25	31
	Winter	-0.511	-0.039	13.1:1	.259	<.005	42
P. tenuinodis	Summer	-0.030	-0.397	13.2:1	.130	<.05	39
	Winter	-1.351	0.627	2.5:1	.585	<.001	28
T. rufescens	Summer	-1.177	0.575	2.1:1	.444	<.001	39
	Winter	-0.860	0.131	6.6:1	.533	<.001	45
Monomorium sp. C	Summer	-0.277	0.421	1:1.5	.352	<.005	23
	Winter	-0.815	0.279	2.9:1	.324	<.01	25
Monomorium sp. B	Summer	-0.761	0.490	1.6:1	.246	<.05	20
	Winter	-0.331	-0.261	1.3:1	.106	<.10	27
T. sericeiventre	Summer	0.132	-0.579	1:4.4	.143	<.10	21
	Winter	-0.378	-0.086	4.4:1	.077	<.25	21
O. barbiger	Summer	0.378	-0.227	1.7:1	.206	<.10	19
	Winter	-0.485	0.083	5.8:1	.113	<.25	13

Table 5.6. Field determined upper (Tmax) and lower (Tmin) thermal limits for surface activity and the temperature coinciding with maximal activity (Tpref). Values are black body temperatures at ant height (°C).

Species	Activity period*	Tmin	Tmax	Tpref	N**
M. denticornis	N	7	39	20-23	8
M. viator	N	7	42	19-24	8
P. tenuinodis	FN	7	41	19-23	8
T. rufescens	FD	7	42	31-36	8
Monomorium sp. C	D	19	46	35-40	8
Monomorium sp. B	D	20	46	39-42	8
T. sericeiventre	D	26	46	38-42	8
O. barbiger	D	33	>49	46-48	8

* N = nocturnal, FN = facultative but predominantly nocturnal, FD = facultative but predominantly diurnal, D = diurnal.

** The number of colony days from which the data were derived.

maximum tolerated temperatures. In contrast, in diurnal species there was a tendency for 'preferred' temperatures to approach the upper tolerance limits.

5.3.3 Critical Thermal Limits

Laboratory determined Critical Thermal Maxima and Minima were fairly similar for all species irrespective of their activity period (Table 5.7). Critical Thermal Maxima ranged from 42.9 - 51.5 °C and Critical Thermal Minima ranged from 8.5 - 13.3 °C. Despite these similarities, individual variation within a species was small and most interspecific comparisons were significantly different. In general Critical Thermal Maxima for the diurnal species were higher than for the more nocturnal species, with the most diurnal species, O. barbiger, having the highest Critical Thermal Maximum. Although M. denticornis is predominantly nocturnal it had a high Critical Thermal Maximum relative to the more diurnal species T. rufescens and P. tenuinodis. The predominantly nocturnal and crepuscular-nocturnal species, M. denticornis, M. viator and P. tenuinodis, had the lowest Critical Thermal Minima, all less than 10 °C, whereas for the more diurnal species Critical Thermal Minima were in excess of 10 °C.

5.3.4 Behavioural interactions

Of 104 encounters between M. denticornis and T. rufescens

Table 5.7. Laboratory determined critical thermal limits# for eight common Namib Desert ant species. Critical Thermal Maxima = CTMAX and Critical Thermal Minima = CTMIN.

Species	Activity*	CTMAX (°C)			CTMIN (°C)		
		$\bar{X}$	±SE	n	$\bar{X}$	±SE	n
M. denticornis	N	47.5	0.2	15	8.6	0.3	15
M. viator	N	46.7	0.3	15	9.1	0.2	15
P. tenuinodis	FN	42.9	0.3	15	8.5	0.1	15
T. rufescens	FD	46.9	0.1	15	11.4	0.1	15
Monomorium sp. C	D	49.0	0.2	10	13.3	0.2	8
Monomorium sp. B	D	49.0	0.3	15	10.9	0.3	15
T. sericeiventre	D	47.9	0.2	15	11.6	0.1	15
O. barbiger	D	51.5	0.2	15	12.1	0.2	15

* N = nocturnal, FN = facultative but predominantly nocturnal, FD = facultative but predominantly diurnal, D = diurnal.

\# All species pair comparisons were significantly different (Mann-Whitney U-test, $p < 0.05$) except for _M. viator_-_T. rufescens_, _M. denticornis_-_T. sericeiventre_, _Monomorium_ sp. B-_Monomorium_ sp. C (CTMAX) and _T. sericeiventre_-_O. barbiger_, _T. rufescens_-_Monomorium_ sp. B, _M. denticornis_-_P. tenuinodis_ (CTMIN).

individuals, 58 resulted in aggressive responses being exhibited by one or both individuals and 15 resulted in avoidance responses. Therefore, 73 of 104 encounters (70%) resulted in interference behaviour. Three of the encounters resulted in obvious physical injury and all three injured ants were _T. rufescens_ which sustained an immobilized leg. _Messor denticornis_ was significantly more dominant than _T. rufescens_ ($p < 0.001$, Chi-square test), dominating in 56 of 58 aggressive encounters.

5.4 DISCUSSION

A convenient way of looking at the determinants of ant activity is to assign them to two groups, stimulatory-inhibitory and regulatory factors (Briese & Macauley, 1980). The stimulatory-inhibitory factors control the absolute levels of activity whereas the regulatory factors determine the relative rates of activity, particularly during the diel cycle. The most important biotic stimulatory-inhibitory factor, particularly for harvester ants, appears to be the availability of food (Briese & Macauley, 1980; Whitford & Ettershank, 1975), although this will be modified by colony hunger. The activity levels of _M. denticornis_ and _T. rufescens_ increase significantly with increases in food abundance (see section 6.3.4). An important physical stimulatory-inhibitory factor is rainfall (Briese & Macauley, 1980; Schumacher & Whitford, 1976; Whitford, 1978a; Whitford & Ettershank, 1975). The present study supports this latter notion, as activity increased substantially for most species immediately after rain. These increases in activity were not only a consequence of the increased duration of activity period as at any given moment activity levels were considerably greater in most species. The increase in activity duration after rain may in part have been a consequence of cloud cover and moist sand which reduced thermal and desiccation stress throughout the 24 h sampling period. Observations on some nests indicated that the increased activity subsequent to rainfall was caused by an increase in both foraging effort and nest construction. The increase in foraging effort may have been in response to an increase in food availability such as the availability of insect prey. The principal food of most of the ant species is however seeds, and could not have increased in abundance in the time available. Furthermore, it is unlikely that seed availability could have increased through being uncovered as the rainfall in question was very gentle (1.3 mm in 6 h). In the absence of quantitative data on feeding habits and insect availability on either side of a rainfall event this remains speculative. Naturally occurring and experimentally induced increases in food availability, however, invariably result in increased levels in harvester ant activity (Briese & Macauley, 1980; Whitford & Ettershank, 1975; Whitford _et_ _al_., 1980; see section 6.3.3). Much of the increase in activity after rainfall is attributable to nest construction, particularly debris removal. It appears that rainfall stimulates ants to expand nest size, probably in anticipation of seed production and the resultant storage requirements and increases in colony size. Some of this activity may also be related to nest entrance expansion to facilitate the departure of reproductives which occurs typically after rainfall (Conway, 1980; Curtis, 1983; Delye, 1968; pers. obs.).

Temperature is undoubtedly one of the most important activity regulating factors in ants, although other factors such as vapour pressure deficit and light intensity may also have a controlling action (Briese & Macauley, 1980). In the present study variations in the thermal and humidity environment explained a significant amount of the observed variation in activity patterns although a substantial amount of variation could not be attributed to these two factors. Similar unexplained variation has been found in studies of ant activity in the Chihuahuan Desert (Whitford & Ettershank, 1975; Whitford et al., 1981) and in semi-arid Australia (Briese & Macauley, 1980). In general the nocturnal species had lower Critical Thermal limits than the diurnal species and the trends were similar to those that have been reported for ants in North American deserts (Kay & Whitford, 1978; Whitford & Ettershank, 1975).

North American desert ants do not utilize the entire spectrum of thermal conditions available to them (Whitford & Ettershank, 1975; Whitford et al., 1981). In general, nocturnal species tend to approach their Critical Thermal Minima while foraging but stop activity considerably below their Critical Thermal Maxima. Conversely, diurnal species typically commence surface activities when conditions are substantially hotter than their Critical Thermal Minima and forage until temperatures are just below their Critical Thermal Maxima. In contrast, some of the Namib Desert ant species were active over virtually the entire range of thermal conditions that they could tolerate physiologically. Examples of this were Monomorium sp. C., M. viator, P. tenuinodis and T. rufescens (Tables 5.6 & 5.7). Indeed some species apparently were active at temperatures less than their Critical Thermal Minima but this presumably indicates the difficulties involved in assessing locomotor dysfunction precisely in response to increasing cold in the laboratory.

In general, the preferred temperatures of desert ants are lower in nocturnal than in diurnal species (Delye, 1968; Kay, 1978). Most species prefer temperatures between 20 and 30 °C but values of 35 - 40 °C have been reported for Cataglyphis spp., Saharan ants reknowned for their extreme diurnalism (Delye, 1968; Wehner et al., 1983). The Namib Desert ant species studied here conform to these general trends with the predominantly nocturnal species 'preferring' temperatures below 24 °C while the diurnal species 'prefer' temperatures close to and slightly above 40 °C.

Briese & Macauley (1980) suggest that wind speeds > 8 m s^{-1}

have an inhibitory effect on ant activity. The notion that strong wind inhibits ant activity is also mentioned by Curtis (1983) and by Sheata & Kaschef (1971). For the Namib Desert ant species the critical wind speed was about 6 m s^{-1} (pers. obs.). Above this speed ants were occasionally lifted up and blown off course. During the study period wind strength seldom exceeded this critical limit (Table 5.1) and thus wind _per se_ probably had little direct effect on the overall results. Wind may however have had an indirect effect on ant activity by modifying the thermal environment.

There are several possible reasons for interspecific differences in the activity patterns of desert ants. Temporal partitioning could reduce competitive interactions (Briese & Macauley, 1980; Chew, 1977; Hansen, 1978; Mehlhop & Scott, 1983; Schumacher & Whitford, 1976; Whitford & Ettershank, 1975; Whitford _et al._, 1976; Whitford _et al._, 1981). For animals in general, Carothers & Jaksic (1984) suggest that temporal partitioning is an expected consequence of interference competition. Intra- and interspecifically directed aggression, as well as avoidance responses, are common among ants (Holldobler, 1974; Holldobler & Lumsden, 1980; Mabelis, 1979; Samways, 1983; Steyn, 1954; Whitford _et al._, 1976; Wilson, 1971). The present data suggests that individuals of the two dominant species, _M. denticornis_ and _T. rufescens_, will probably exhibit interference interactions when they encounter one another and although no quantitative data on the extent of interference interactions between the other ant species exist such interactions do occur (pers. obs.). The observed temporal differences in activity patterns could reduce the probability of interspecific encounters. The seasonal shifts in activity patterns are best interpreted as responses to the physical environment. The reduction of temporal overlap among diurnal species in summer, for instance, probably reflects the longer daylight period and consequent broader spread of temperatures during this period.

Another possible explanation for interspecific differences in temporal activity periods is that different species have different navigational requirements. Two of the predominantly nocturnal species, _M_. _denticornis_ and _P_. _tenuinodis_, are trunk-trail foragers that are dependent upon pheromone trails for successful navigation between the nest and foraging area. Pheromone persistence may be enhanced during the comparatively cool and moist nocturnal period although there are diurnal ants in other environments that utilize trunk-trails (Gamboa, 1976; Greenaway, 1981; Wheeler & Rissing, 1975). In the Namib Desert many of the diurnal foragers do not exhibit typical pheromone-trail laying behaviour. These ants presumably rely on solar navigation and therefore could not forage at night.

It has also been suggested that differences in activity patterns in ectotherms may merely reflect different thermal preferenda and that temporal partitioning is essentially an epiphenomenon (Carothers, 1983; Huey & Pianka, 1981, 1983).

The above explanations for interspecific partitioning of time are not necessarily mutually exclusive. All or some of them may be relevant. Some could be the proximal reasons for the observed differences while others may be the ultimate reason why interspecific differences have evolved.

SECTION SIX

FORAGING ECOLOGY OF TWO DOMINANT HARVESTER ANT SPECIES IN THE CENTRAL NAMIB DESERT

6.1.1 INTRODUCTION

Seed-storing harvester ants are important components of desert ecosystems as they are able to exploit the large quantities of nutrient-rich seeds that are typically produced by desert plants following rainfall events. In the past decade there has been a surge of interest in harvester ant ecology in North American deserts and to a lesser extent in the arid and semi-arid regions of Australia (see references below). One of the general ideas to emerge from these studies is that seed-harvesting ants occur in interactive communities (*sensu* Wiens, 1984), that is, harvester ant communities are structured primarily as a result of biotic interactions between species. Brown *et al*. (1979) have reviewed the considerable indirect evidence for competitive interactions, particularly for food resources, between granivorous ants. With reference to animal communities in general, Noy-Meir (1979/80) and Wiens (1977, 1984), however, have suggested that in fluctuating environments such as deserts, where rainfall and hence productivity are unpredictable, non-interactive communities can be expected. In these communities the observed patterns would largely be epiphenomena resulting from independent responses of species to the environment. Community patterns of North American granivorous birds largely support the non-interactive community concept whereas community patterns of granivorous ants in North American deserts appear to be an exception to this concept (see references in Noy-Meir, 1979/80). Most granivorous ant and bird studies have, however, primarily been in environments receiving approximately 100 to 400 mm of rain each year. In these habitats seed production occurs at least once a year (Brown _et al._, 1979).

In contrast, the Namib Desert environment fluctuates more than that of North America and Australia. Mean annual rainfall in the most productive region is less than 100 mm (Lancaster _et al._, 1984) and seed production may not occur for several years (Louw & Seely, 1982). In such a system seeds are not as reliable a resource as they are in North American and Australian arid zones and community patterns may be even less tied to biotic interactions. Ecological studies of harvester ants in African deserts have not kept pace with those in America and Australia and this report represents the first published investigation of the foraging ecology of harvester ants in a southern African desert. The study concerns the two principal species occurring in a 13 species ant community. _Messor denticornis_ is a large polymorphic species (5.5 - 11.0 mm total length) whereas _Tetramorium rufescens_ is a medium sized (4.0 - 5.1 mm TL) monomorphic species. Together these species comprise 60 % of the community forager density and 90 %

of the community forager biomass (see section 4.3). *Messor denticornis* is a trunk-trail forager and *T. rufescens* is a diffuse forager (Marsh, 1984). Patterns of diet, food abundance, forager behaviour and spatial occurrence are considered in relation to the interactive versus non-interactive community concepts.

6.1.2 STUDY SITE

The study site was situated in the central Namib Desert on the gravel plains near Ganab (28°08'S; 15°37'E) and was selected for its apparent uniformity. The site was located on an approximately 100 ha flat sandy plain. The major portion of the study occurred within a 16 hectare plot in the centre of this plain. The sand was compacted and approximately 0.5 m deep. Above the sand was a 2-5 mm layer of small quartz pebbles. Underlying the sand was a hard, porous calcrete layer which was several metres deep (J. Ward, pers. comm.) Ant nests were all subterranean and were located within the calcrete as well as in the sand.

Mean annual rainfall at Ganab, 3 km from the study site, was 87.2 ± 91.8 mm (range 9.9 - 375.0 mm, N = 16) (Lancaster *et al*., 1984). The large range and standard deviation indicate that this is an extremely variable environment. Effective precipitation, i.e. sufficient to cause germination of annual plants is 17 - 20 mm in the Namib Desert (Seely, 1978) and the longest recorded period without effective rainfall at Ganab is 22 months (Lancaster *et al.*, 1984). Perennial grasses which exist as dry but rooted stubble during drought can, however, grow and set seed after as little as 12 mm of rain (pers. obs.). The period during and just prior to the present study spanned extreme fluctuations in rainfall. In 1981, one year prior to observations, 30 mm of rain fell over a period of six months and was insufficient to cause seed set. In 1982, 97.2 mm was recorded with resultant germination of annual plants, growth of perennial plants and seed set by both groups. No effective rain fell in 1983. During the first half of 1984 15.8 mm of rainfall was recorded. Of this 12.9 mm fell in March and was sufficient for perennial grasses to produce seed.

For the major part of the study the habitat was devoid of photosynthetically active vegetation. The only indications of vegetation were scattered clumps of grass stubble, typically 10 - 20 mm high. In May 1982, after heavy rains stimulated plant growth, a survey using the point quadrat technique (Greig-Smith, 1964) revealed the presence of 14 species (N = 1033 point strikes). Eight species were grasses and in terms of proportion by number 86.9 % of the plants comprised three grass species, *Stipagrostis ciliata* (43.8 %), *S. uniplumis* (22.6 %) and *Enneapogon brachystachyus* (20.5 %).

6.2 PROCEDURE

6.2.1 Forager abundance

Surface active foragers were censused once a month for 17 months from January 1983 to May 1984 inclusive in a 16 ha plot that was subdivided into 256 25 m x 25 m cells. An observer moved slowly within the plot on a pedal-powered vehicle, averaging 170 ± 30 m h^{-1} (SD). The observer lay face-down upon a platform situated 40 cm above the substrate. All ants that were encountered within a 50 cm wide transect were aspirated and stored in 70 % alcohol for later identification. The transect was spatially dynamic in that it was demarcated by two antennae 50 cm apart and projecting 60 cm from the front end of the moving vehicle. An odometer measured the length of the transect. Each census was conducted for a minimum period of 24 consecutive hours with many running for 48 h. A fluorescent lamp was used for nocturnal observations. The location and direction of the transects were determined by consulting random number tables. The observer endeavoured to steer a straight course until the boundary of the 16 ha plot was reached at which point the random number table was consulted and a new direction was adopted. Throughout each census the location, at a resolution of 25 m x 25 m, and the time when ants were encountered were recorded.

Activity patterns of the two species were determined by computing hourly forager densities. To obtain sufficient data for analysis, the data from the first four months of the census, January to April 1983 inclusive, were pooled. The activity data were therefore obtained from 216 census hours in summer. Interspecific similarities in activity pattern were determined with Pianka's (1973) measure of resource overlap:

$$O_{ij} = \frac{\sum p_{ia} \quad p_{ja}}{\sqrt{\sum p_{ia}^2 \sum p_{ja}^2}}$$

where P_i and P_j are the proportions of the a^{th} time period used by the i^{th} and j^{th} species respectively. Resource overlap can range in value from zero for completely different activity patterns to unity for identical activity patterns.

Spatial patterns within the 16 ha plot were analyzed using presence/absence data in 25 m x 25 m or 50 m x 50 m cells obtained during the 17 census months. Actual ant densities were not used in this analysis as it was not possible to account adequately for differences in diel activity levels and sampling effort per cell. All cells that were not censused at some stage during the 18 month study period at times when both species were active were omitted from the analysis. A Chi-square test was used to determine whether there was any degree of association between the two species. The dispersion of foraging ants within the 16 ha plot was determined at a resolution of 50 m x 50 m using presence/absence data from 25 m x 25 m cells. Thus each 50 m x 50 m cell was assigned a value ranging from 0 - 4 depending on how many of the four 25 m x 25 m cells that occurred within each larger cell contained ants. The variance/mean ratio (Pielou, 1969) was used to determine the dispersion pattern of each species and departures from random expectation were assessed with a Chi-square test.

6.2.2 Nest abundance

Densities of T. rufescens nests were obtained from nest counts in five 1600 m^2 plots. Plot positions within the study area were selected randomly. Nests were located by luring ants to a grid of bait (cheese and seed) and following foragers back to their nests. Bait points were 5 m apart and each plot was searched periodically over 48 h. Because of the relatively low density of M. denticornis nests the 1600 m^2 plots were too small for reliable nest density estimates in this species. Nests of M. denticornis were however relatively conspicuous and density estimates were obtained by visual inspection during walking transects. Each transect was 1000 m long and 2 m wide. A total of 10 randomly located transects were walked within the study area.

Nest dispersion patterns were determined for both species using nearest-neighbour techniques (Clark & Evans, 1954). A number of nests (24 T. rufescens, 16 M. denticornis) were selected at random, the nearest conspecific nest was located and the distance between the two nests was measured to the nearest 10 cm (T. rufescens) and nearest 1 m (M. denticornis). Significant departures from random expectation were assessed by determining the standard variate of the normal curve (see Clark & Evans, 1954). A Mann-Whitney U-test was used to compare interspecific differences in inter-nest distances.

6.2.3 Food and foraging

To determine foraging distances individuals were followed from the nest (*T. rufescens*) or from the end of a trunk-trail (*M. denticornis*) until they had located and picked up a food item and the radial distance from the nest to the food item was measured to the nearest 10 cm. Nocturnal observations were made using fluorescent light, which did not appear to influence the behaviour of the ants. Interspecific comparisons of foraging distances were assessed statistically with a Mann-Whitney U-test.

Twice a month observations were made of forager activity at 16 marked *M. denticornis* nests. All active trails were followed to their terminal end and the radial distance from the nest to the foraging site and the azimuth direction of each trail were recorded.

