BEHAVIOURAL AND PHYSIOLOGICAL ECOLOGY OF THE NAMIB DESERT DUNE ANT, *CAMPONOTUS DETRITUS* EMERY.

by

Barbara Anne Curtis

A thesis submitted in partial fulfillment
of a Master of Science degree in the
Department of Zoology,
University of Cape Town.

March 1983

THE ANT

by Ogden Nash

The ant has made himself illustrious
Through constant industry industrious.
So what?
Would you be calm and placid
If you were full of formic acid?

TABLE OF CONTENTS

RESULTS AND DISCUSSION

ABSTRACT

The ecology of *Camponotus detritus* was examined over two years at six sites across the Namib Desert. This common species was found to fill an important role in the dune ecosystem as the major honeydew consumer, apparently limited chiefly by intraspecific competition for food. Each colony, comprising one to four nests with a mean of 3 404 workers per nest, maintained a discrete foraging territory. Nests were constructed in sand beneath perennial vegetation. Nest density was 0,3 - 0,9 ha^{-1}. Worker abundance was lowest near the coast, highest in the central dunes and intermediate inland toward the east. The abundance of honeydew-producing scale insects showed a similar pattern.

There was no marked seasonality in the intensity of foraging activity or in brood production, suggesting a constant food supply which is in turn maintained by the regular occurrence of advective fog. Both light and temperature affected surface activity, which was bimodal in summer and unimodal in winter, ceasing when surface temperature exceeded about 55°C. Due to a steep thermal gradient above the sand during midday in summer the air temperature experienced by ants at 5 mm was 10 - 15°C lower than surface temperature. Although primarily diurnal, some workers remained at their foraging grounds overnight.

Laboratory studies showed that the mean preferred temperature of workers and brood was 35°C at 100 % rh and 31 - 33°C at 30 % rh. The CT_{max} of workers was 53°C at 100 % and 30 % rh and CT_{min} was 4,57°C at 100 % rh. Workers tolerated -1°C, 95 % rh; 45°C, 95 %rh and 45°C, 45 % rh for 24 hours. Water loss increased with increasing saturation deficit at 35°C, but was lower at 25°C and 24 mm Hg than at 35°C and 21 mm Hg. Large workers had lower rates of water loss and survived longer than smaller workers. Groups lost significantly less water at 25°C and 24 mm Hg than individuals. Rate of water loss was high relative to other desert arthropods but comparatively low for an ant.

ACKNOWLEDGEMENTS

I acknowledge with thanks the assistance of the following:

Professor G.N. Louw for supervision of the thesis; Dr M.K. Seely, D.E.R.U., for co-supervision, advice and encouragement; the Desert Ecological Research Unit (D.E.R.U.), Gobabeb, funded by the C.S.I.R. and Transvaal Museum, for use of vehicles, equipment and other research facilities; the Department of Agriculture and Nature Conservation, South West Africa/Namibia for use of facilities and permission to work in the Namib-Naukluft Park; the C.S.I.R. for a post-B.Sc.(Hons) bursary for two years; the University of Cape Town for a Twamley post-graduate bursary for one year and other financial support; D.E.R.U. technicians for help with fieldwork; Dr E.L. McClain and Alan Marsh for reading preliminary drafts of the thesis and for helpful discussions; Rose Leggott and Fiona Harris for typing the preliminary drafts and final manuscript respectively; Professors R.M. Crewe, V.C. Moran, C. Crawford, Dr G.L. Prinsloo, Dr C.Celliers and Christian Peters for helpful discussions; Professor C. Crawford for advice on statistics; Dr A.J. Prins, South African Museum, for identification of ants; Dr. F. Wanless, British Museum, for identification of the spider, *Cosmophasis* sp. and Dr A.S. Dippenaar for sending the specimen to him; Dr Y. Ben-Dov, Agricultural Research Organisation, Israel, for identification of scale insects; Mr T. Longman for constructing the temperature choice chamber and for assistance with experiments performed in the laboratory at the University of Cape Town and to every one at Gobabeb for encouragement and support.