Once a month, for 18 months, food items were removed from ants returning to the nest. An effort was made to collect a minimum of 50 food items per species from a minimum of four nests. This was not however always possible as activity levels became much lower after six months and remained low for the majority of the study period. Thus for certain months no food, or very little food, was collected and in other cases the majority of food was collected from one to two nests only. Because of the unpredictable nature of harvester ant activity it was also not possible to sample the same nests each month. The only feasible approach therefore was to search within the study plot for active nests and collect food opportunistically from these nests. Each food item was assigned to one of six taxonomic categories; four devoted to various types of seed, one to non-seed plant matter and one to arthropod matter. Dietary niche breadths were calculated using the inverse of Simpson's (1949) diversity index: $B = 1/\sum p_i^2$, where p_i is the relative proportion of the i^{th} food category in the sample. Values of B, calculated in this manner, can range from one for a species that utilizes one food category only, to six for a species that utilizes all six categories equally. Each food item was dried for three days at 70 °C and weighed to the nearest 0.01 mg. Interspecific comparisons of food mass were performed on a monthly basis using the Mann-Whitney U-test to detect significant differences.

During October 1983, when forager activity levels had been depressed for several months, a food supplementation experiment was performed to test the hypothesis that the low levels of activity were partly attributable to reduced food availability. Twenty nests of each species were marked and randomly placed into two groups of 10 nests per species. The level of forager activity of each nest was estimated by counting the number of ants that occurred on the surface in a 1 m^2 quadrat which included the nest entrance. Activity counts were made between 20h00 and 21h00 for M. denticornis and between 07h00 and 08h00 for T. rufescens. These periods in the diel cycle coincided with relatively high levels of activity (see section 5.3.2). Three activity counts, each count separated by 15 to 20 min, were made at each nest and the highest of the three values was taken as the activity count for that nest. Maize meal granules (0.2-1.5 mm diameter) were then broadcast, at a density of 100 granules m^{-2}, within a 10 m radius of 10 nests of T. rufescens and M. denticornis and activity levels were estimated 24 h later. The results were subject to a two-way analysis of variance.

At the same time that food items were collected from ants the availability of food items in the environment was quantified. Ten square quadrats (900 cm^2) were placed at random within the 16 ha census plot and all material lying on and approximately 1 - 3 mm below the soil surface was collected. The contents from each quadrat were passed through a series of graded sieves and sorted by hand. All items known to be taken by ants were noted. The dispersion of the food resources was assessed each month using Morisitas index of dispersion (see Elliott, 1977). Departures from randomness were determined using a Chi-square test.

Following the rainfall events of 1982 when a standing crop of seed-bearing grass existed, 20 M. denticornis nests were selected at random and the most intensively used trunk-trail was followed to its termination. The standing crop of grass 1 m beyond the terminal end of the trail and 1 m to the left side of the trail midway between the nest and trail end was removed from a 0.25 m^2 area. Each sample was dried for three days at 70 C and weighed to 0.01 g. Differences in standing crop in the areas where ants chose to feed (at the terminal end of the trunk-trails) and in the areas by-passed by the ants (midway along the trails) were assessed with a Mann-Whitney U-test.

6.3 RESULTS

6.3.1 Forager abundance

Tetramorium rufescens was more abundant than *M. denticornis* for the majority of censuses during the 18 month study period (Fig. 6.1). There were large fluctuations in forager density during this period with both species exhibiting very similar patterns of change. Abundance values peaked in April in both years and thereafter decreased markedly. The density of foragers was relatively high during five months in the first year and only relatively high for one to two months in the second year. Ant abundance was greater during the summer of 1982/83 than during the summer of 1983/84.

Over a diel cycle *M. denticornis* and *T. rufescens* had

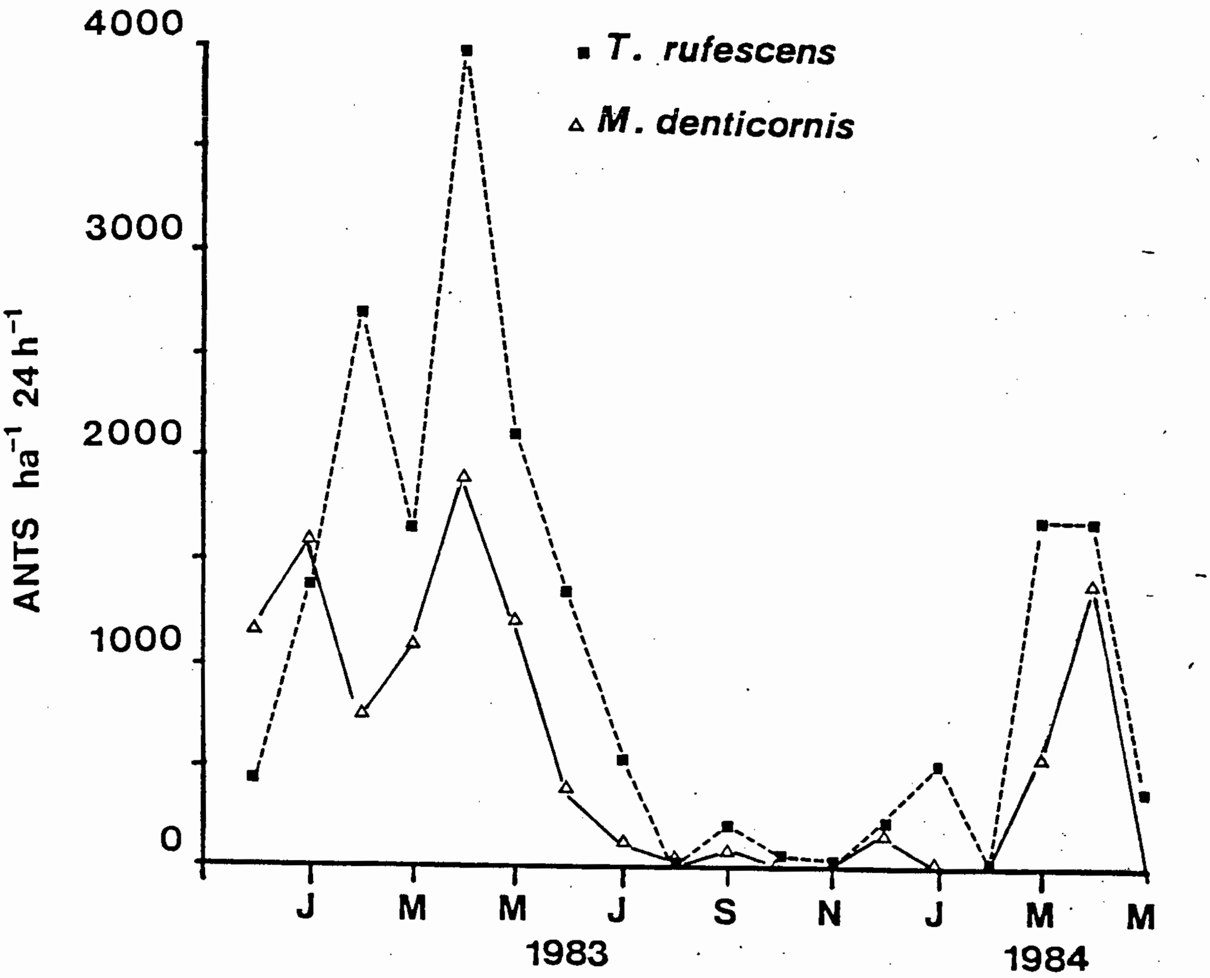

Figure 6.1. Temporal changes in forager density expressed as the number of foragers encountered per hectare per day.

similar activity patterns (Fig. 6.2, overlap in activity periods, O, = 0.71). *Tetramorium rufescens* was more diurnal than *M. denticornis* although for both species most foraging occurred at night. During the day *T. rufescens* activity ceased for 5 h whereas that of *M. denticornis* ceased for 8 h. Activity appeared to fluctuate from hour to hour but these fluctuations may reflect a sampling artifact in that each sample is pooled across several days, thereby introducing possible variation from micro-climatic differences.

Of the 256 25 m x 25 m cells occurring within the 16 ha plot, 241 were sampled during periods when both species were active on the study plot. Of these 241 cells, 207 contained one or both of the species. No significant spatial association, between the two species was apparent at this resolution ($P > 0.1$).

At a resolution of 50 m x 50 m *M. denticornis* foragers occurred in 53 of 64 cells and *T. rufescens* foragers occurred in 56 of 64 cells (Fig. 6.3). Thus *M. denticornis* occupied 13.25 ha of 16 ha and *T. rufescens* occupied 14 of 16 ha. The two species were sympatric in 45 cells, equivalent to 11.25 ha. Every cell was occupied by at least one species. Cells in which a species was absent tended to cluster together. Thus there were three regions in the 16 ha plot where *M. denticornis* were not found and two regions where *T. rufescens* were not found. At the above mentioned

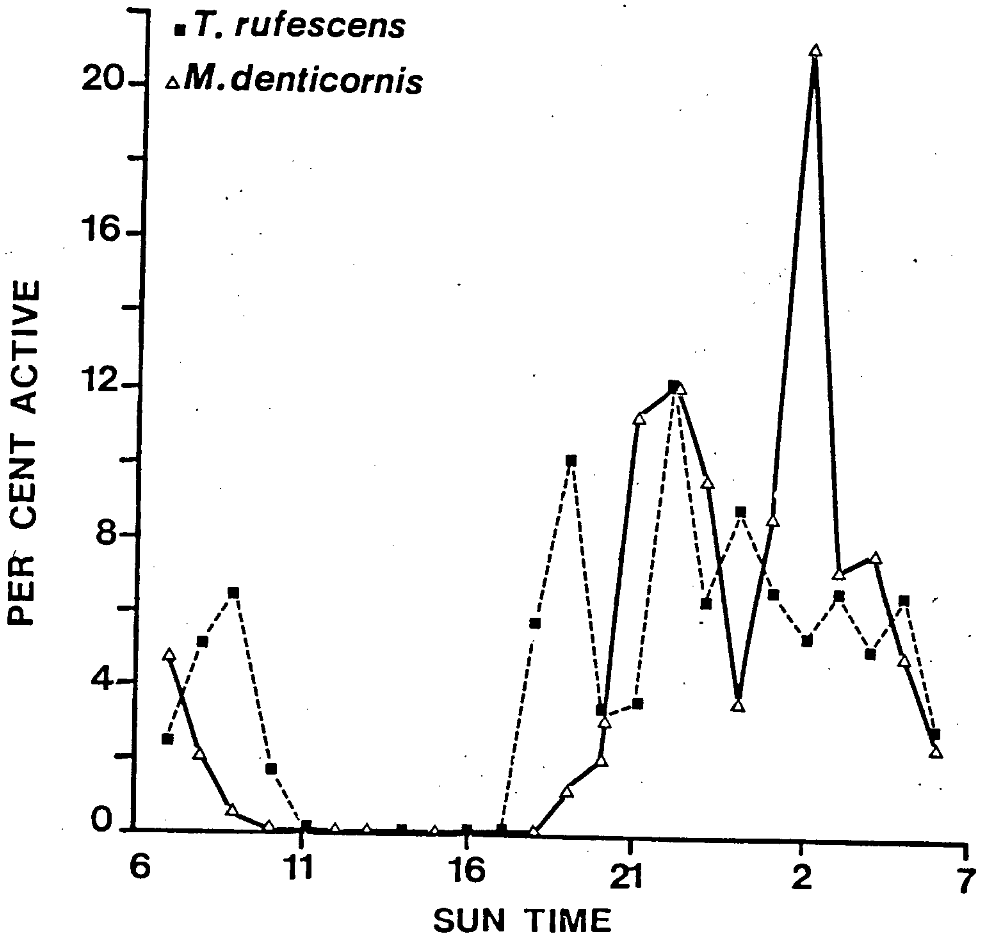

Figure 6.2. Diel activity patterns of M. denticornis and T. rufescens. Data are expressed as a proportion of total activity occurring over a 24 h cycle.

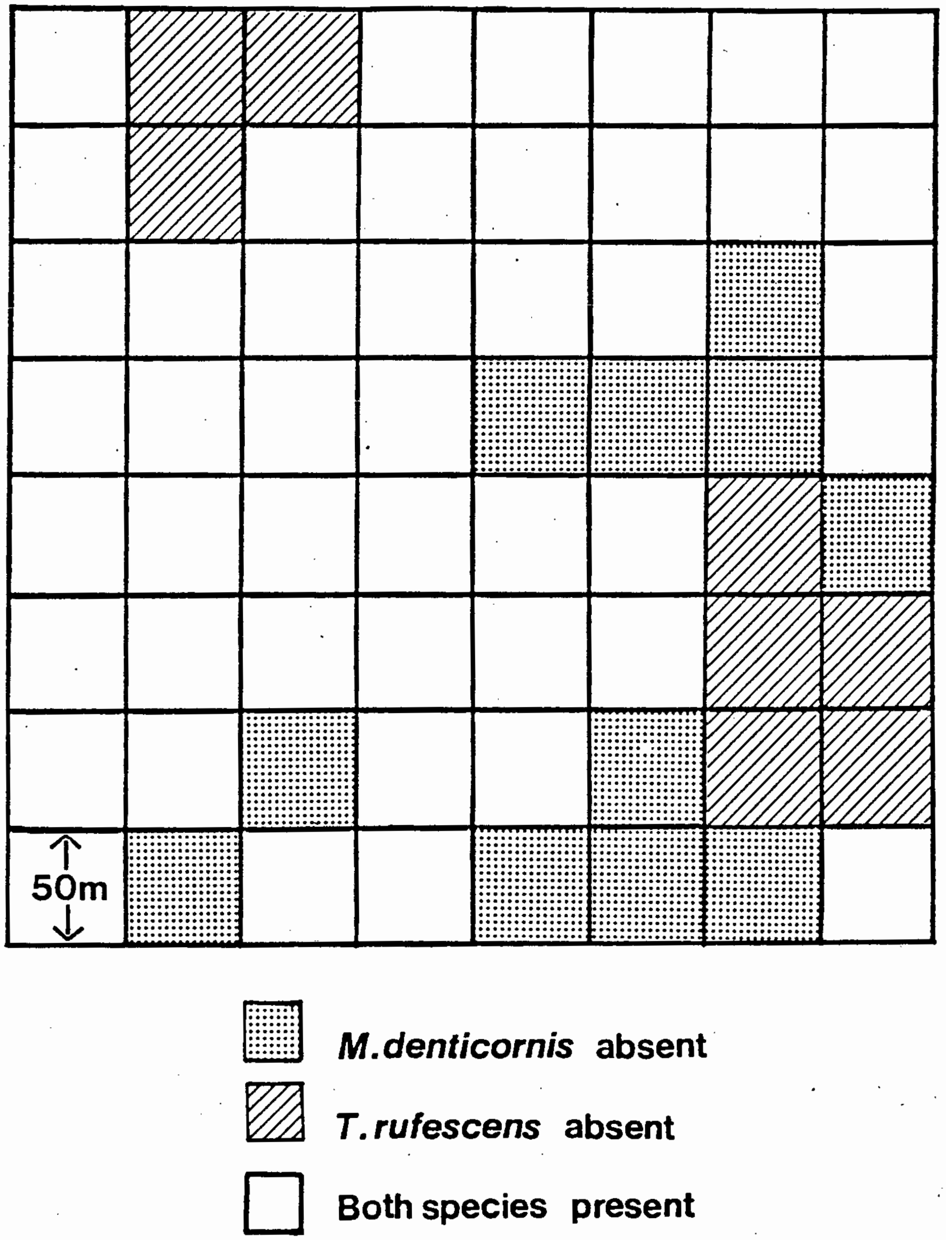

Figure 6.3. Spatial occurrence of foragers of M. denticornis and T. rufescens.

resolution the variance/mean ratios of both species were close to unity (Table 6.1) and the distribution of foraging ants did not deviate significantly from random ($p > 0.05$).

6.3.2 Nest abundance

The nest density of *T. rufescens* was over five times higher than that of *M. denticornis* (Table 6.1). Dispersion of nests of *T. rufescens* did not deviate significantly from random, whereas *M. denticornis* nests were significantly over-dispersed ($p < 0.001$, Table 6.1). The distance between conspecific nearest neighbour nests was significantly greater in *M. denticornis* than in *T. rufescens* ($p < 0.001$). On the average *M. denticornis* nests were approximately twice as far apart from one another as were *T. rufescens* nests (Table 6.1).

6.3.3 Food and foraging

Foraging distances of *T. rufescens* were considerably shorter than those of *M. denticornis* (Table 6.1; $p < 0.001$). Mean foraging distance of *T. rufescens* was less than 50 % of the mean inter-nest distance although maximum foraging distance (11 m) exceeded 50 % of the mean inter-nest distance (Table 6.1). This indicates that there was little or no intraspecific, inter-nest overlap in foraging area. In contrast, mean foraging distance of *M. denticornis* exceeded 50 % of the mean inter-nest distance indicating possible

Table 6.1. Spatial statistics of *M. denticornis* and *T. rufescens* foragers and nests.

STATISTIC	SPECIES	
	T. RUFESCENS	*M. DENTICORNIS*
DISPERSION OF FORAGERS		
$S/\bar{X}$	0.832	0.937
N (# of 50 x 50 m cells)	64	64
P	> 0.05	> 0.05
DISPERSION OF NESTS		
R	1.19	1.75
N	24	16
P	> 0.05	< 0.001
NEST DENSITY (#/hectare)		
$\bar{X}$	22.5	4.4
SE	9.4	0.9
INTERNEST DISTANCE (m)		
$\bar{X}$	14.3	31.9
SD	3.5	13.2
N	28	43
FORAGING DISTANCE (m)		
$\bar{X}$	4.6	22.4
SD	2.8	14.8
Maximum	11.0	67.0
N	41	50

inter-nest overlap in foraging area. Examination of the patterns of space utilization by foragers at 16 M. denticornis nests however revealed no simultaneous utilization of a feeding site by any two nests and very few instances of the use of the same feeding site by neighbouring nests at different times. The spatial distribution of six M. denticornis nests and their corresponding trunk-trails illustrate patterns typical to all conspecific nests studied (Fig. 6.4). For each nest, at any given moment, foraging was very directional with one, occasionally two to three, trunk-trails being used. The same foraging area was used for up to four weeks before another was selected. Over a period of several months the majority of the area about each nest had at some stage been searched although search patterns were markedly asymmetric in some nests (Fig. 6.4). During many of the nest observations on M. denticornis some diffuse foraging, within a radius of 1 - 3 m of the nest, occurred although the majority of ants utilized trunk-trails to reach more distant foraging sites. The maximum recorded foraging distance for M. denticornis was 67 m.

The trunk-trails of M. denticornis terminated in regions supporting considerably higher standing crops of annual grass than surrounding areas in all 20 nests examined. On the average, 17 times more grass occurred in these foraging areas than in areas ignored by foragers. The differences were statistically significant ($p < 0.001$). The standing crop of

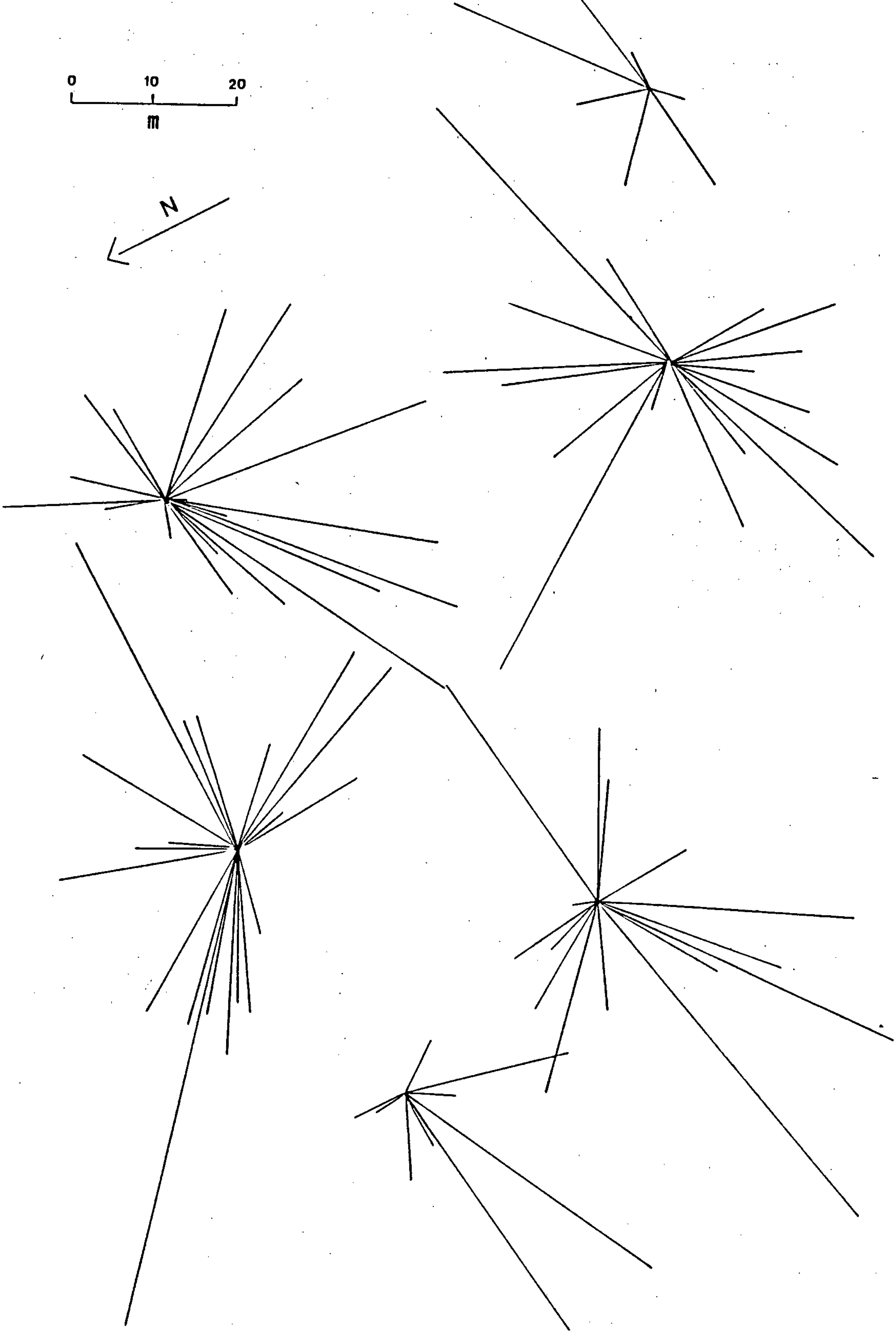

Figure 6.4. Distribution of trunk-trails at six M. denticornis nests.

grasses reflects past seed reserves in the soil as well as present seed reserves attached to the plants. At the time of observation, foragers exploited the foraging sites by climbing the grasses and removing the seeds which were then carried individually to the nest.