This thesis is dedicated to Mary Seely whose love of the Namib is infectious.

Section One

INTRODUCTION

1.1 Purpose

A common and conspicuous arthropod of the central Namib Desert dune-field is the large ant, *Camponotus detritus*. Towards the west it is the only ant species present, whereas in the east, where other ant species also occur, *C. detritus* still appears to be the most abundant. The genus *Camponotus*, known from Tertiary fossils, comprises 1 500 species and has a worldwide distribution (Wilson 1971). Despite the fact that *C. detritus* is so common in the Namib dune-sea, very little is known about its biology and ecology. Holm and Scholtz (1980) described it as a detritivore and Seely (1978a) records it drinking fog moisture from the sand and vegetation. Robinson and Cunningham (1978) noted that the ants are occasionally preyed on by the lizard, *Aporosaura anchietae*. Apart from these observations on natural history, no detailed or comprehensive study exists on this species.

Since ants are ecologically one of the most dominant groups of terrestrial animals and are particularly important in desert ecosystems (Bernard 1964a, Délye 1968, Wilson 1971, Whitford 1978a, Bernstein 1979a), the present study was initiated to determine the role played by *Camponotus detritus* in the Namib dune ecosystem. As virtually nothing was known about this species, it was felt that an extensive approach would be more beneficial to future research on the Namib fauna than a detailed study of a single aspect of its biology. The aim of the study was twofold : to examine the general ecology of the species as well as its ecophysiological tolerances and to compare and contrast these findings with those in other ant species. Part of the study was to determine the effect of the environmental gradient, which occurs from west to east across the dune-field, on the distribution and abundance of this species.

For most of the study, behavioural observations were made on *C. detritus* in its natural environment at Gobabeb, midway across the dune-field (Fig. 1.1). Nests were excavated, feeding behaviour observed and activity patterns studied. Simple laboratory experiments were performed to examine temperature tolerances and water loss. To study the effect of the environmental gradient on this species, nest density and abundance of workers was determined at six sites across the dune-field (Fig. 1.1) and correlated with climatic data, vegetation cover and abundance of scale insects.

1.2 Study Area

The Namib is a long, narrow desert stretching for over 2 000 km along the western coast of southern Africa from Moçamedes in Angola southwards to the Orange River (latitudes 15 - 30°S) (Louw 1972). The central Namib, seldom wider than 130 km, is divided into two geomorphologically distinct areas by the ephemeral Kuiseb River. To the north lie gravel plains bordered by a narrow strip of transverse dunes along the coast. South of the Kuiseb a vast dune-sea stretches from the coast to the foothills of the central escarpment (approximate longitudes 14°30'E -