For both species approximately 50 or more food items were collected for 14 months, 12 of them consecutive months (Tables 6.2 & 6.3). Activity levels and foraging success were very low in August 1983 and from November 1983 to February 1984 inclusive. Consequently little or no food could be collected for these periods. Overall dietary patterns are illustrated in Fig. 6.5 where food items have been placed into three categories; seed, non-seed plant matter and arthropods. *Messor denticornis* consistently collected more seed than *T. rufescens*. Both species, however, primarily collected seed for roughly the first year of sampling i.e. January 1982 to February 1983, thereafter the amount of seed in the diet declined considerably with concomitant increases in the amounts of non-seed plant matter and arthropods. Seeds again became relatively common in the diet of both species in the final sampling period, May 1984. In *M. denticornis* the dietary shifts were consistent relative to those in *T. rufescens*. In *M. denticornis*, the amount of arthropod matter in the diet increased progressively as the proportion of seeds declined. In contrast, although arthropods were consistently more abundant in the diet of *T. rufescens* relative to that of *M. denticornis*, the

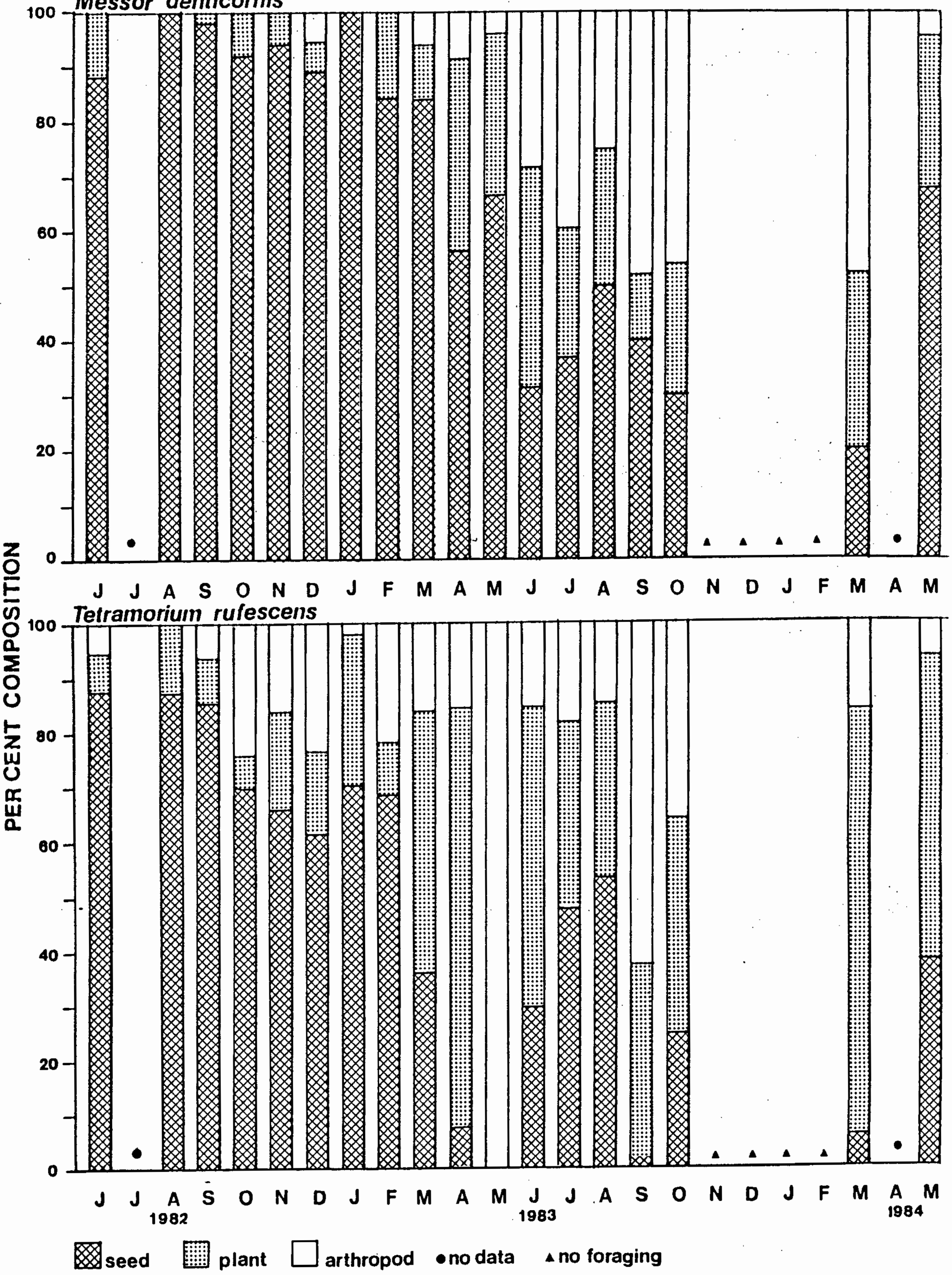

Figure 6.5. Composition of forage of M. denticornis and T. rufescens. Data are expressed as a per cent of the number of items taken from returning ants each month.

contribution that arthropods made to the diet of _T. rufescens_ varied considerably from month to month (Fig. 6.5). For example, arthropods made up 15 % of the diet in April and June 1983 and 100 % in May 1983.

From time to time, miscellaneous plant matter made up considerable proportions of the diet of both species. Typical items in this category were grass stems and leaves. These were normally dry, brown and photosynthetically inactive. In March 1984, however, after the first significant rainfall event since 1982, both species of ant and especially _T. rufescens_ collected large quantities of fresh green grass shoots and leaves.

The majority of arthropods collected by both species were termites. Termites were on occasion collected alive but most were dead on arrival at the nest and were frequently very dry and dismembered, suggesting that they had been scavenged by the ants. Two species of termite were collected by the ants. The large _Hodotermes_ sp. (dry mass per individual ~ 2-5 mg) were primarily taken by _M. denticornis_ and comprised the majority of the arthropod fraction of the diet in September and October 1983 and March 1984. The smaller _Trinervitermes_ sp. (dry mass per individual ~ 0.7-1.5 mg) were frequently taken by _T. rufescens_ and made up the entire diet sample in May 1983. _Tetramorium rufescens_ also collected _Hodotermes_ sp. on occasion and the arthropod component of the diet in September 1983 was made up almost exclusively by this species of termite.

More detailed analyses of the seed component of the diets of the two ant species are given in Tables 6.2 and 6.3. It is evident that the majority of seeds collected by both ants belonged to one species only, *Enneapogon brachystachyus*. This species of grass produces two types of seed, aerial seeds which are borne at the distal portion of the plant and basal seeds which are located at ground level at the base of the stem. The basal seeds were typically collected in clusters of up to ten seeds surrounding a piece of grass stem. Each seed was situated within a hard woody capsule. In contrast the aerial seeds occurred as discrete individuals surrounded by light feathery capsules. Aerial seeds were collected individually by the ants. Before the relatively heavy rains of 1982, and hence before new seed had been introduced into the environment, no aerial *Enneapogon* seed occurred in the diet of either ant species but basal *Enneapogon* seed, various other grass seeds (particularly *Stipagrostis* spp.) and unidentified dicotyledon seeds were taken. From June 1982 onwards, after the rains, aerial *Enneapogon* seed was a prominent seed type in the diets of both species for several months. From February 1983, when aerial *Enneapogon* seeds started becoming less prominent in the diets of both ants, *M. denticornis* started taking progressively more basal *Enneapogon* seeds. *Tetramorium rufescens*, in contrast, took very little basal *Enneapogon* seed with the exception of the August 1983 sample. The presence of other seed types in the diets of both species fluctuated greatly from

Table 6.2. Proportion of different seed categories in the diet of *Tetramorium rufescens*. The data are expressed as a percentage of N, the number of food items collected each month. See text for explanation of the terms aerial and basal *Enneapogon* seed.

YEAR	MONTH	N	*ENNEAPOGON*		*STIPAGROSTIS*	DICOT.
			AERIAL	BASAL		
1982	Jan	97	0	4.1	15.5	12.4
1982	Jun	57	86.0	0	1.8	0
1982	Aug	128	73.4	0	3.2	10.9
1982	Sep	49	73.5	0	8.2	4.0
1982	Oct	50	60.0	2.0	4.0	4.0
1982	Nov	50	54.0	0	6.0	6.0
1982	Dec	52	53.8	0	1.9	5.8
1983	Jan	54	68.5	0	1.9	0
1983	Feb	51	49.0	0	2.0	17.6
1983	Mar	50	18.0	0	14.0	4.0
1983	Apr	52	2.0	0	5.7	0
1983	May	50	0	0	0	0
1983	Jun	47	2.1	0	0	27.7
1983	Jul	50	0	4.0	20.0	24.0
1983	Aug	28	0	25.0	21.4	7.1
1983	Sep	53	0	0	1.9	0
1983	Oct	28	0	0	21.4	3.6
1984	Mar	51	2.0	0	2.0	2.0
1984	May	50	0	2.0	32.0	4.0

Table 6.3. Proportion of different seeds in the diet of Messor denticornis. The data are expressed as a percentage of N, the number of food items collected each month. See text for explanation of the terms aerial and basal Enneapogon seed.

YEAR	MONTH	N	ENNEAPOGON		STIPAGROSTIS	DICOT.
			AERIAL	BASAL		
1982	Jan	91	0	18.7	19.8	8.8
1982	Jun	86	40.7	0	47.7	0
1982	Aug	79	92.4	0	5.1	2.5
1982	Sep	51	92.2	2.0	3.9	0
1982	Oct	50	88.0	4.0	0	0
1982	Nov	50	90.0	6.0	0	0
1982	Dec	56	78.6	7.1	3.6	0
1983	Jan	50	86.0	12.0	2.0	0
1983	Feb	50	36.0	30.0	16.0	2.0
1983	Mar	50	48.0	24.0	12.0	0
1983	Apr	48	12.5	33.3	6.3	4.2
1983	May	51	13.7	15.7	7.8	29.4
1983	Jun	35	5.7	22.8	2.9	0
1983	Jul	51	3.9	23.5	9.8	0
1983	Aug	4	0	50.0	0	0
1983	Sep	50	0	40.0	0	0
1983	Oct	50	2.0	24.0	2.0	2.0
1984	Mar	40	7.5	2.5	2.5	7.5
1984	May	50	2.0	4.0	56.0	6.0

month to month.

For both ant species dietary diversity varied considerably during the study period. Changes in diet niche breadth facilitate intra- and interspecific comparisons (Fig. 6.6). The niche breadth of *T. rufescens* fluctuated markedly from month to month with no apparent order to the pattern. In contrast, although the niche breadth of *M. denticornis* varied widely during the study period, the pattern of change was less random. For example, niche breadth in *M. denticornis* remained consistently low for six consecutive months, August 1982 to January 1983 inclusive. Thereafter the niche breadth increased and, although it exhibited greater fluctuations than during the previous six month period, it remained relatively high for the remainder of the study period. Niche breadth in both species fluctuated more when seeds did not form a major dietary component.

Messor denticornis collected significantly larger food items than *T. rufescens* for the majority of sample months (Table 6.4) and a combined probability test (Sokal & Rohlf, 1981) revealed that over the entire study period this relationship was significant ($p < 0.001$). During the period June 1982 to January 1983, however, when aerial *Enneapogon* seeds were common dietary components for both species, food particle sizes did not differ between the species except for August 1982 when *M. denticornis* took significantly smaller

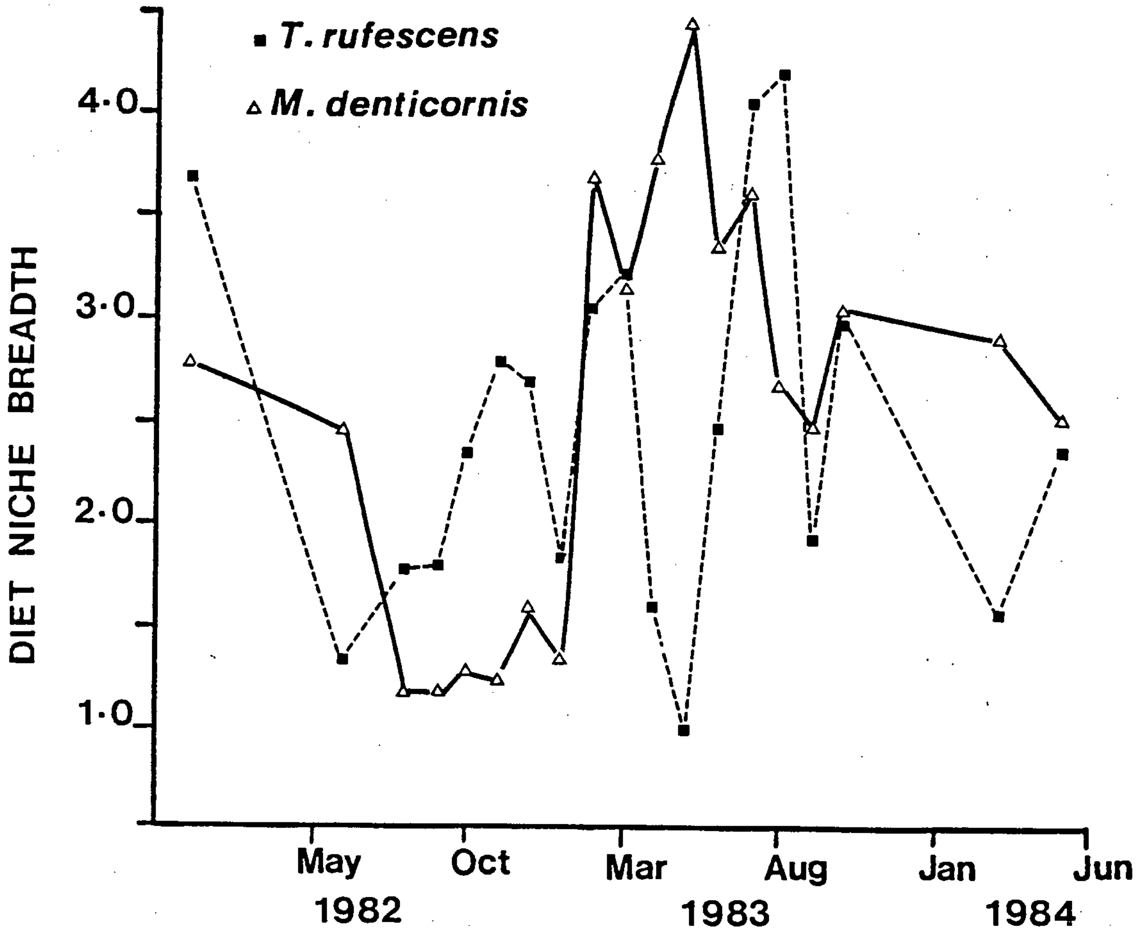

Figure 6.6. Temporal changes in the dietary niche breadth of M. denticornis and T. rufescens.

Table 6.4. Monthly dry masses of food particles for *M. denticornis* and *T. rufescens*. Levels of significance determined by Mann-Whitney U-test.

YEAR	MONTH	*M. DENTICORNIS*			*T. RUFESCENS*			P
		$\bar{X}$	± SE	N	$\bar{X}$	± SE	N	
1982	Jun	0.40	0.03	86	0.33	0.03	57	NS
1982	Aug	0.32	0.02	81	0.36	0.03	129	< 0.001
1982	Sep	0.36	0.05	52	0.31	0.31	48	NS
1982	Oct	0.52	0.14	50	0.50	0.07	50	NS
1982	Nov	1.24	0.48	50	0.35	0.05	48	NS
1982	Dec	1.28	0.55	54	0.41	0.06	49	NS
1983	Jan	1.04	0.32	50	0.42	0.06	54	NS
1983	Feb	1.73	0.38	50	0.42	0.12	50	< 0.001
1983	Mar	2.64	0.67	50	0.53	0.07	50	< 0.02
1983	Apr	3.26	0.51	45	0.37	0.07	46	< 0.001
1983	May	1.92	0.53	46	0.91	0.47	50	< 0.01
1983	Jun	1.96	0.64	33	1.20	0.98	46	NS
1983	Jul	2.59	0.56	44	0.75	0.10	43	< 0.001
1983	Aug	no data			0.81	0.12	27	--
1983	Sep	3.07	0.49	50	1.13	0.11	44	< 0.001
1983	Oct	2.49	0.49	50	0.43	0.06	26	< 0.001
1984	Mar	2.21	0.86	41	0.37	0.05	51	< 0.001

items than *T. rufescens* (Table 6.4). The smallest food item taken was 0.05 mg (both species) whereas the largest item was 35.0 mg (*M. denticornis*). The largest item collected by *T. rufescens* was 24.0 mg.

Adding food to the environment resulted in an increase of forager activity in both species (Table 6.5). There were significantly increased levels of activity in all nests that received additional food relative to activity levels in the same nests 24 h previously (ANOVA, df 1 36, F 10.087, $p < 0.005$) and relative to unmanipulated control nests assessed on the same day (ANOVA, df 1 36, F 25.675, $p < 0.001$). Pretreatment control and experimental nests supported the same levels of activity dependent on species (ANOVA, df 1 36, F 0.388, $p > 0.5$) whereas control groups showed a significant decrease in activity level from Day 1 to Day 2 (ANOVA, df 1 36, F 4.608, $p < 0.05$). Thus the response to food supplementation was probably even more pronounced than that indicated in Table 6.5. *Messor denticornis* nests supported higher levels of activity than *T. rufescens* nests in all treatment groups (ANOVA, df 1 36, F 24.848, $p < 0.001$).

Temporal changes in food abundance are shown in Fig. 6.7. During the study period food abundance increased for the first few months, peaked in November 1982 and thereafter declined rapidly. For 15 consecutive months levels of food abundance were very low finally showing a slight increase in May 1984.

Table 6.5. Means and standard errors of the numbers of ants from control nests (unmanipulated throughout) and experimental nests (food added to environment after activity counts of day 1). N = 10 nests per species per treatment group.

	SPECIES			
	<u>T. rufescens</u>		<u>M. denticornis</u>	
	$\bar{X}$	SE	$\bar{X}$	SE
CONTROL				
Day 1	4.4	0.9	17.1	4.8
Day 2	2.1	0.5	6.4	3.5
EXPERIMENTAL				
Day 1	4.5	0.7	20.6	3.0
Day 2	14.8	2.8	36.5	7.1

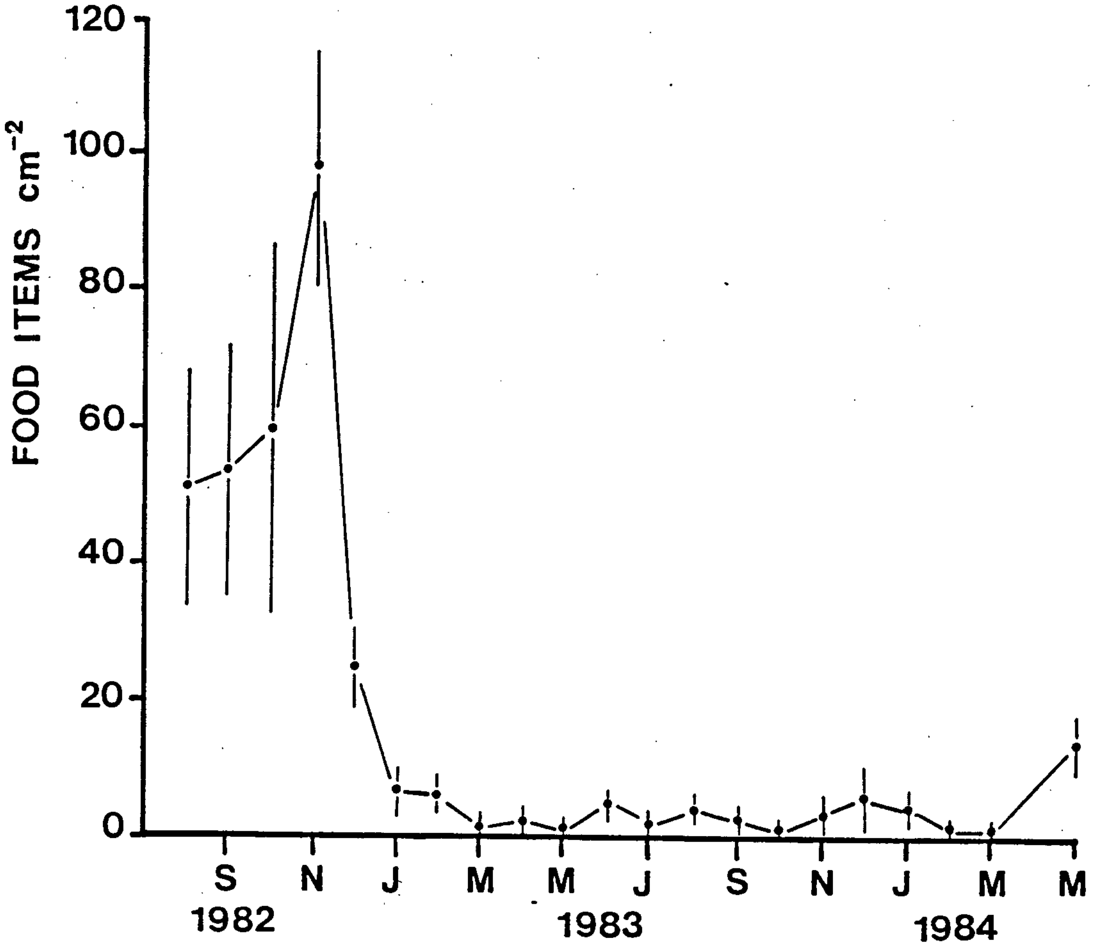

Figure 6.7. Temporal changes in environmental food density, expressed as one standard error (vertical lines) about the mean (dots).

The large standard errors about the means reflect the variability in food particle dispersion. Morisitas indices of dispersion were significantly greater than unity for all months with the exception of May 1983 ($p < 0.05$), indicating that the food items had a clumped dispersion throughout most of the study period. The majority of food items (63 %) were aerial *Enneapogon* seeds.

6.4 DISCUSSION

The two harvester ants exhibited very similar patterns of abundance during the study period suggesting similar responses to the same environmental factors. Food has usually been considered a limiting resource to harvester ant populations (Brown *et al.*, 1979) and in the Namib Desert low food availability was definitely related to low levels of forager abundance. This is supported by the food supplementation experiment (Table 6.5) and the concurrent increase in naturally occurring food (Fig. 6.7) and forager abundance (Fig. 6.1) towards the end of the study. A correlation between food availability and activity has also been documented for harvester ants in North American deserts (Whitford & Ettershank, 1975; Whitford *et al.*, 1980) and in a semi-arid region in Australia (Briese & Macauley, 1980). In the earlier part of the present study, however, forager abundance did not closely track food availability (Figs. 6.1 & 6.7). For example, the peak in ant activity occurred five months after the peak in food availability when environmental food levels were already substantially reduced. This suggests that forager activity was not limited by food availability alone but by food availability in conjunction with some other factor, possibly climatic conditions. Alternatively, it may reflect the lag time between collecting the food resources and converting them into ants. From the forgoing it appears that food may have been superabundant for several months following seed set. Assuming that the foraging success of individuals did not increase with declining food availability, the major portion of food collected by a colony over the duration of the study period would have occurred during the initial period when seed production exceeded the ants capacity to collect and store them.

It seems unlikely that competition for food occurred during the study period as most food was collected when food was superabundant and not limiting. Once the granaries of colonies were replete with seed the pressure to forage would have relaxed. Low levels of activity during the period of food scarcity support this notion. Food brought in during this period would have supplemented the diet and retarded the rate of seed store depletion but may not have been essential for survival. Only after a protracted drought when seed stores are near depletion would a 'bottleneck period' (_sensu_ Wiens, 1977) arise during which competition could be intense. At least for _M. denticornis_, seed stores were not depleted during the study period. *Messor denticornis* colonies occasionally relocate their nests and during such events workers transport food stores to the new site. Such events were observed throughout the study period, and even early in 1984, after over 20 months without effective rain, aerial *Enneapogon* seeds predominated in these food stores. Similar observations of superabundant seed production have been noted for North American harvester ants where activity in one year was considerably reduced relative to the previous year despite high seed production (Whitford, 1978b). The reduced activity was attributed to the ants having nearly full granaries from the previous years foraging activity.

Numerous researchers have shown that harvester ants in some North American deserts partition food resources on the basis of body size (Bernstein, 1979; Brown *et al.*, 1979, Chew & De Vita, 1980; Davidson, 1977a, 1978; Hansen, 1978) and have inferred that species size differences are competitively determined. The evidence for competitively determined size differences within communities is however weak (Simberloff & Boecklen, 1981) and the very similar dietary niches of *M. denticornis* and *T. rufescens* (Tables 6.2 & 6.3, Fig. 6.5), despite the large discrepancy in body size, suggest that in the Namib Desert ant community body size does not have a strong influence on seed size utilization. Similarly, Morton (1982) indicates that the relationship between harvester ant body size and seed size utilization is not sharply defined in an Australian arid zone.

In the Namib Desert differences in body size appear to influence food utilization during periods of scarcity. During these periods T. rufescens on the average took smaller food items than M. denticornis although the mean masses did not differ in proportion to the differences in ant size. For example, M. denticornis collected a reasonably high proportion of the large basal Enneapogon seed clusters. Not only are these food items large, but they are also fairly firmly attached to the rooted grass stubble, and T. rufescens may be at a considerable disadvantage in exploiting them. This may explain the paucity of these dietary items in the smaller species' diet.

Although harvester ants are considered to be food specialists (Brown et al. 1979; Petal, 1978), dietary flexibility, reflecting the opportunistic character of a generalist has been noted for many species. Whitford (1978b) reviews information on the forage of North American harvester ants and indicates that numerous genera, including Veromessor = Messor (synonomy by Bolton, 1982) prey heavily upon termites when they are present on the surface. During eruptions, termites constitute up to 50 % of the forage brought to colonies. Furthermore, Whitford (1978b) indicates that Novomessor and Veromessor regularly take up to 50 % non-seed matter, including stems, leaves, floral parts, faecal matter and exoskeletons. In the Namib Desert, M. denticornis and T. rufescens exhibit similar but more extreme dietary flexibility. Of the two species *T. rufescens* appears to be the least specialized in terms of diet. The apparently random fluctuations in the dietary niche breadth of *T. rufescens* reflects its opportunistic foraging behaviour. In contrast, *M. denticornis* exhibited more stable dietary patterns. *Messor denticornis*, for example managed to collect considerable amounts of seeds long after seeds had become inconsequential in the diet of *T. rufescens*. This suggests a greater efficiency at locating seeds in *M. denticornis*.

The superior seed locating ability of *M. denticornis* relative to *T. rufescens* is probably related to the degree of seed clumping relative to foraging distance and degree of coordination between foragers. Theoretical and empirical studies indicate that trunk-trail foraging is an efficient way of exploiting patchily distributed and relatively stable food sources such as seeds (Holldobler & Lumsden, 1980; Holldobler & Moglich, 1980). The large foraging areas of each *M. denticornis* nest are likely to contain numerous high density seed patches within them. It has been shown that *Veromessor pergandei* and *Pheidole militicida* workers shift the direction of trunk-trails when seed supplies in an area diminish (Holldobler & Moglich, 1980; Rissing & Wheeler, 1976) and the frequent changes in *M. denticornis* foraging directions presumably reflect similar responses to resource abundance. Furthermore, *Pogonomyrmex rugosus* foragers utilize trunk trails to collect seed during the peak in seed production but foraging becomes more diffuse when seed availability declines (Davidson, 1977b). The density of P. rugosus foragers also declines with decreases in seed availability. Similar patterns were exhibited by M. denticornis in the present study. In contrast, the exact location of a T. rufescens colony, which has a much smaller foraging area than M. denticornis, will determine whether it has access to a productive or non-productive area. The most efficient way to exploit a relatively evenly distributed food resource would be for a colony to forage diffusely. The more or less diffuse foraging that T. rufescens exhibits (Marsh, 1984) may therefore indicate that food patchiness is on a scale greater than the average T. rufescens foraging area.

The absence or rarity of one or both species from certain regions within the 16 ha plot may reflect regional differences in colonization and extinction rates. There were, however, no apparent edaphic differences within the plot which suggests that the availability of nest sites was not likely to be a factor influencing colonization. Towards the end of the study when the patchiness in ant distribution had become apparent, the absence of vegetation and low levels of seed in the environment unfortunately precluded investigating the possibility that large scale food patchiness may have enhanced extinction rates in food-scarce regions. The patchiness in ant distribution therefore remains unexplained.

Diel activity patterns (Fig. 6.2) were also enigmatic. In another study of activity, based on counts of ants leaving and returning to nests, these two species exhibited highly dissimilar activity patterns (see section 5.3.2). In that study there was a 19 % similarity in activity in both summer and winter 1982, whereas the present study revealed a 71 % similarity in activity time. Calculations of temporal niche overlap indices (Pianka, 1973) between the two different studies reveal that the activity patterns of *M. denticornis* remained more or less constant (O = 0.91) whereas *T. rufescens* changed considerably (O = 0.58). Thus the high overlap between species in the early part of 1983 was a consequence of *T. rufescens* shifting its activity period from predominantly diurnal to predominantly nocturnal. This constitutes another example of the greater flexibility in foraging behaviour that *T. rufescens* exhibits relative to *M. denticornis*.

The reason for the activity shift is however not apparent. Encounters between the two species frequently result in interference interactions (see section 5.3.4) and a reduction of activity overlap during periods when encounters are likely, i.e. when forager density is high, would be expected if interference interactions have a significant negative effect on one or both species. It is unlikely, however, that the density of foragers in December 1982 would have been greater than that in early 1983. If anything the progressive increase in forager density that occurred in successive months in early 1983 suggests that December 1982 forager density would have been less. Alternatively the niche shift may bear no relationship to interactions with *M. denticornis*. Diet may explain the niche shift in that it coincided approximately with the decline in importance of seeds in the diet of *T. rufescens*. However, in view of the large fluctuations in diet diversity it was not possible to detect any correlation between the shift to nocturnalism and the utilization of a prey item, such as termites, that may have been more available at night.

6.5 CONCLUSIONS

The data collected on the two dominant harvester ant species reveal patterns which are not readilly reconciled with competition theory. Despite large differences in body size between ant species there was a high degree of overlap in diet, particularly during the most important foraging period when storable seeds were available. No spatial segregation of foraging areas was apparent at a resolution of 25 m x 25 m. When food was scarce both species responded opportunistically to transient resources, frequently taking identical prey types such as Hodotermes. Both species were nocturnal.

Despite the apparent absence of competitively determined patterns, the occurrence of competition between these two species cannot be discounted. For example, a more detailed investigation of space utilization may reveal predominantly non-overlapping foraging areas which may be a result of interspecific competition. At present nest densities there are large interstices between *T. rufescens* foraging areas and it is conceivable that *M. denticornis* predominantly uses these interstitial areas for foraging. Furthermore, an overdispersion of nests is indicative of intraspecific competition (Levings & Traniello, 1982) and the spatial patterns discussed therefore indicate intraspecific competition in *M. denticornis* but not in *T. rufescens*. Finally, even if competition did not occur during the study period it remains conceivable that, during severe droughts when seed stores become depleted, 'bottleneck periods' could occur and interspecific competition could be intense. The detection of such events would however require a longer term study.

The existence of patterns in North American harvester ant communities that are consistent with competition theory (Brown *et al.*, 1979) and the lack of clearly defined competitive patterns in the Namib Desert study may reflect the greater dependability and diversity of the seed resource in the North American deserts. Diversity in seed type and size should facilitate partitioning according to body size. The annual production of seeds should enable populations to more closely approach an equilibrium situation where seeds could become limiting and regular, perhaps frequent, competitive interactions could occur. In contrast, in the Namib Desert the lower seed diversity, with essentially only one staple seed, precludes partitioning on the basis of body size between those species which are large enough to handle them with reasonable efficiency. The unpredictable production of seeds prevents ant populations from realizing the carrying capacity of the environment and competitive interactions are therefore not a continuous phenomenon, only occurring during widely spaced and unpredictable 'bottleneck periods' or not at all.

SECTION SEVEN

THERMAL RESPONSES AND TEMPERATURE TOLERANCE IN A DIURNAL DESERT ANT, OCYMYRMEX BARBIGER

7.1 INTRODUCTION

Deserts characteristically receive large radiant energy inputs during the day and, due primarily to edaphic factors, the desert surface can become very hot with an attendant high output of long-wave radiation (Oke, 1978). Small invertebrates, living close to or on the surface in such environments, would be exposed to high thermal loads and consequently tend to retreat from the surface during periods of the day when thermal stress is greatest (e.g. Crawford, 1981; Louw & Seely, 1982). Typically, desert ants have subterranean nests which form ideal refuges from environmental extremes. Some ant species, however, voluntarily forage during the hottest times of the day. For example, in the Sahara desert, Cataglyphis bicolor has been observed foraging on surfaces exceeding 70°C (R. Wehner, pers. comm.). In the Namib desert certain Ocymyrmex species forage at similar surface temperatures.

Owing to their small size it is not posible, using conventional methods, to obtain direct measurements of ant body temperature under natural conditions. However, operative environmental temperature (Bakken, 1976, 1980), an integrated measure of radiant and convective thermal exchange in an organism, gives an indication of the equilibrium temperature that an organism would attain if it lacked metabolic heat production and evaporative heat loss. For most small, non-flying insects this is approximately equal to body temperature (Casey, 1981). Thus with a knowledge of heat flux rates, of operative environmental temperatures in pertinent positions in the habitat and of the use of the habitat by foraging ants it should be possible to arrive at a reasonable approximation of body temperatures under a variety of conditions.

This section describes how O. barbiger foragers exploit the micro-climatic mosaic in their habitat and thus modify their body temperature. These predicted field body temperatures are compared to laboratory determined thermal limits.

7.2 PROCEDURE

The ants were studied in the dry Kuiseb river bed (Fig. 7.1) near the Namib Research Institute at Gobabeb (23°35'S; 15° 03'E). In this habitat there are numerous large patches of sand, which are barren save for the occasional clump of grass, Eragrostis spinosa. Foraging ants regularly spend their entire period of surface activity in these patches. Scattered on the sand are numerous small objects such as goat faecel pellets,

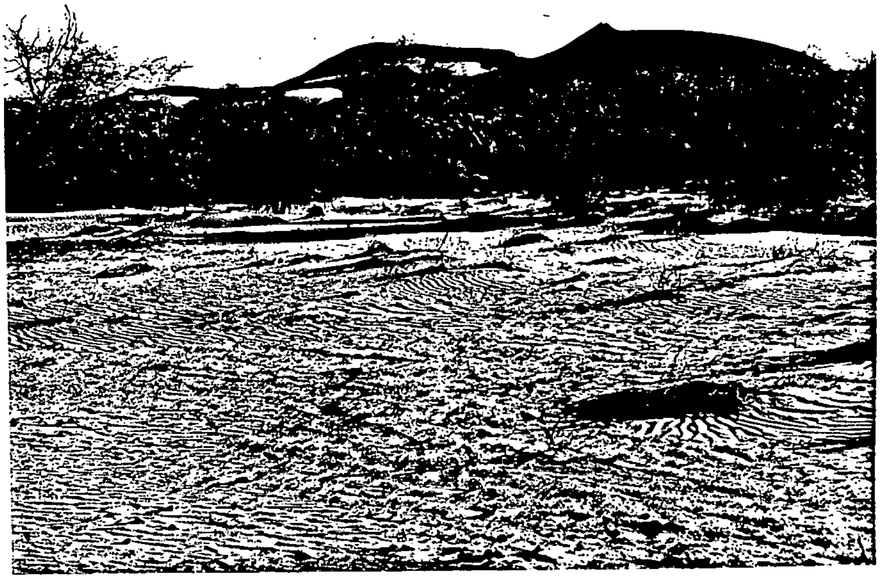

Figure 7.1. The Kuiseb River bed study site. The foreground is typical of the habitat in which Ocymyrmex barbiger workers forage.

dried mud clumps, and broken twigs. The sand patches receive direct insolation throughout most of the day.

Ocymyrmex barbiger workers are monomorphic and small with a mean live mass of 4.1 ± 1.2 mg (SD) per worker (N = 30). Relative to their body size, their legs are long and they usually hold their head, thorax and gaster approximately 4 mm above the substrate.

7.2.1 Field observations

Ocymyrmex barbiger is a diurnal forager (see section 5.3.2). Marked nests were observed for 10 min every 30 min from sunrise to sunset and the number of ants returning from foraging excursions was counted. Prior to each observation period the following measurements were taken: Wind strength at 4 mm elevation, using a hot-wire anemometer; sand surface temperature (T_s) and operative environmental temperature (T_e), at various elevations up to 1 m, using copper-constantan thermocouples and a digital recorder (Bailey Instruments, Model BAT-12). T_e was sensed with a fine copper-constantan thermocouple (40 guage) inserted into the thorax of an O. barbiger exoskeleton. T_s and T_e at an elevation of 4 mm were also recorded in the shade. The effect of air movement on T_e was investigated by monitoring the temperature of an ant exoskeleton at 4 mm elevation every 5 s for 10 min during which a light but variable breeze prevailed. In between temperature recordings, wind speed was measured using a hot-wire anemometer held at the same height.

Ocymyrmex barbiger workers are conspicuous against the pale brown river sand and were easy to follow and observe from a distance of 2 - 4 m. At this distance the ants showed no signs of being aware of the observer. It was possible therefore to accompany them on their foraging excursions and record their behaviour. Every occasion on which the ants paused in the shade, or climbed and perched on objects above the sand surface, and the amount of time spent in each of these micro-habitats and on the insolated sand surface, were recorded with the aid of a digital stop watch and a hand-held cassette recorder. At the end of each foraging excursion, T_s, and T_e at 4 mm elevation, were measured.

7.2.2 Laboratory observations

All experiments were run at room vapour pressure, which ranged from 1.10 - 0.95 kPa. To determine the Critical Thermal Maximum (CTM) of O. barbiger workers, individual ants were placed in 100 ml Erlenmeyer flasks, containing a 3 mm layer of river sand, and the temperature in the flask was progressively raised $1^{\circ}C\ min^{-1}$ by immersing it in a water bath above a heating element. Flask temperature was sensed 4 mm above the sand layer with a copper-constantan thermocouple linked to a digital thermometer. The temperature at which each ant began to have muscle spasms and/or indicated signs of paralysis was considered to be the CTM. A total of 76 individuals, collected from five colonies, was tested.

The relationship between temperature tolerance and exposure time was investigated by placing four ants in constant temperature environments at 49.5, 51.4, 53.0, 56.5 and 62.9°C, and measuring the time each ant took to exhibit signs of muscle spasm and/or paralysis.

The survival value of brief thermal respites was investigated by imposing the following three experimental treatments: ants were exposed to a thermal environment alternating between 25 s periods at 51 ± 1°C (SD) and 5 s at 30 ± 1°C; a second group of ants was exposed continuously to 30 ± 1°C; a third group of ants was exposed continuously to 51 + 1°C. Ants were exposed to the above treatments for 30 min, and at the end of the treatment period they were maintained at 30 ± 1°C, and their behaviour monitored for two hours. The ants were considered to have tolerated the treatment if they were able to walk in a coordinated manner, with none of the jerky movements associated with heat stress. To perform these experiments ants were suspended from a wooden spindle by means of thin, insulated copper wire tied loosely around their petioles. The spindle was moved by hand to flasks maintained at the different temperatures. Ten ants were used in each treatment.

Heat flux rates were determined by measuring the rate of cooling of an ant exoskeleton in still dry air and under various regimes of constant air movement. Thoracic temperatures were recorded using a fine copper-constantan thermocouple (40 guage) and digital recorder. The exoskeleton was heated to approximately 80°C, the heat source (a hand-held hair dryer) was then rapidly removed and the rate of cooling monitored with a video camera filming a stop watch and digital readout of the thermocouple thermometer at 24 frames s^{-1}. Air flow was created with a small electric fan, which ran continuously throughout the experiments. To allow sufficient time for constant air flow conditions to be established, cooling rates were only recorded when exoskeleton temperature dropped below 68 °C.