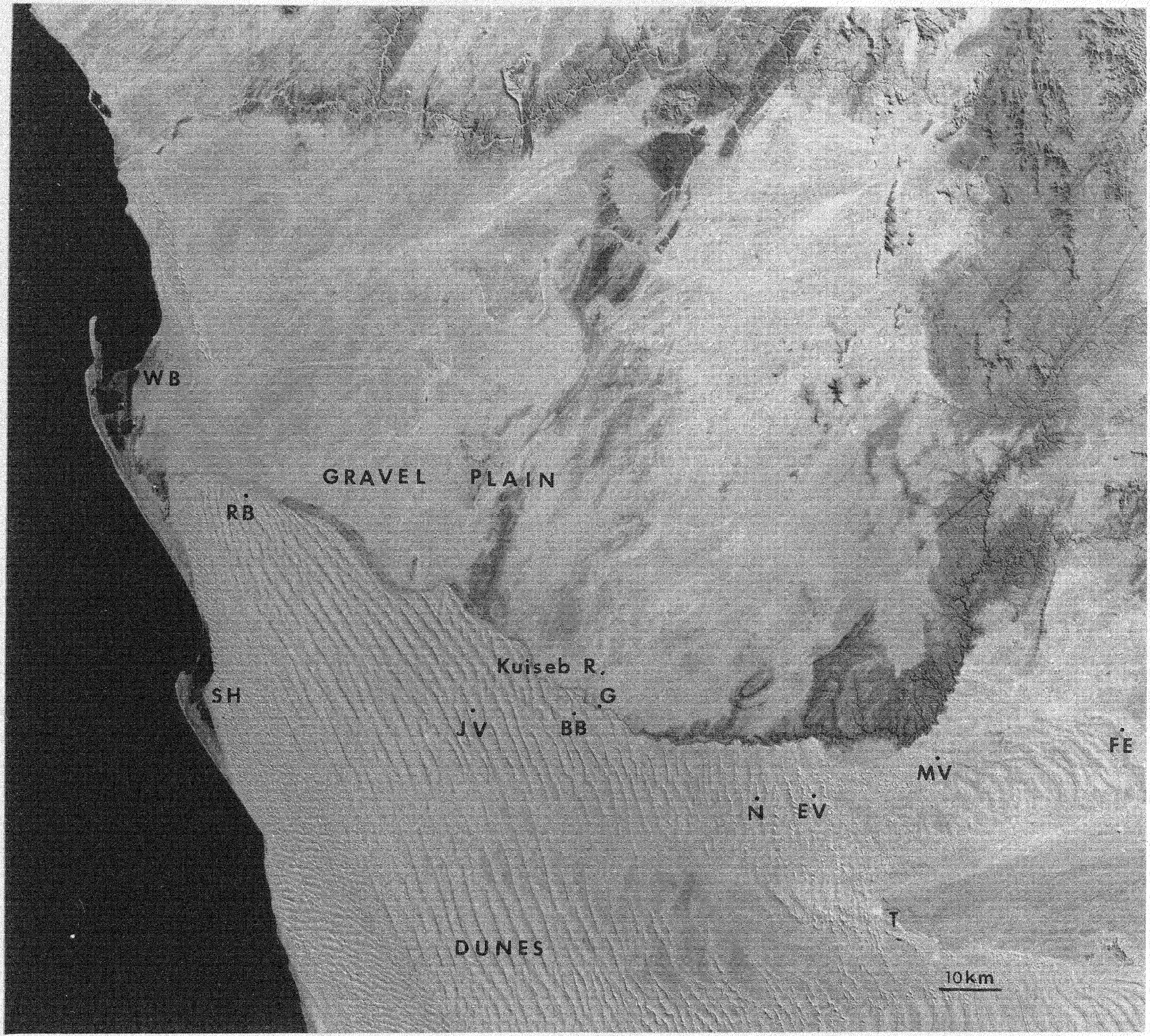


Fig. 1.1 Satellite photograph of the central Namib Desert showing the positions of the study sites. The ephemeral Kuiseb River divides the gravel plain to the north from the dune-field to the south. (Photo: NASA)

WB = Walvis Bay
SH = Sandwich Harbour
EV = Elephant Valley
T = Tsondab Vlei

Study sites:

RB = Rooibank
JV = Jumbo Valley
BB = Bannoch Burn
G = Gobabeb Res. Station
N = Noctivaga
MV = Mniszechi's Vlei
FE = Far East

15°45'E) (Fig. 1.1).

Barnard (1973 in Robinson and Seely 1980) recognises three geomorphological sections to the dune-sea, from west to east : a narrow coastal strip of transverse dunes with no interdune valleys, parallel linear dunes in the centre and multifaceted dunes in the east. The linear dunes of the central region lie along a north-north-west to south-south-east axis, and are separated by interdune valleys of variable width (0,5 - 3,0 km) and substrate. To the west, dune sand covers the interdunes (Figs. 2.1 and 2.2), whereas further east the substrate is gravel (Figs. 2.3 and 2.4), supporting a distinctly different fauna and flora from the dunes and sandy interdunes (Robinson and Seely 1980). The dunes themselves have a very characteristic morphology (Fig. 1.2). The crest is the highest point of the dune where the windward and leeward slopes meet. Below the crest, the sand on the windward side is compacted whereas on the leeward side it is continuously shifting and falling, forming the slipface. Since the prevailing winds in the Namib are from the north-west and south-west, the slipface is usually on the eastern side of the dune. In winter, however, strong winds from the east cause the slipface to move across to the western side. Lower down, on both sides are the more stable, less steep, vegetated dune plinth and dune base. In the east the dunes are lower and more stable than those in the centre or along the coast. Often there are no clearly defined interdunes but instead hollows and depressions with coarser sand between the dunes (Figs. 2.5 and 2.6).