7.3 RESULTS

Below a T_s of 51 °C, foraging ants spent 93 % of their extranidal time on the sand surface. At higher T_s, foragers made frequent pauses after having climbed up objects such as grass stalks, goat faecal pellets and dried mud clumps, or in shaded areas, often in the shadows cast by grass stalks (Fig. 7.2). Typically, the ants attained elevations of 10 - 20 mm, although occasionally they climbed up to 100 mm above the desert floor. Pause duration in these localities was usually short 5.4 ± 8.6 s ($\bar{X} \pm$ SD), although at high thermal loads ants sometimes paused for up to 85 s before proceeding on their journey. Short pauses occurred at all $T_s > \sim 48$°C but pauses > 10 s primarily occurred at high thermal loads, $T_s > 58$°C (Fig. 7.3). All of

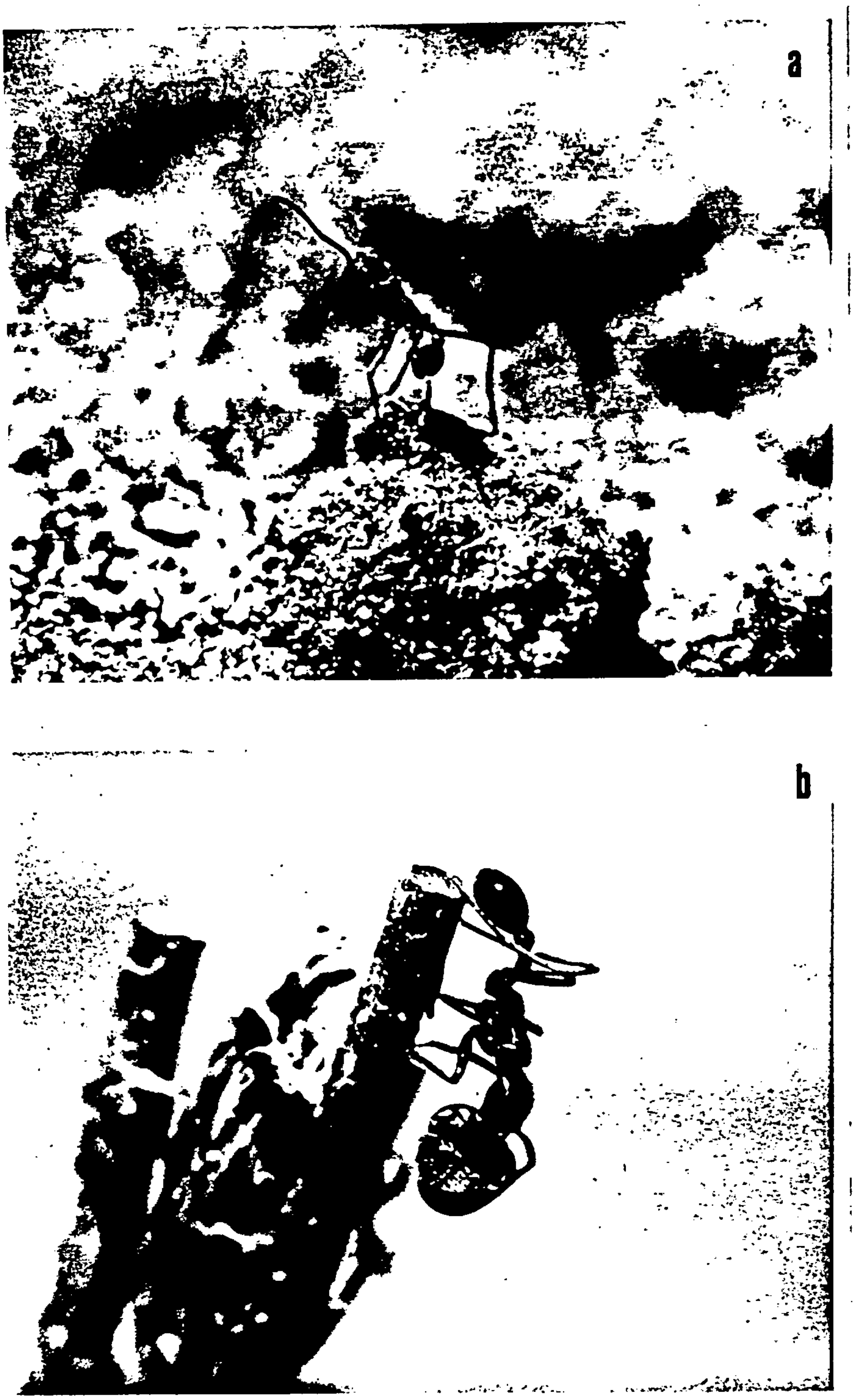

Figure 7.2. (a) An O. barbiger forager pausing on a clump of sand while searching for food. (b) A successful forager, with the head of a beetle in its mandibles, pausing on a grass stalk during its return to the nest. Surface temperature was greater than 60 °C on both occasions.

the sites where ants paused served as thermal refuges for the ants in that they were cooler than the surrounding sand surface and air layer 4 mm above the sand (ant height). The frequency of thermal respite behaviour increased with $T_s > \sim 51$ °C (Fig. 7.4). During particularly hot conditions ($T_s > 60$°C), foraging ants spent over 50 % of their extranidal time in thermal refuges.

T_e varied considerably in that part of the habitat utilized by the ants. Observations on 12 colonies on separate days, spanning a range of climatic conditions, showed that the majority of surface activity occurred between T_s 40 - 50°C. Ants were nevertheless active on the surface between T_s 27 - 67 °C, and over this range T_e at ant height varied from 25 - 55 °C in direct sunlight and from 20 - 43 °C in the shade (Fig. 7.5). The discrepancy between T_e in sun and shade increased with T_s. The variation in T_e at any given T_s can probably be attributed to differences in air movement. For example, at a constant T_s of 56 °C, T_e at 4 mm elevation fluctuated rapidly by as much as 3.2 °C when air movement oscillated between 0 and 1.7 m s^{-1} (Fig. 7.6).

Temperature lapse profiles were steep above the sand and lapse profile steepness increased with T_s (Fig. 7.7). T_e 10 - 20 mm above the sand surface were up to 6.6 °C lower than those at an elevation of 4 mm (ant height).

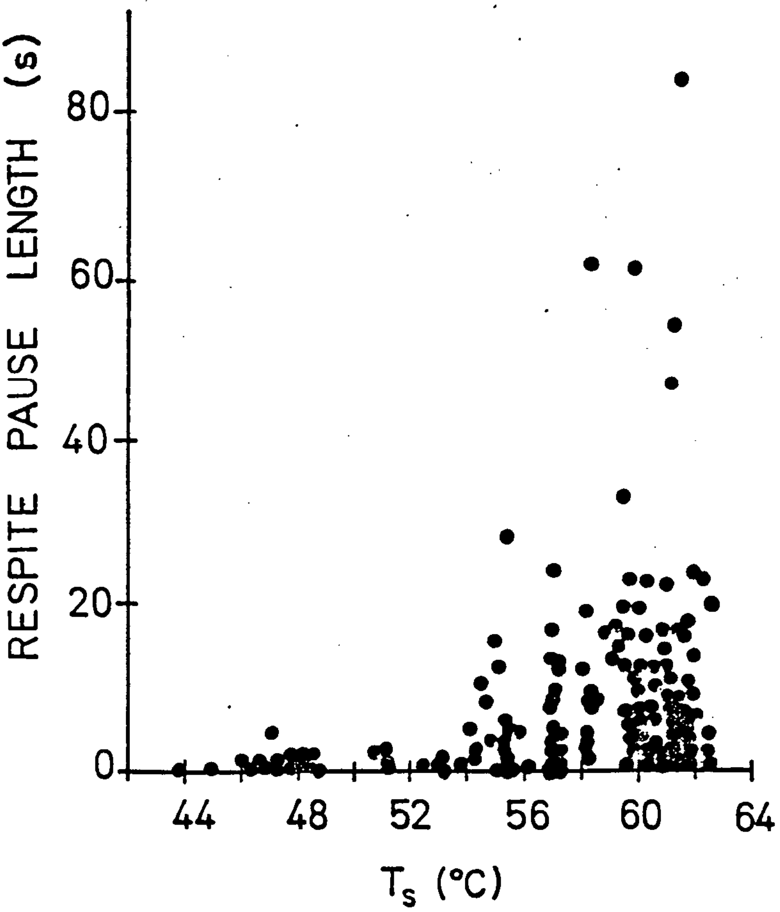

Figure 7.3. Relationship between the length of time spent in a thermal refuge and sand surface temperature. Each dot represents one pause by one individual.

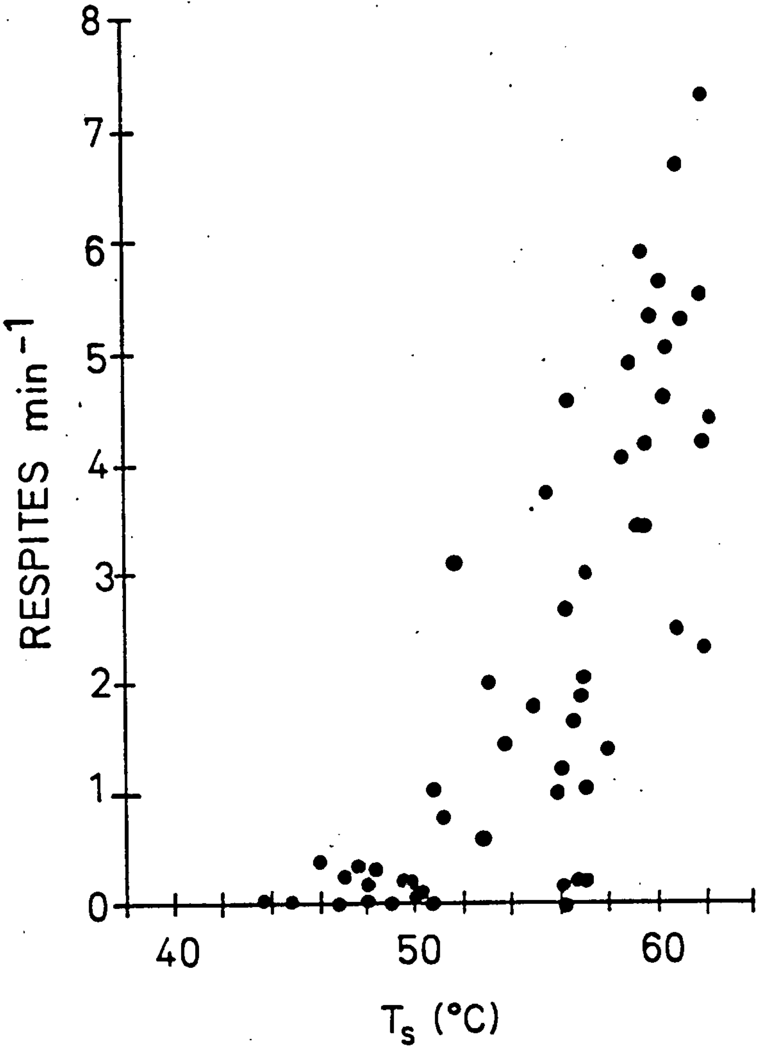

Figure 7.4. Relationship between sand surface temperature and the frequency of thermal respite behaviour. Each point represents data obtained from one individual during one foraging excursion.

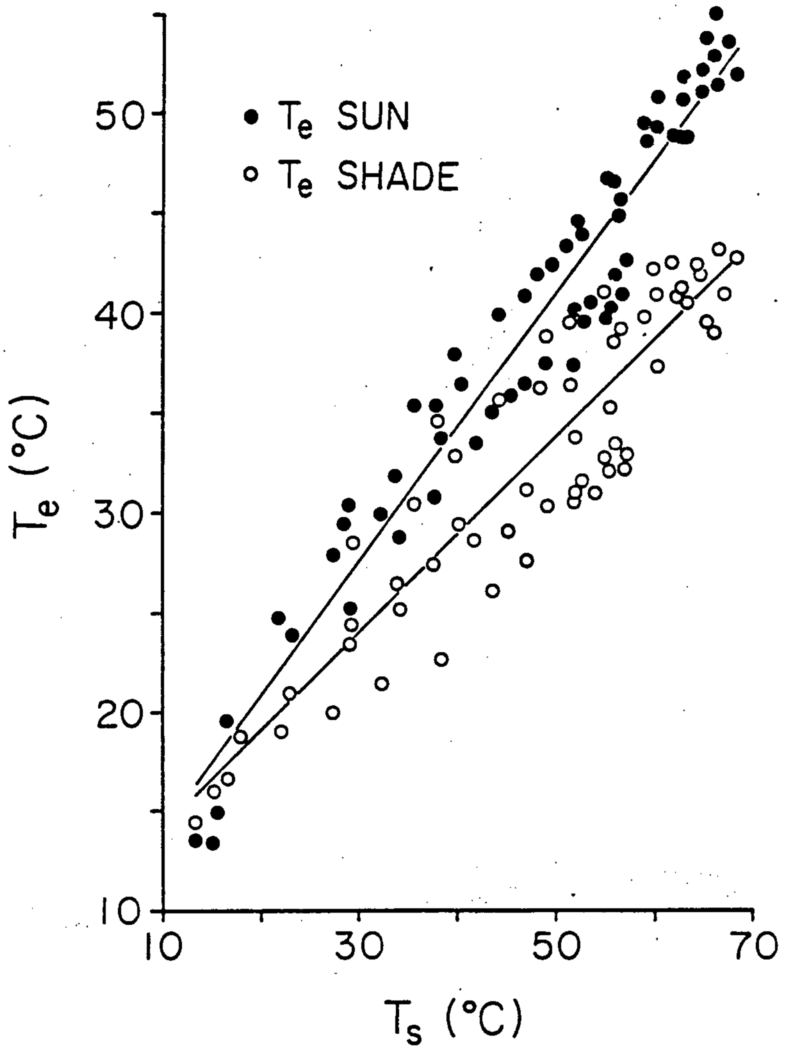

Figure 7.5. Relationship between insolated sand surface temperature and operative environmental temperature at 4 mm elevation in direct sunlight [$y = 7.18 + 0.68x$ ($r^2 = 0.95$)] and shade [$y = 8.89 + 0.49x$ ($r^2 = 0.87$)].

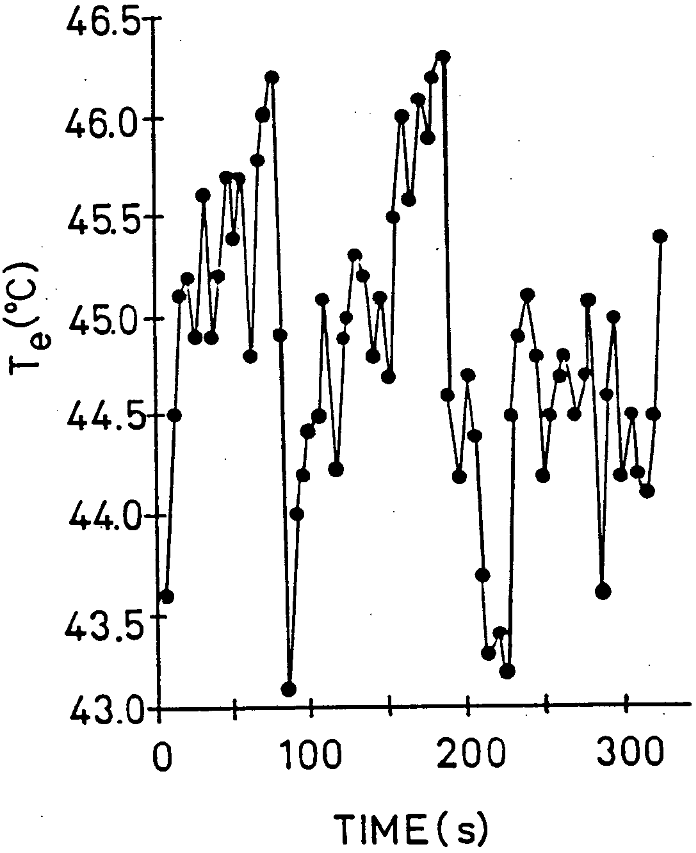

Figure 7.6. Changes in operative environmental temperature at 4 mm elevation in response to fluctuating air movement (0 - 1.7 m s^{-1}).

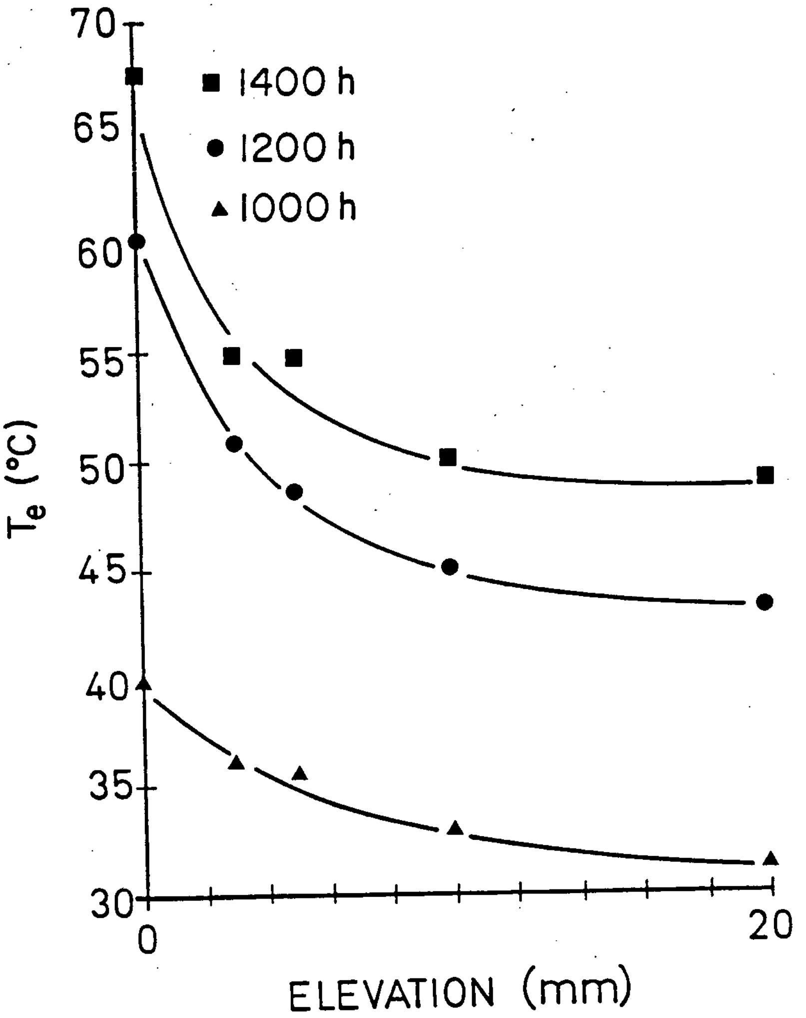

Figure 7.7. Operative environmental temperature lapse profiles at different times of the day on 31 March 1983.

The foraging activity of an ant colony on a hot day (maximum air temperature in the shade at 1 m elevation = 39 °C, 31 March 1983) and relevant micro-climatic data are presented together (Fig. 7.8). Ant activity was bimodal, with a complete cessation of activity during the hottest period of the day. T_e in direct sunlight, at ant height, were similar when morning activity ceased and afternoon activity commenced (50 - 52 °C). Corresponding T_s , however, were 60.0 - 63.0 °C and 66.6 - 67.8 °C repectively for the morning activity cessation and afternoon activity commencement times. In the morning most activity occurred at a T_e of 44 °C, whereas the corresponding temperature for the afternoon peak in activity was 49 °C. Wind speed increased progressively throughout most of the day, peaking coincidentally with the afternoon peak in forager activity. Thermal respite behaviour occurred during 79 % of the foraging period. The shaded band, between T_e at ant height in the shade and direct sunlight, represents the range of T_e available to foragers on this particular day. Refuge temperatures were 7 - 15 °C lower than those which an ant would experience on the insolated sand surface.

The CTM for O. barbiger workers was 51.5 ± 0.7 °C ($\bar{X}$ ± SD, range 49.5 - 52.7 °C, N = 76). The length of time required to produce a state of partial paralysis decreased with increases in temperature (Fig. 7.9). At 62.9 °C, the extreme investigated, ant movement remained coordinated for 11.5 s only. In the

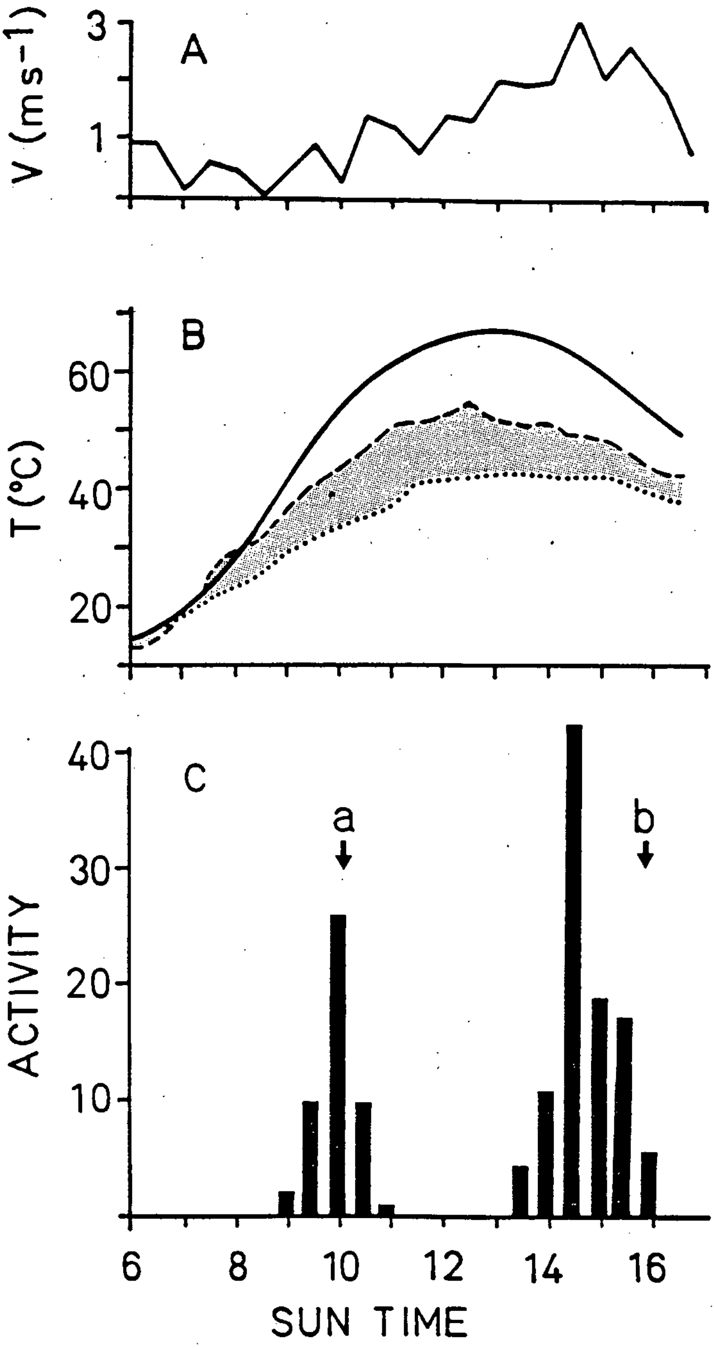

Figure 7.8. Wind speed (A); temperature (B), surface temperature (————), operative environmental temperature in sun (-------), operative environmental temperature in shade (··············) and foraging activity of an ant colony (C) on 31 March 1983. Histogram height represents the number of foraging ants returning to the nest in 10 min. Thermal respite behaviour occurred between a and b.