Despite its narrow width, the Namib has a distinct climatic gradient from the coast inland (Besler 1972) (Fig. 1.3). The effects of the cold Benguela current which flows northwards along the western coast of

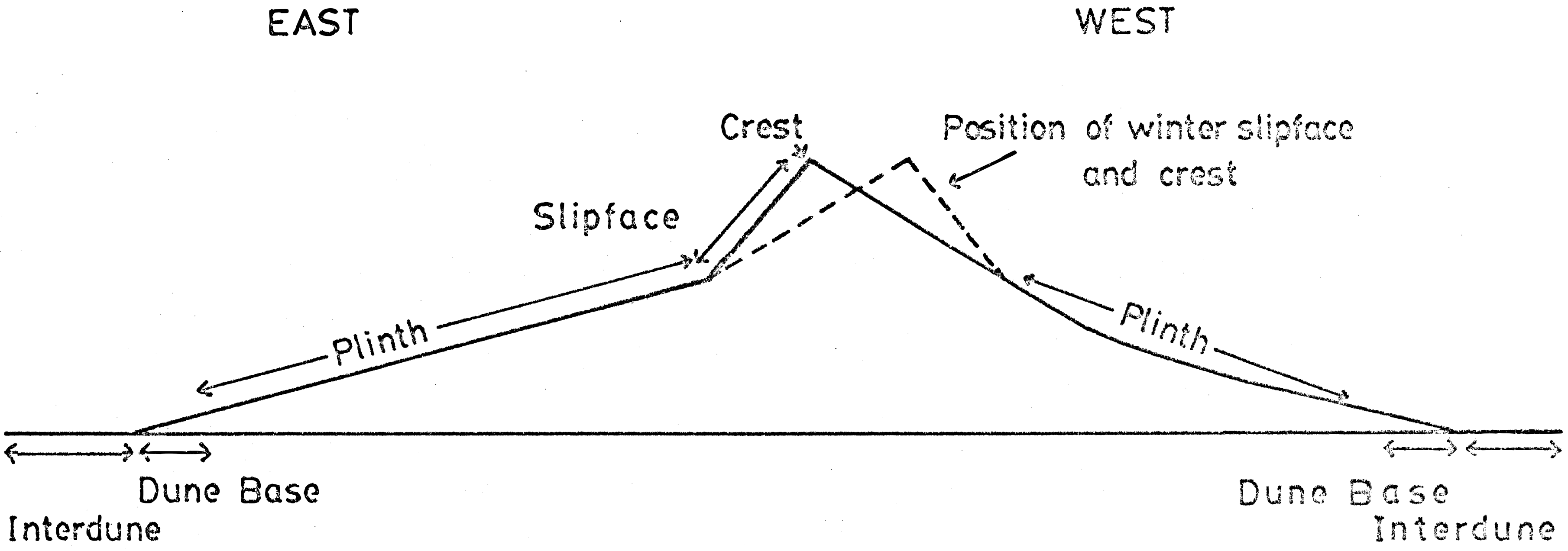
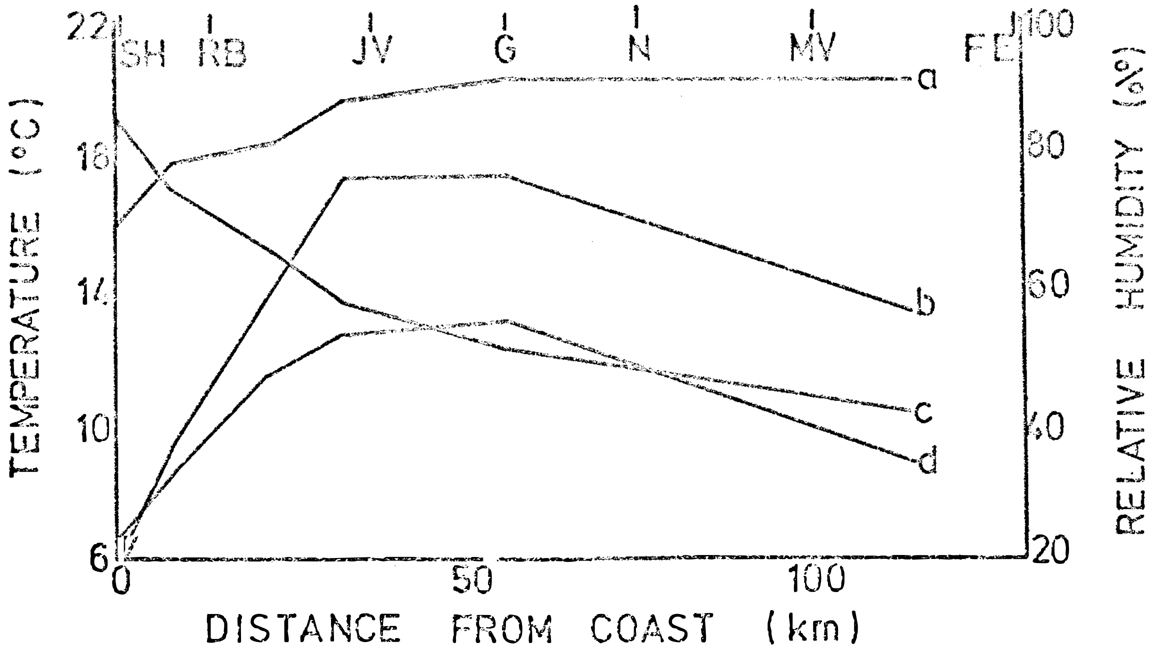