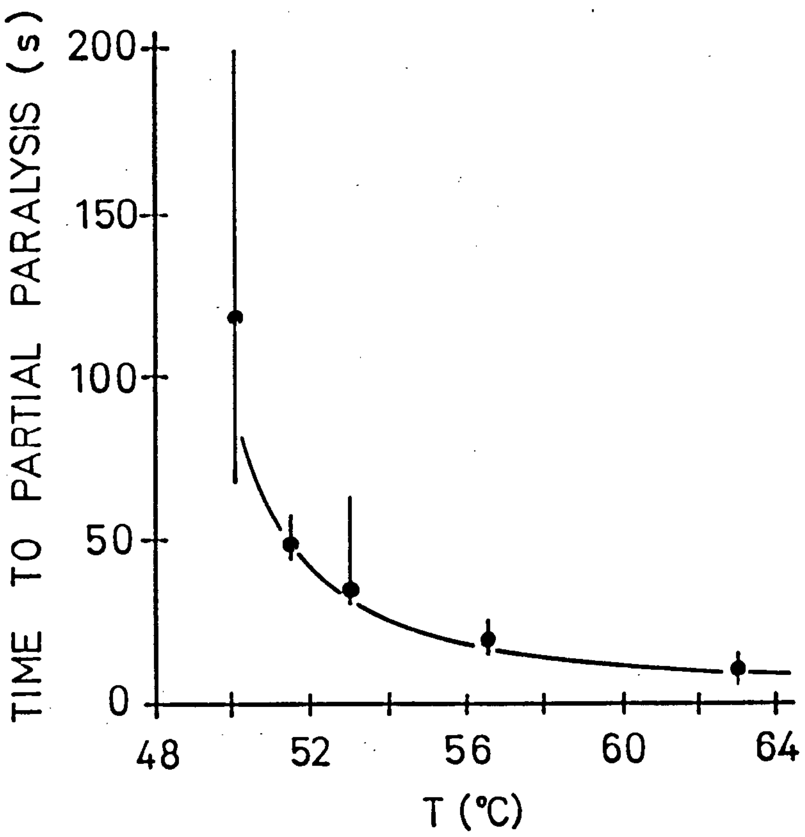

Figure 7.9. Relationship between temperature and time to produce a state of partial paralysis. Vertical lines represent the range and dots the mean (n = 4 for each temperature).

laboratory, all ants survived a continuous 30 min exposure at 30 °C, no ants survived a continuous 30 min exposure at 51 °C, whereas, 80% of those ants which experienced periodic but brief thermal respites (5 s in each 30 s) survived a 30 min exposure to 51 °C.

Cooling rates for O. barbiger, relative to air movement conditions commonly encountered in their natural habitat, are given in Fig. 7.10. As expected the rate of heat exchange was very sensitive to air movement. The cooling rate at a wind speed of 4 m s^{-1} was five fold that in still air.

7.4 DISCUSSION

7.4.1 Efficacy of thermal respiting

Small insects are very efficient heat exchangers (Gates, 1980) and thus it is not possible for them to maintain a body temperature independent of ambient temperature. Willmer & Unwin (1981) however have suggested that the thermal lability of small insects may be an advantage in hot environments. Although small insects heat up more rapidly than large insects, they also cool down more rapidly in any available thermal refuge. As expected the rate of heat exchange in O. barbiger is dependent on both the temperature differential and air speed. Depending on conditions, even brief pauses in thermal refuges can result in a substantial lowering of body temperature. The following

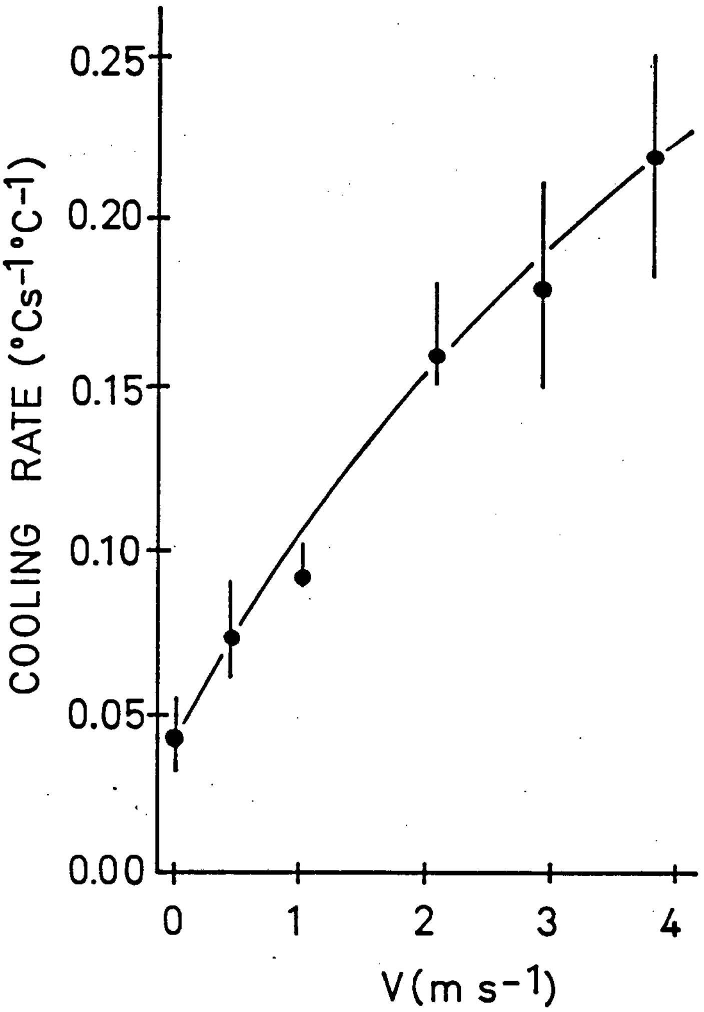

Figure 7.10. Relationship between cooling rate (°C s^{-1} °C^{-1}) of an O. barbiger exoskeleton and air movement (m s^{-1}). Vertical lines represent the range and dots the mean (n = 4 for each wind regime).

examples from Fig. 7.8 illustrate how effective, in lowering body temperature, thermal respiting can be: An ant running on the sand surface at a T_s of 66.7 °C would have had a body temperature of about 51.0 °C. In view of the prevailing wind speed (2 m s^{-1}), and temperature differential (8.5 °C) a pause of 7 s in the shade would have resulted in a 6 °C depression in body temperature. During the afternoon peak in activity, when T_s was 62 °C, an ant running on the insolated surface would have had a body temperature of about 49 °C, but with the prevailing wind of 3 m s^{-1} and the 6.4 °C temperature differential a pause of 7 s in the shade would have reduced the body temperature of an ant to 44 °C. In contrast, during the morning peak in activity, the rate of heat exchange would have been less in view of low wind speed (0.2 m s^{-1}). In this situation, with a 9.8 °C differential between T_e in the sun and shade, it would require a pause of 10 s in the shade to lower body temperature by 4 °C and equilibration to the refuge temperature of 34 °C would have taken in excess of 40 s.

These differences in the efficiency of thermal respiting behaviour may explain why activity peaked at a lower T_s and T_e in the morning relative to the afternoon. The morning peak in activity occurring during circumstances when ants could forage on the surface without needing to use thermal refuges; probably less than 1 % of a forager's extranidal time would have been spent in thermal refuges at that surface temperature (Figs. 7.3 & 7.4). In the afternoon, the ants could afford to forage at higher temperatures because of the increase in air movement and therefore heat flux; at the peak in activity 55 % of a forager's extranidal time would have been spent in thermal refuges (Figs. 7.3 & 7.4). Efficient heat exchange, however, is a two edged sword, and ants foraging during the afternoon period would have heated up more rapidly once they left a thermal refuge to forage. In contrast, equilibration to T_e on the insolated sand would have been slower during the morning period.

A factor which complicates estimates of body temperature is heat exchange from forced convection during locomotion. Ocymyrmex barbiger foragers can run at speeds of 23 m min^{-1} (see section 8.3), equivalent to a relative air movement of 0.38 m s^{-1}. In relatively still air, such forced convection could increase the rate of equilibration to ambient conditions substantially. Ants may also increase the rate of heat loss in thermal refuges by vigorously moving some of their limbs, thereby disturbing the boundary layer of air in contact with their bodies. Frequently, under high thermal loads, ants seek places of higher elevation, and while maintaining a grip on the refuge object with some limbs, rapidly flail their other limbs about in the air.

7.4.2 Temperature tolerance

In addition to O. barbiger, a number of other diurnal desert ants are known to voluntarily tolerate high body temperatures relative to their physiological limitations (Table 7.1). However, most of these species only occasionally experience high body temperatures, whereas, *O. barbiger*, because of its dependence on heat stressed arthropod prey items (see section 8.3) is regularly exposed to high thermal loads.

Although CTMs have not been determined for the *Cataglyphis* species of the Sahara desert, which like *O. barbiger* utilize heat-stressed arthropod prey (R. Wehner, pers. comm.), they appear to have considerably higher physiological tolerances to heat than *O. barbiger*, and any other ant species tested. For example, five *Cataglyphis* species take from 10 - 25 min to enter heat coma when exposed to an environment of 55 °C (Delye, 1967), whereas, under similar conditions, *O. barbiger* workers entered a heat coma after 25 s. Similarly, at 50 °C the *Cataglyphis* species take from 45 - 55 min to enter heat coma (Delye, 1967) as opposed to 70 s in the case of *O. barbiger*. Even allowing for their relatively large size and hence higher thermal inertia, the *Cataglyphis* species exhibit a remarkable physiological tolerance to high temperatures. However, the maximum recorded T_s tolerated by one of these species, *C. bicolor*, is just over 70 °C (R. Wehner pers. comm.), which is not very much greater than the 67 °C tolerated by *O. barbiger*. Furthermore, because of its greater height, *C. bicolor* foragers probably experience an ambient temperature no greater, and possibly lower, than *O. barbiger* experiences

Table 7.1. Critical Thermal Maxima (CTM), maximum surface temperature (T_s) tolerated and the amount (%) that surface temperature exceeds the CTM of some diurnal desert ants. The lower two species are from the Namib Desert, while all other species are from the Chihuahuan Desert.

SPECIES	T_s (°C)	CTM (°C)	DIFFERENCE (%)
Trachyrmyrmex s. neomexicanus *	49	36.7	33.5
Pogonomyrmex desertorum '	50	53.3	-6.0
Formica peripilosa *	55	45.2	21.7
Pogonomyrmex rugosus '	55	53.8	2.2
Myrmecocystus romainei +	60	46.1	30.2
Myrmecocystus depilis +	60	47.4	26.6
Myrmecocystus mimicus +	60	48.4	24.0
Pogonomyrmex californicus '	~60	52.9	13.4
Camponotus detritus ©	63	53.8	17.2
Ocymyrmex barbiger	67	51.4	30.4

* Schumacher & Whitford 1974; ' Whitford & Ettershank 1975; + Kay & Whitford 1978; © Curtis 1983.

while running over the sand at maximum T_s.

7.4.3 Importance of thermal respiting

In addition to *O. barbiger*, thermal respiting behaviour has been reported for certain Chihuahuan desert ants (Kay & Whitford, 1978; Whitford & Ettershank, 1975) and it was suggested that such behaviour facilitated survival during thermally stressful conditions. The present study on *O. barbiger* confirms the notion that thermal respiting facilitates survival, and foraging, under high thermal loads. If prevented from using thermal refuges *O. barbiger* workers soon become disorientated, incapable of coordinated locomotion and finally die. For example, an ant that was deprived of a thermal refuge at a T_s of 62 °C became paralysed within 60 s.

The adaptive value of voluntarily tolerating high thermal loads is that the time available for foraging is substantially increased. *Ocymyrmex barbiger* are arthropod scavengers and there is reasonable evidence that the availability of prey increases on hot days (see section 8.3). Similarly, Whitford *et al.* (1980) have demonstrated that the Chihuahuan desert ant, *Novomessor cockerelli*, will extend its foraging time and increase foraging intensity during physiologically stressful conditions if the amount of proteinaceous food is artificially increased. Thus, it appears that there are situations in nature in which it is advantageous to risk near-lethal temperatures in order to maximize foraging success.

For a number of reasons, foragers of social insect species may be able to approach more closely their upper thermal limits than other insects before being penalized with reduced fitness. The sterile workers contribute indirectly to producing the next generation (Wilson, 1971). The death, or incapacitation, of a forager may, therefore, reduce, but not prevent, a colony's reproductive output. In insects reproduction is affected adversely by temperature extremes more readily than most other physiological functions (Bursell, 1964). Foraging is typically the task of old workers relatively close to death (Wilson, 1971; Oster & Wilson, 1978; Porter & Jorgensen, 1981; Wehner et al., 1983) and the loss, or incapacitation, of a worker, that has progressed through various other worker roles, is less detrimental to colonial ergonomic efficiency than that of a younger worker.

SECTION EIGHT

MICRO-CLIMATIC FACTORS INFLUENCING FORAGING PATTERNS AND SUCCESS OF THE THERMOPHILIC DESERT ANT, *OCYMYRMEX BARBIGER*

8.1 INTRODUCTION

Schoener (1971) has suggested that animals should forage in such a manner that their net rate of food intake is maximized. This suggestion is both intuitively sensible and consistent with the theory of natural selection. It is, however, surprising that organisms should subject themselves to near-lethal temperatures in order to maximize their intake of food (Whitford *et al.*, 1980). Nevertheless, there are situations where animals tolerate high thermal loads in their quest for food. For example, Dreisig (1980) has shown that the optimal foraging temperature of predatory tiger beetles, *Cicindela hybrida*, is close to their upper tolerance limit. This is a consequence of prey availability being greatest at such temperatures. In the Chihuahuan desert, the ant *Novomessor cockerelli* will forage under near-lethal thermal loads if the amount of proteinaceous food is increased artificially (Whitford *et al.*, 1980).

In the Namib desert, workers of the ant *Ocymyrmex barbiger* regularly forage on barren ground until surface temperature approaches 67 °C. During these foraging excursions the ants are exposed to near-lethal thermal loads, where failure to locate thermal refuges at frequent intervals can be fatal (see section 7.4.3). The present section is concerned with the adaptive value of occupying this unusual thermal niche. To examine this problem, the diet and foraging behaviour of *O. barbiger* have been studied in relation to environmental conditions.

8.2 PROCEDURE

The foraging ecology of *O. barbiger* was studied in the dry Kuiseb river bed, near the Namib Research Institute at Gobabeb (23°35'S; 15°03'E). The river bed is sandy and supports numerous *Acacia* spp. trees. Between the trees there are large patches of barren sand which receive direct insolation throughout most of the day. Foraging ants regularly spend their entire period of surface activity in these patches.

The ants live in small colonies in subterranean nests which are situated typically at the base of some living or dead vegetation, particularly grass clumps (*Eragrostis spinosa*), or in dry mud beds. Four nests that were excavated contained from 160 to 240 individuals. *Ocymyrmex barbiger* workers are monomorphic and have a live mass of 4.1 ± 1.2 mg ($\bar{X} \pm$ SD, N = 30). Nests were located by following ants from a grid of bait. The distance from each nest to its nearest neighbour was measured.

Prey items were removed from ants as they approached their nest, and placed individually into sealed vials. The items were identified under a dissecting microscope, weighed, and then dried at 60 °C for 24 h to determine moisture content. A minimum of 20 food items was collected every day, for six consecutive days, in October 1983. During this period climatic conditions varied considerably so that food collected during cool-moist days could be compared with that collected during hot-dry days. Food items were also collected in January and February 1982. During each collecting period, food was taken from ants as they returned to each of three nests.

Nests were observed for 10 min every 30 min from sunrise to sunset, and the number of ants that returned from foraging excursions was recorded. The total number of foraging excursions per day was computed by interpolation. Prior to each observation period, the following climatic data were noted: wet and dry bulb temperature at 1 m elevation using a sling psychrometer, and sand surface temperature using a copper-constantan thermocouple and digital recorder (Bailey Instruments, Model BAT-12). The wet and dry bulb temperatures were used to calculate vapour pressure deficits, a measure of the drying power of the air. By interpolation, vapour pressure deficit was totalized between 10h00 and 17h00 (the period when most ant activity occurred) and this value was considered to be an index of the physiological stressfulness of that day.

<u>Ocymyrmex</u> <u>barbiger</u> workers were easy to follow and observe,

and showed no signs of being disturbed from a distance of 2 - 4 m. Individual foragers were followed for entire foraging excursions and the following data collected: the time that individual foragers were active on the surface relative to the total time the ant was out of the nest, the radius from the nest to the most distant point that each ant reached and the distance from the nest to the position where an item of food was located. Sand surface temperature was measured before and after each foraging excursion.

The speed of locomotion was determined for a range of sand surface temperatures by measuring the time ants took to move 1 m. To facilitate these observations, ants were lured to bait and only those ants which ran without hesitation toward the bait were considered.

8.3 RESULTS

Ocymyrmex barbiger is principally an arthropod scavenger (Table 8.1). Of 242 items of food 95 % were insects, 2.4 % spiders and the remaining 2.6 % plant matter, specifically fruits. With the exception of two termites, all prey items were dead on arrival at the nest and many were fairly desiccated. The mean wet mass of prey items was 2.4 mg (range 0.12 - 24.7 mg) and the mean moisture content per item of forage was 19.1 %. The composition of the diet was similar during spring (October) and summer (January and February), the most notable difference

Table 8.1. Taxonomic composition of the diet of *O. barbiger*. The data are expressed as percentages of the total number of dietary items collected (n = 107 for the January/February sample and n = 135 for the October sample).

Food category	January/February (%)	October (%)
Lepidopteran larvae	20.6	27.4
Hymenoptera	34.6	14.8
Coleoptera	1.9	14.8
Hemiptera	9.3	13.3
Diptera	2.8	6.7
Isoptera	7.5	3.7
Thysanura	4.7	3.7
Neuropteran larvae	1.9	1.5
Insect remains	12.0	8.9
Araneae	4.7	0
Plant matter	0	5.2

being the greater importance of coleopterans in October (Table 8.1).

Despite the considerable range in maximum air temperature (24.3 - 37.3 °C) and vapour pressure deficit (0.59 - 1.46 kPa) that occurred during the six days of sampling in October, there were no detectable differences in taxonomic composition of diet from day to day. The dry mass of food particles also did not differ from day to day ($p > 0.05$, t-test).

The activity patterns of ants from one nest on three different days are shown in Fig. 8.1. Day 1 was a cool-moist day, characterized by low vapour pressure deficits and surface temperatures. Days 2 and 3 were hot-dry days, characterized by high vapour pressure deficits and surface temperatures. Day 3 was exceptionally stressful in that, although the temperature profile was similar to that of Day 2, the vapour pressure deficit started off higher and remained higher throughout the day than Day 2. On the hot-dry days, foraging activity was bimodal, with morning and afternoon peaks and a cessation of activity at midday. In contrast, on the cool-moist day foraging activity was unimodal. Similar patterns were exhibited from numerous other nests. The morning activity peaks on all three days occurred at surface temperatures between 52.0 and 56.5 °C, whereas the afternoon peaks in activity on the two hot days occurred at a surface temperature of about 60 °C. Despite similar surface temperature conditions, foraging activity ceased

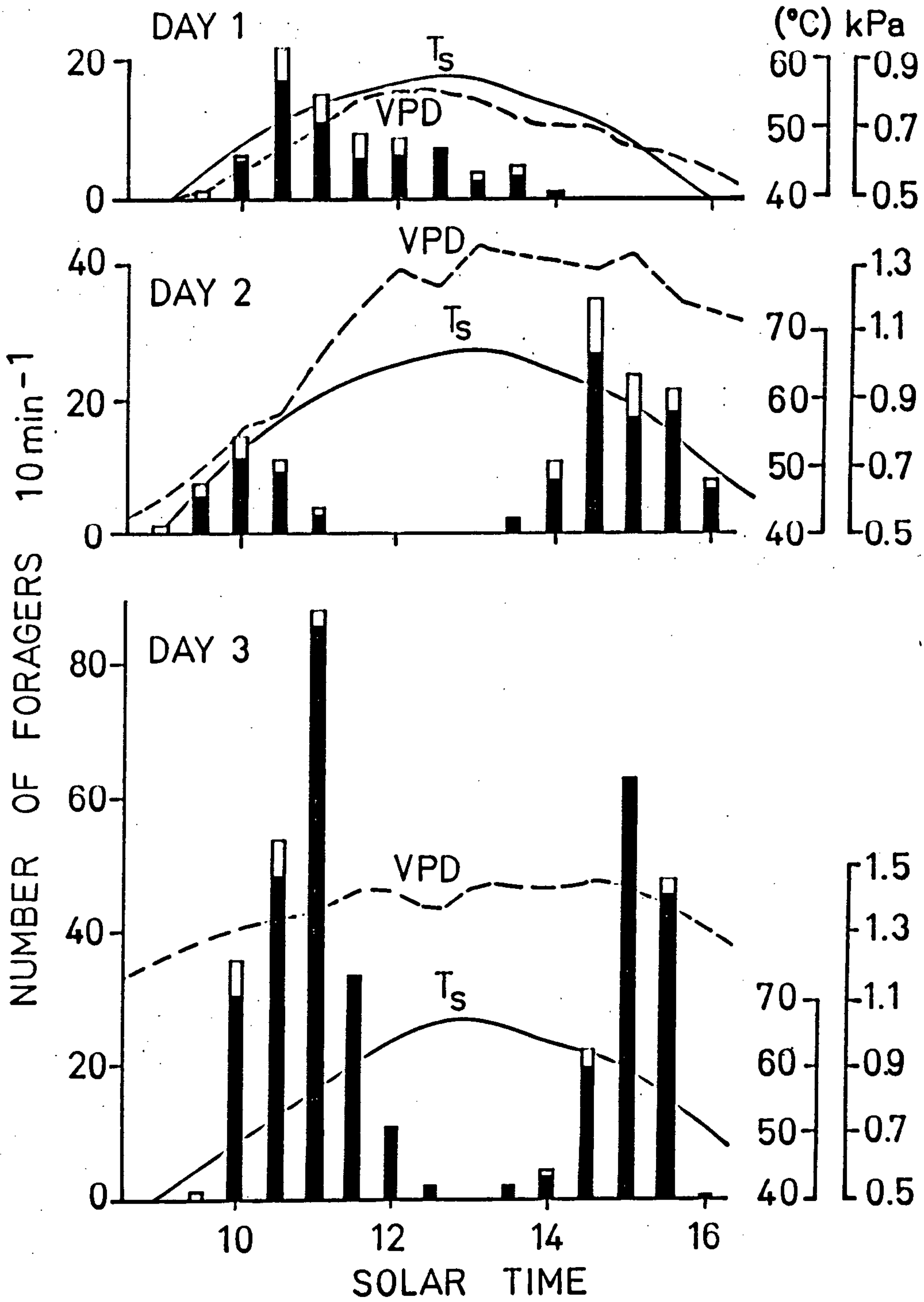

Figure 8.1. Foraging activity patterns of an _O. barbiger_ colony on three separate days in relation to climatic conditions. Activity is expressed as the number of ants returning to the nest in 10 min. Shaded areas correspond to successful foragers. T_s = surface temperature (°C), VPD = vapour pressure deficit (kPa).

for about 180 min on Day 2 as opposed to 60 min on Day 3. The differences between the foraging activity on these three days are best illustrated by considering the total number of foraging excursions made during each day. Despite the relatively mild conditions on Day 1 only 232 foraging excursions occurred, whereas 423 occurred on Day 2, and on Day 3, the most stressful day, 1086 foraging excursions took place; foraging activity increased with increasing environmental stress. Foraging efficiency, the number of ants returning with food relative to the total number returning to the nest, was similar on all three days (Fig. 8.1).

The relationship between the number of successful foraging excursions per day (excursions in which ants retrieved prey items) and totalized daily vapour pressure deficit is presented in Fig. 8.2. These data were obtained over a period of 18 months from five different colonies and there is a significant correlation between environmental stress and foraging success ($p < 0.05$, t-test). Two of the five nests were observed for three to four days respectively (in the latter case observations were on consecutive days) and the relationship also held.

Ocymyrmex barbiger workers typically searched for and retrieved food items independently. Recruitment was, however, observed on numerous occasions. The recruiting ant emerged from the nest, with her gaster directed downwards in a typical trail laying posture, followed immediately by up to 10 recruits. The

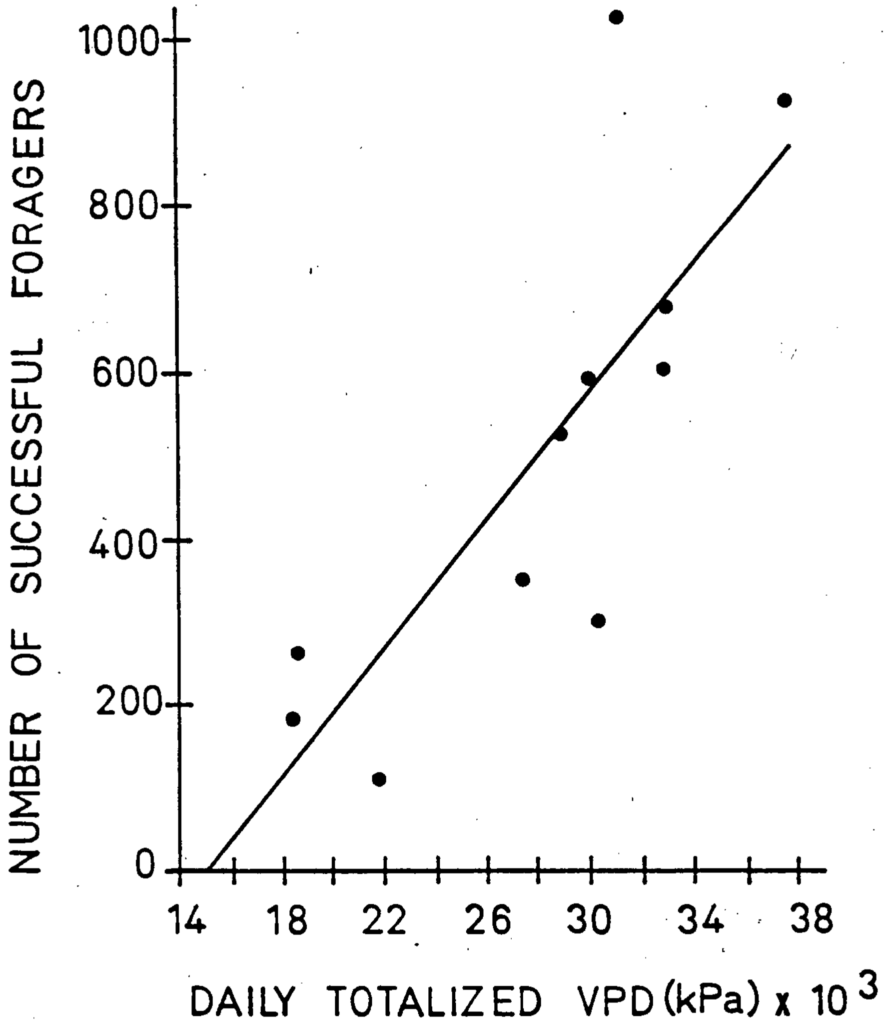

Figure 8.2. Relationship between the number of successful foraging excursions from one colony per day and totalized daily vapour pressure deficit (kPa). $y = -595.9 + 0.04x$; $r^2 = 0.64$.

recruiter advanced at a relatively slow pace making frequent pauses, often appearing to pause until bumped by one of the recruits. The recruits darted rapidly from side to side, advancing less directly than the recruiter, but frequently overtaking her. Often, after a few metres, some recruits lost contact with the recruiter but invariably some were successfully directed to a prey item. For example, five recruits were successful in locating a large lepidopteran larva 40 m from the nest. Typically, recruitment occurred when an item of prey, too large for an individual to retrieve, was located. Cooperative retrieval of the intact prey items did not occur, instead the ants dissected the prey into pieces that individuals could carry.

Foraging excursions lasted for up to 35.6 min (= 2134 s), and ants travelled up to 50 m from their nests in search of food. The distance covered on foraging excursions varied with climatic conditions. On a cool-moist day (maximum air temperature 30.0 °C, surface temperature 57.0 °C, vapour pressure deficit 0.70 kPa) the mean radius from the nest to the location of food particles was 31 ± 9 m ($\bar{X}$ ± SD, N = 16), whereas, on a hot-dry day (maximum air temperature 40.2 °C, surface temperature 68.0 °C, vapour pressure deficit 1.43 kPa) foraging distance was only 16 ± 9 m (N = 19). These values are significantly different ($p < 0.05$, Mann-Whitney U-test).

Relative to foraging distance, inter-nest distance was small ($\bar{X}$ 32.2 m, range 13-50 m, N = 17). Thus colonies probably have overlapping foraging areas. This was confirmed by the frequent occurrence of ants from two to three colonies at the same bait point. Also, in the course of following foragers, there were occasions when an individual passed within a few cm of another colony's nest entrance.

Typically prey items were located on the exposed sand surface (N = 50 observations) and not in shaded areas. However, at surface temperatures greater than 51 °C foraging ants make periodic retreats into thermal refuges, such as in the shade or by climbing up objects such as grass stalks (see section 7.3), where food does not occur. With increasing sand surface temperatures beyond 51 °C the effective time ants spent searching for prey, relative to the total time away from the nest, decreased progressively (Fig. 8.3).

Running speed was a function of temperature, showing a linear increase between sand surface temperatures of 27 - 62 °C (Fig. 8.4). The maximum recorded speed was 23 m min^{-1} . At the lowest recorded temperatures, when the first individuals emerged to forage, ant movements were erratic and uncoordinated, relative to locomotion at higher temperatures. There were no apparent impairments to coordination at the highest recorded temperatures.

8.4 DISCUSSION

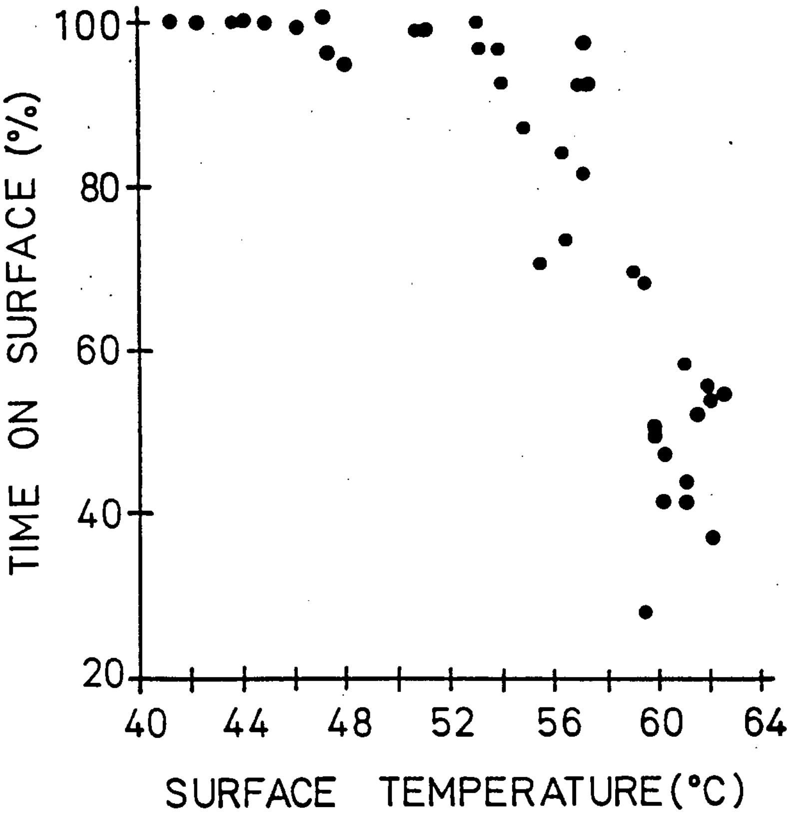

Figure 8.3. Relationship between sand surface temperature and the proportion of time spent away from the nest that foragers spent on the insolated sand surface.

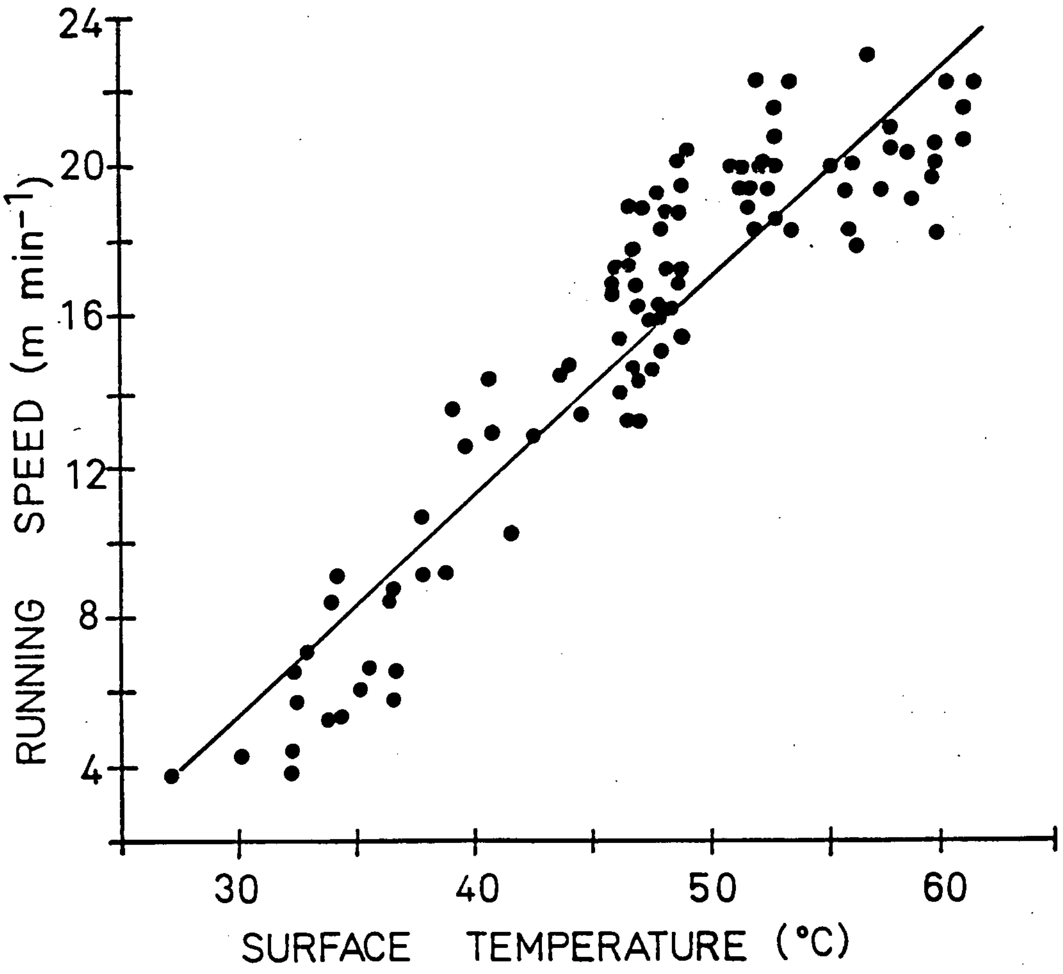

Figure 8.4. Relationship between running speed and sand surface temperature. $y = -11.79 + 0.58x$; $r^2 = 0.86$.

The present study indicates that *O. barbiger* is an arthropod scavenger. Furthermore, less detailed observations on *O. turneri* and *O. velox*, in the Namib desert, and on *O. velox* and an unidentified congener in the Etosha National Park, Namibia, indicate that these species are also primarily insectivorous (unpubl.). All of these observations have been in arid habitats and are in marked contrast to the observations of Prins (pers. comm.) who in more mesic regions of southern Africa (Cape Town and Namaqualand) has collected large amounts of seed from the nests of *O. barbiger*. Furthermore, Prins (pers. comm.) has made similar observations on *O. weitzeckeri* in the Kruger National Park, South Africa and these observations have led to the generalization that all members of the genus *Ocymyrmex* are highly granivorous (Prins, 1963; 1965). From the available evidence it thus appears that *O. barbiger*, and other members of the genus, are capable of switching their diet depending on locality but more detailed data from localities other than the Namib desert are required to confirm this.

It appears that *O. barbiger* foragers occupy their temporal/thermal niche in order to maximize the exploitation of dead arthropods. Although, in the short term, the size and type of prey remained the same irrespective of climatic conditions, recovered prey originated substantially closer to the nest during hot-dry periods than during cool-moist conditions. The most acceptable explanation for this observation is that prey density increases during hot-dry conditions.

In hot deserts high temperatures and desiccation could be important mortality factors for small arthropods. The apparent increase in prey availability and the increase in forager activity attending hot-dry periods supports this hypothesis. Furthermore, many of the soft-bodied arthropods taken by *O. barbiger* were visibly moist and therefore, had died that same day as dead insects dehydrate rapidly (Edney, 1977).

Studies, on the behavioural ecology of *O. velox* (Wehner & Marsh, in prep.) and the present investigation on *O. barbiger*, indicate that the genus *Ocymyrmex* (Subfamily Myrmicinae) occupies the same ecological niche as *Cataglyphis* species (subfamily Formicinae) occupy in the Sahara desert and southern Greece (Harkness & Wehner, 1977; Schmidt-Hempel, 1983; Wehner *et al.*, 1983). Both genera are arthropod scavengers, forage during the heat of the day, run very rapidly and are single prey loaders. Both genera are adapted to utilizing a low density, spatially unpredictable food source and occupy their thermal niche in order to take advantage of environmentally stressed prey.

One of the major differences between the two genera is colony size. While *Ocymyrmex* colonies comprise a few hundred individuals, *Cataglyphis* colonies are larger, frequently containing several thousand workers. Furthermore, recruitment behaviour does not occur in Cataglyphis species the workers of which exhibit life-long fidelity to specific foraging areas. In contrast, Ocymyrmex species have a well developed recruitment system and workers appear to have little fidelity for specific foraging areas (Wehner & Marsh, in prep.; present study).

With increasing thermal loads O. barbiger move more rapidly over the surface (Fig. 8.4) but beyond a critical temperature they cannot remain continuously on the surface (Fig. 8.3). As prey items do not occur in thermal refuges, time spent in refuges reduces the amount of extranidal time available for foraging per se. It follows that there should be a temperature at which the area searched by foraging ants per unit time is maximal. By combining the information from Figs. 8.3 and 8.4 it can be seen that the optimal searching surface temperature for an individual is 52.4 °C (Fig. 8.5). As temperature changes continuously throughout the day it would be unreasonable for ants to forage only at this optimal temperature. It would, however, be reasonable to predict that at the colony level foraging activity should peak at this temperature. The morning activity peak coincides closely with this temperature ($\bar{X}$ 53.5 °C, range 51.8 - 56.3, N = 11), and on relatively cool days (maximum sand surface temperature 62°C) the afternoon peak in forager activity also occurs in this range ($\bar{X}$ 51.8 °C, range 50.5 - 52.5, N = 6). In contrast, on exceptionally hot-dry

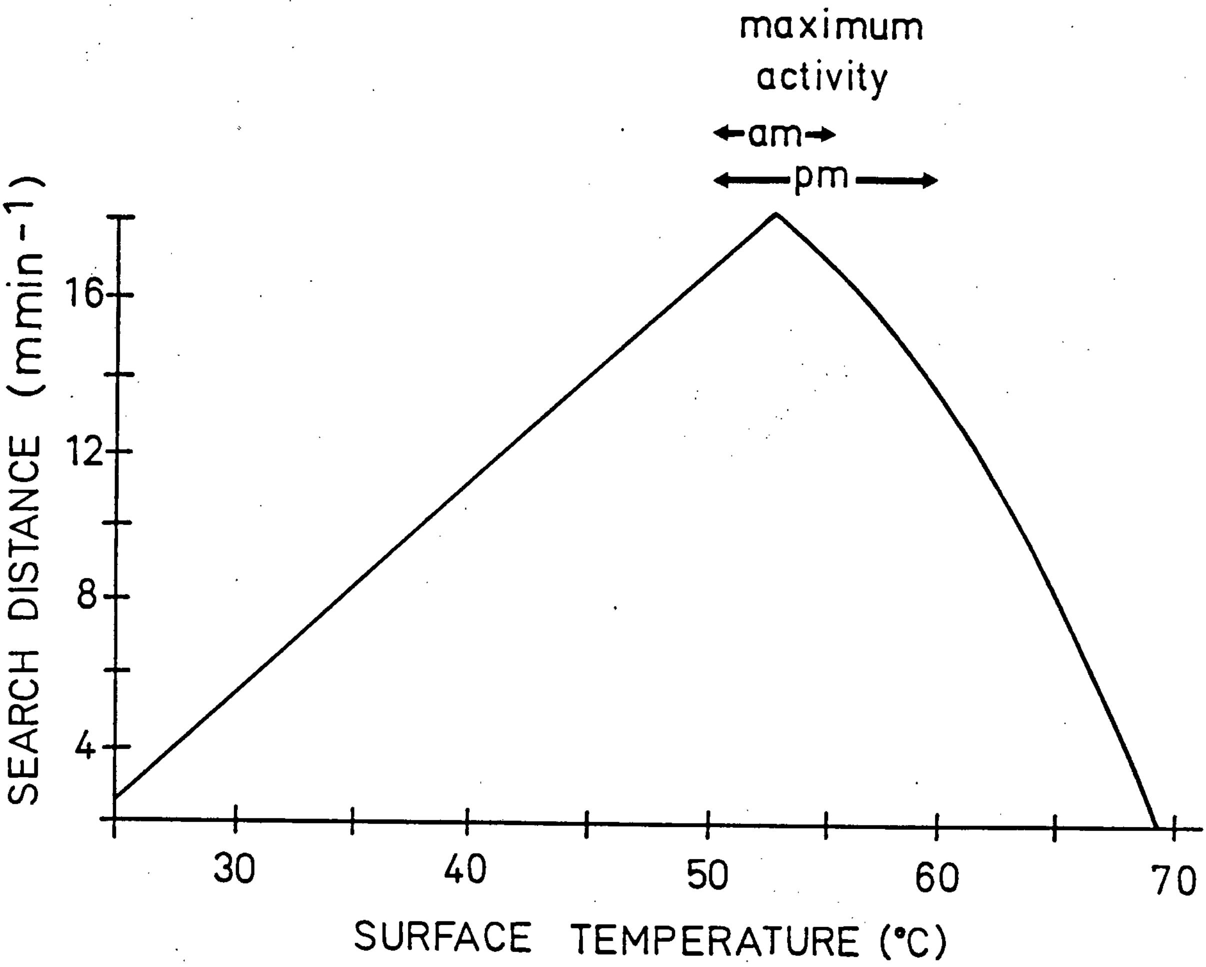

Figure 8.5. Relationship between search distance per unit time and sand surface temperature. "am" and "pm" indicate the range of temperatures over which colony activity peaked during the morning and afternoon activity periods respectively.

days (maximum surface temperature > 67 °C) foraging activity is apparently maximal at high, suboptimal temperatures ($\bar{X}$ 59.0 °C, range 57.0 - 62.0, N = 3) but more data is required to confirm this tendency.

Although there will be a loss of foraging efficiency at temperatures greater than optimum, provided prey density is higher during such conditions than at the optimal searching temperature, the reward per unit time can still be greater. For example, the prey retrieval rate would be the same at 64 °C and at the optimal temperature provided prey density was double that at the optimal temperature. The evidence provided here suggests that changes in prey density of this magnitude do occur and that they are related to the fluctuating thermal environment.

SECTION NINE

CONCLUSIONS

In deserts, where environmental conditions are unpredictable and productivity is low, organisms can be expected to exhibit opportunistic and flexible characteristics (Noy-Meir, 1979/80; Louw & Seely, 1982). Such characteristics would enable these organisms to take advantage of favourable conditions whenever they occur. Animals with generalist diets are particularly common in very arid environments and it is primarily the relatively long-lived species which exhibit such features (Louw & Seely, 1982). Desert ants have several attributes which make behavioural plasticity an advantageous if not essential feature. Colonies are relatively long lived, permanently "rooted" in the soil and individuals are small. These attributes limit a colony to a small area from which it has to obtain all the resources necessary for survival, growth and reproduction. In an environment where food is spatially and temporally patchy, the ability to utilize diverse food types is clearly adaptive. Epigaeic desert ants also forage in regions where thermal conditions vary most during a diel and seasonal cycle. Flexibility in the periods used for surface activity is therefore of adaptive value in enabling ants to both select suitable micro-climatic conditions and utilize transient food types which may occur at times other than the usual activity time.

The present study was designed to achieve a broad perspective of Namib Desert ant ecology emphasizing the adaptations which contribute towards the success of ants in the desert. The study commenced by examining distributional patterns of the component species. Attention was then focused progressively from the general to the more specific aspects of ant ecology. The structure and function of one community was studied in some detail for an extended period of time. Here emphasis was directed towards quantifying species composition, activity patterns and trophic relationships. This led to a study in greater depth of the foraging ecology of the two dominant ants in this community. Finally attention was directed towards an examination of the behavioural and physiological ecology of the unusually arid-adapted, thermophilic species, *Ocymyrmex barbiger*. Here the emphasis was on elucidating behavioural mechanisms that facilitate the exploitation of a thermally stressful environment and on gaining an understanding of the adaptive value of occupying this unusual niche.

A major conclusion which can be drawn from the present study is that Namib Desert ants are highly opportunistic. Throughout the study there have been frequent examples of opportunistic responses by the ants to changes in their environment. This opportunism is undoubtedly a key adaptation facilitating survival in an harsh and unpredictable environment. There were several facets of opportunism in evidence. Examples are the considerable flexibility in diet exhibited by virtually all species that were studied; behavioural flexibility, such as *M. denticornis* switching from trunk-trail foraging to diffuse foraging when food was scarce; the extension of activity periods immediately after rain; *T. rufescens* switching from predominantly diurnal to nocturnal foraging activity for no apparent reason; *O. barbiger* foragers tolerating near-lethal temperatures when food was particularly abundant; the collection and storage of food when supplies were abundant.

None of these adaptations are unique to the ants of the Namib Desert: they have been reported for ants in most deserts where adequate studies have been carried out. There does, however, appear to be a difference in the degree to which these adaptations are employed, with the Namib Desert species exhibiting greater plasticity in behaviour and especially diet. This undoubtedly reflects environmental differences. In comparison to the deserts of North America and Australia, where most quantitative studies of ant ecology have been carried out, the Namib Desert is a more arid, more variable, less predictable environment and supports a lower diversity of food items, especially seeds.

The science of ecology is presently going through a revolutionary period where theories, which had almost become accepted dogma, are being challenged and new ideas are being searched for and offered as alternatives (Price et al., 1984). One of the dominant and influential theories during the past decade, which is currently being questioned, concerns the role of competition in ecosystems. There is, for example, a substantial amount of evidence that competition is not important to the structure and dynamics of a diverse array of insect communities (Strong, 1981; Strong et al., 1984). Noy-Meir (1979/80) has recently argued persuasively that "direct, unidirectional and independent responses of plant and animal populations to environmental variations may be sufficient to explain most ecological phenomena in deserts". According to this "autecological hypothesis" desert ecosystems lack strong and intricate interactions and regulatory feedbacks between the various organisms and between the environment. Desert populations are primarily influenced by the weather, in particular rainfall, and the effect of water availability becomes "overwhelming" in hot arid ecosystems. In short, in hot arid ecosystems competition and other biotic interactions such as predation will not play important roles in ecosytem dynamics. Although there is good support for the "autecological hypothesis" there are also inevitable exceptions. One of the exceptions made by Noy-Meir (1979/80) concerns desert granivorous ants, birds and rodents. For these organisms there is some evidence that seeds may be a limiting resource (Brown et al., 1979). Arid-adapted granivores should have ample time and opportunity to exploit and deplete their food resource and as a consequence competition and predation may be expected. Virtually all of the evidence that Noy-Meir (1979/80) invokes to establish granivores as an exception to his "autecological hypothesis", however, comes from studies conducted in North American deserts and none are from extremely arid environments. Furthermore, Noy-Meir appears to have overlooked some good evidence that North American granivorous birds, occurring in shrub-steppe habitats, do not occur in competitively structured communities (Wiens, 1977).

In the present study of ant community structure and function in the Namib Desert, it was found that, because of their highly variable nature, the observed community patterns were not readily reconciled to competition theory. The patterns were more in line with what would be expected of a non-interactive community and therefore support the "autecological hypothesis". However, several factors mitigate arriving at a firm conclusion concerning the role of competition in the Namib Desert ant communitiy. Perhaps most important of all is the fact that "many ecological phenomena that might be due, in whole or in substantial part, to the effects of interspecific competition can also be explained by alternative hypotheses not involving competition" (Lawton & Strong, 1981). In the absence of well designed tests the results obtained are, therefore, frequently ambiguous and subject to biased interpretation. Unfortunately, it is notoriously difficult to test adequately for competitive effects. Pontin (1982) has stated that the basic approach will involve the experimental removal of one species from its normal habitat followed by the monitoring of population size changes in the remaining species compared with controls. Such an ideal approach is, however, frequently either not possible or prohibitively impractical. A second factor preventing a firmer conclusion concerning the role of competition in the Namib Desert ant community is the lack of data on certain aspects where competition could possibly have an influence. For example, data are required on the utilization of feeding space by the various species. Data on the influence of predation on ants are also of possible importance to an understanding of ant community structure and function and could have a substantial effect on the importance of competitive interactions.

Finally it should be borne in mind that the role of rare events that generate occasional but potentially intense competition cannot be ignored as a force structuring ecological communities just because they are rare (Lawton & Strong, 1981). Thus even if the observed community patterns during the brief study period are most readily reconciled with those expected of a non-interactive community, and if "bottleneck periods" do occur only infrequently, competition could still have an influence on community structure. Because of the time scale at which these events occur they will remain "tantalizingly plausible but extremely difficult to test" (Connell, 1980).

APPENDIX

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THE EFFICACY OF PITFALL TRAPS FOR DETERMINING THE STRUCTURE OF A DESERT ANT COMMUNITY

by

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Pitfall trapping was found to be an unreliable way of determining the structure of a Namib Desert epigaeic ant community. There were considerable intra- and interspecific differences in the probability of encountering randomly distributed pitfall traps and in the vulnerability to capture when pitfall traps were encountered.

INTRODUCTION

Various methods for quantifying the structure of epigaeic ant communities have been reported in the literature. These methods are based on colony density (Briese & Macauley 1977; Whitford 1978; Bernstein 1979), censusing ants at baits (Culver 1974; Chew 1977; Davidson 1977), soil-core sampling (Boomsa & De Vries 1980), searching (Room 1975) and pitfall trapping (Muhlenberg et al. 1977; Majer 1978a; Samways 1981, in press). Pitfall trapping is a superior method in that it can be employed with ease on a regular basis to monitor temporal changes in community structure, it can be operated throughout the day and night thereby avoiding problems associated with interspecific differences in activity rhythm and several sites can be sampled concurrently for intersite/habitat comparisons. Furthermore, Samways (in press) found that in the citrus orchards of Nelspruit, South Africa, 'pitfall trapping gave the most individuals, the most species and the most constancy of proportions of ant species in each trap from week to week' when compared with other methods employing sticky traps, nest counting, quadrat sampling and counting by eye per unit time.

The mathematical model of Jansen & Metz (1979) indicates that pitfall trapping should give reliable data on the community structure of epigaeic arthropods, provided the animals move independently according to Brownian motion. This model also makes the implicit assumption that all individuals that encounter pitfall traps are equally vulnerable to capture regardless of species. Alternatively, it should be possible to derive specific correction factors which take into account differences in vulnerability to capture. Certain characteristics of ants, however, suggest that they may not be ideal pitfall trap candidates. All ant species have elaborate social behaviour and many exhibit recruitment responses to food sources such that the movements of foragers are not independent of one another (see Wilson 1971). Furthermore, owing to interspecific differences in size, shape, foraging behaviour and speed of locomotion it seems unlikely that all species within a community will be equally vulnerable to capture.

The purpose of the present investigation was to test the efficacy of pitfall trapping as a method to obtain reliable data on the structure of a Namib Desert epigaeic ant community. The following two questions were posed: 1) Do foraging workers of the component ant species in the community have the same probability of encountering randomly distributed pitfall traps? 2) Do all individuals that encounter pitfall traps have the same probability of capture?

METHODS

Study Site and species

The study was conducted on the gravel plains near Ganab (28°08' S;15°37' E) on the eastern edge of the Namib-Naukluft Park. The habitat is a uniform flat plain and was almost devoid of vegetation and litter during the investigation thus facilitating observations. Previous intensive searching using a variety of baits to attract ants revealed that 13 ant species occurred in this habitat. Only eight species were sufficiently common to provide adequate data for this study. Three of the species belong to the genus *Monomorium* which is currently being revised by B. Bolton of the British Museum (Natural History), London, and consequently it is not possible to use specific names. Reference specimens of these species are lodged at the British Museum (Natural History) as follows: *Monomorium* sp. A = M. Namib sp. A; *Monomorium* sp. B = M. Namib sp. B. *Monomorium* sp. C = M. Namib sp. C.

Probability of trap encounter

Most of the surface activity of ants is concerned with foraging and it is during foraging excursions that ants are likely to encounter pitfall traps. Typically, ants leave their nests and travel in one general direction when searching for food. For example, *Messor denticornis* Forel workers frequently travel up to 60 m from their nest to their foraging sites without deviating more than 1 cm from their path (pers. obs.). Likewise *Ocymyrmex barbiger* Emery foragers regularly travel for 30 m or more in a path which deviates no more than 2 m from a straight course. The foraging behaviour of all the common ant species at Ganab conforms to this general pattern and the direction of leaving a nest is thus indicative of movement in the environment. This behavioural characteristic was therefore used to detect interspecific differences in foraging direction patterns and consequently interspecific differences in the probability of encountering randomly distributed pitfall traps. To avoid localized depletion effects, pitfall trap sample period should be of limited duration. Majer (1978a) used seven day sample periods whereas Samways (1981) used three day sample periods. Here the foraging direction patterns of individual colonies were plotted over three day periods. Every day, for three consecutive days, the azimuth foraging directions of 20 randomly selected ants from each of 20 marked nests were determined as the ants crossed the circumference of a 50 cm radius circle drawn around the nest entrance. Observations were made during peak activity periods for each species and individual nests were observed at the same time each day. The 20 nests included 4 *M. denticornis*, 3 *Tetramorium rufescens* Stitz, 3 *T. sericeiventre* Emery, 1 *Monomorium* sp. A, 3 *Monomorium* sp. B, 2 *Monomorium* sp. C, 1 *O. barbiger* and 3 *Pheidole tenuinodis* Mayr. The Rayleigh test (Batschelet 1981) was used to determine whether the 60 azimuth directions obtained for each nest conformed to a random pattern or exhibited directionality. In one instance, where the foraging directions appeared to be trimodal, Rao's spacing test (Batschelet 1981) was used to test whether the pattern departed from random.

Vulnerability to capture

A pitfall trap was inserted 0.5 - 1.0 m from the entrance of each of 36 selected nests. The nests included 6 *M. denticornis*, 5 *O. barbiger*, 5 *T. rufescens*, 5 *T. sericeiventre*, 5 *P. tenuinodis*, 5 *Monomorium* sp. A. and 5 *Monomorium* sp. B. The structure and insertion of the pitfall traps was based on the design of Majer

(1978b). A pitfall trap comprised a glass test-tube (18 x 150 mm), inserted into a PVC lined hole in the ground so that the rim was flush with the surface. Each test-tube contained 5 ml ethylene glycol, a preservative commonly used in pitfall traps. Finely grated cheese was placed 0.5 m beyond the traps. The cheese was used as bait to lure ants in the direction of the traps so as to ensure a minimum of 50 encounters per nest per observation period. The response of each individual that encountered a trap was recorded. Individuals carrying bait were not considered in the analysis of the data.

To determine whether capture success was influenced by the type and presence of preservative used or by handling pitfall traps prior to insertion, the following procedure was adopted: One pitfall trap was inserted near each of 16 _M_. _denticornis_ nests, 12 of these traps were inserted in the normal manner by hand whereas care was taken to ensure that four traps remained untouched. Ethylene glycol was added to four of the handled traps (the control group) and to the four untouched traps. Four traps remained empty and an alcohol-glycerine mixture (used by Majer 1978a) and Samways 1981, in press) was added to the remaining four. All traps were monitored in the above mentioned manner and a Chi-square test was used to determine whether the capture success of any of the treatment groups differed from that of the control group.

RESULTS

Probability of trap encounter

Of the 20 colonies observed 8 exhibited statistically significant directional foraging patterns (Table 1). Typically *M. denticornis* travelled for up to 60 m along trunk trails less than 4 cm wide. Between one and three trunk trails were used per nest during any one foraging period. In this species individual trunk trails may be used for up to four weeks before other directions are favoured (pers. obs.). The foraging patterns of *P. tenuinodis* were variable and appeared to be related to the type and spatial distribution of food being exploited. The two colonies which exhibited directional foraging utilized one trunk trail each and these led to specific grass clumps which harboured honey-dew secreting homopterans that were being tended by the ants. These trunk trails were approximately 1 cm wide and 5 m long. Ants from the *P. tenuinodis* colony which exhibited a random foraging pattern were collecting seed. Foraging patterns were also variable in the two *Tetramorium* species. Although these two species do not forage along trunk trails they occasionally show strong recruitment responses in which ten or more individuals emerge from the nest in quick succession behind an ant laying a pheromone trail and travel to the same foraging site.

Thus foraging patterns vary quite considerably in this community. Variation exists both within and between species. Whereas foragers from certain nests moved independently the movements of foragers from other nests were not independent of one

TABLE 1. Summary of foraging patterns for 20 nests. Mean vector length (r) ranges from one for a unidirectional pattern to zero for a perfectly random pattern. Angular deviation (s) is measured in radians and is a measure of dispersion equivalent to the standard deviation of linear statistics. The Rayleigh test was used in all cases with one exception (*) where the foraging pattern was trimodal and a Rao's spacing test was more appropriate (Batschelet 1981).

SPECIES	NEST	r	s	FORAGING PATTERN	SIGNIFICANCE LEVEL
M. denticornis	1	1.000	0	Directional	p<0.001
M. denticornis	2	1.000	0	Directional	p<0.001
M. denticornis	3	0.333	66.1	Directional	p<0.001
M. denticornis *	4	0.341	65.8	Directional	p<0.050
P. tenuinodis	1	1.000	0	Directional	p<0.001
P. tenuinodis	2	1.000	0	Directional	p<0.001
P. tenuinodis	3	0.140	75.1	Random	NS
T. rufescens	1	0.327	66.5	Directional	p<0.001
T. rufescens	2	0.105	76.6	Random	NS
T. rufescens	3	0.094	77.1	Random	NS
T. sericeiventre	1	0.361	64.7	Directional	p<0.001
T. Sericeiventre	2	0.168	73.9	Random	NS
T. sericeiventre	3	0.050	78.9	Random	NS
Monomorium sp. A	1	0.237	70.8	Random	NS
Monomorium sp. B	1	0.080	77.7	Random	NS
Monomorium sp. B	2	0.070	78.1	Random	NS
Monomorium sp. B	3	0.048	79.0	Random	NS
Monomorium sp.c.	1	0.298	67.9	Random	NS
Monomorium sp. C	2	0.120	76.0	Random	NS
O. barbiger	1	0.168	73.9	Random	NS

another. Thus the probability of ants encountering pitfall traps while foraging would vary considerably and would be non-predictive for practical purposes.

Vulnerability to capture

Considerable intraspecific variation in vulnerability to capture was observed and this partially masked any interspecific differences (Table 2). Very few individuals seemed to be captured by surprise upon first encountering a pitfall trap. Most paused at the trap lip and sensed the air with their antennae before further movement. This behaviour suggested that the preservative or human odour on the test-tubes may have been influencing the ants. The tests on *M. denticornis*, however, indicated that there were no detectable differences in behaviour at traps whether they were empty, contained ethylene glycol, an alcohol-glycerine mixture or whether they had been touched or not ($p>0.2$ for all treatment groups).

Having paused at the trap lip many individuals moved around it and continued on their journey. In one instance most individuals from a *M. denticornis* nest consistently avoided the pitfall trap by deviating from their path when about 2 cm from the trap, by-passing the trap and then returning to their original path. This behaviour suggests that a pheromone trail had been laid around the trap.

TABLE 2. Variation in the number of ants captured by pitfall traps. The data are expressed as percentages of the number of individuals that encountered a trap. N1 represents the total number of individuals that encountered the traps and N2 represents the number of nests from which observations were made.

Species	Ants trapped (%)	N1	N2
Messor denticornis	1 - 12	550	6
Ocymyrmex barbiger	0 - 8	270	5
Tetramorium rufescens	16 - 79	507	5
T. sericeiventre	6 - 47	522	5
Pheidole tenuinodis	15 - 72	461	5
Monomorium sp. A	23 - 81	457	5
Monomorium sp. A	3 - 71	341	5

Many ants, particularly the relatively large species such as M. denticornis and O. barbiger, partially entered the traps, by maintaining contact with the trap lip via their meta-thoracic tarsal claws and dangling the remainder of their body in the trap, before resuming their journey. Other ants, particularly the smaller species, entered the traps and walked about on the vertical glass walls. Many of these individuals re-emerged to continue their journey while others fell or were blown into the preservative as they reappeared at the trap lip.

DISCUSSION

The two simple experiments documented in this paper indicated that the major assumptions underlying the use of pitfall trap data to describe community structure were invalid for this Namib Desert ant community. Furthermore, in view of the large intraspecific variation in vulnerability to capture and probability of trap encounter it was not possible to derive correction factors which adequately took into account interspecific differences in trapability. In contrast, at Nelspruit relatively constant proportions of ant species were obtained in each trap through time implying that intraspecific variation in capture success is slight (Samways, in press), however, no data on intertrap comparisons in each habitat was presented. Although it is possible that pitfall trapping may be a more reliable way of obtaining data to describe ant community structure in areas other than the Namib Desert, it is prudent to test the efficacy of the technique before initiating large scale trapping programmes. In view of the possibility of selective trapping it seems unwise to place much reliance on pitfall trapping for obtaining measurements of single communities unless the response of all species to pitfall traps is known and predictable. Similar observations about the reliance of pitfall traps for invertebrates in general have been made by Southwood (1978) and Koch and Majer (1980). Pitfall trapping remains a useful method for interhabitat comparisons (e.g. Muhlenberg et al. 1977; Majer 1978a; Samways 1981, in press) provided intraspecific variation in vulnerability to capture is minimal.

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