Fig. 1.2 Schematic cross-section of a linear dune, not drawn to scale (adapted from Robinson and Seely 1980).



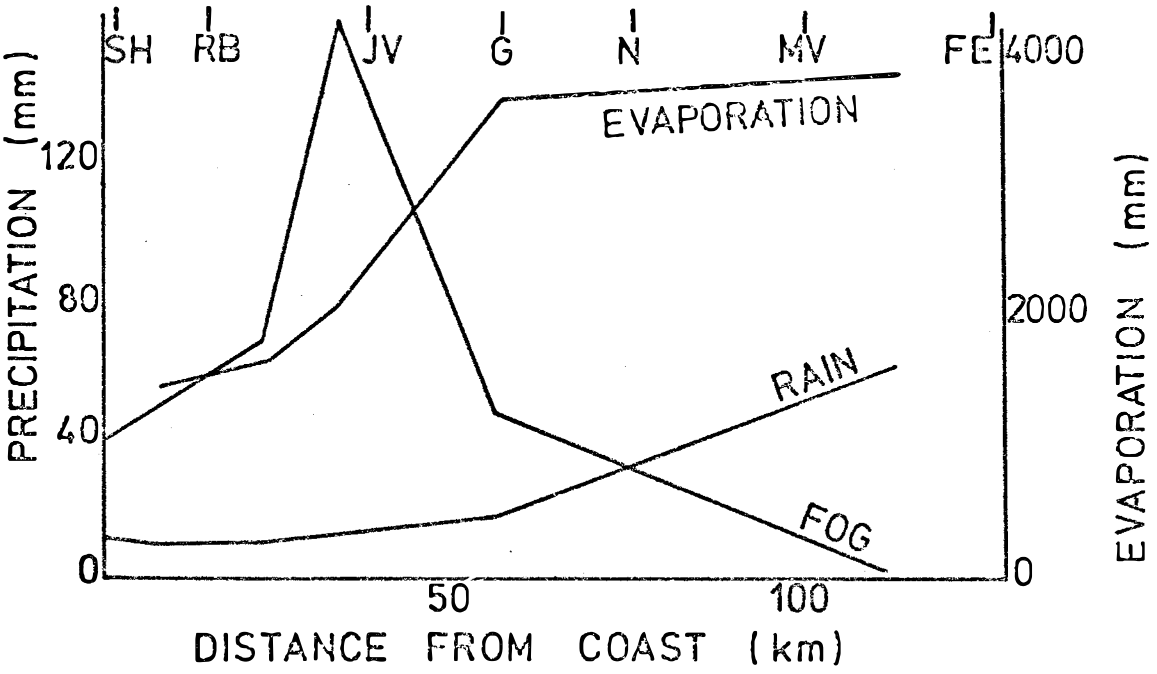


Fig. 1.3 Climatic gradient across the central Namib dune-field (D.E.R.U. records). Study site abbreviations as in Fig. 1.1.

a = Mean annual temp.   b = Mean daily amplitude of temp.

c = Mean annual rh   d = Mean daily amplitude of rh southern Africa, combined with the south Atlantic anticyclone are responsible for the regular occurrence of advective fog, and also for the cool south-westerly winds which prevail during summer (Louw 1972). The coast, where precipitating fog-water provides the main moisture source, experiences about 120 days of fog per annum (Nagel 1962). This decreases to about 36 days in the central regions and to only 5 days in the east (Besler 1972). Fog-water precipitation is greatest 30 km inland, where the low cloud layer comes into contact with the slightly more elevated ground (Anon. 1944 in Seely 1978b).

Because of the coastal fog bank and cool winds, temperatures are lower along the coast than inland, and daily fluctuation in temperature is far less. Relative humidity and evaporation are similarly affected along the coast. Inland, where the moderating effect of the ocean is reduced, fluctuations in temperature and relative humidity are far greater and evaporation is higher. Rainfall is sparse and intermittent throughout the desert, but is greatest in the east, replacing fog as the major moisture source. Rain may occur at any time of the year, but is most common from January to March (Seely and Stuart 1976).

For most of the year fairly mild (approximately 13 km h^{-1}) winds from the north, north-west or south-west prevail at Gobabeb (Seely and Stuart 1976). During the winter months (May - August) strong (approximately 21 km h^{-1}) easterly to south-easterly winds predominate. These are hot, dry berg winds which sweep down the escarpment from the interior and serve to raise the temperature. For this reason the Namib does not experience marked seasonal climatic changes (Robinson and Seely 1980).

Corresponding to the climatic gradient across the dune-sea, plant species diversity and abundance increase from the sparsely vegetated coastal dunes to the relatively complex communities of the eastern section (Robinson 1976) (Fig. 1.4). The dominant plant in the west is the perennial, succulent-leafed *Trianthema hereroensis* which uses fog as a source of moisture (Seely, de Vos and Louw 1977). This plant occurs in the sandy interdune valleys and hollows on the dune plinths. In the central region clumps of perennial vegetation occur on the plinth and dune base with virtually no perennial vegetation on the gravel interdune valleys. The tall grass, *Stipagrostis sabulicola,* occurs across the width of the dune-field, but *T. hereroensis* is gradually replaced by a number of species of perennial grass towards the east. Here the dunes have a more even covering of smaller clumps of perennial vegetation, with *Stipagrostis ciliata* covering the sandy hollows and interdunes.

This vegetation in turn provides food and shelter for numerous arachnids and insects including *Camponotus detritus,* as well as two species of snake, various lizards, birds and small mammals.

The vegetationless dune crests and slipfaces support an unusually diverse endemic fauna (Seely 1978b) of which the major component is tenebrionid beetles (Koch 1962). Due to their abundance, conspicuousness and ease of handling, much of the research in the Namib has centred on this group of insects (Koch 1962, Seely 1978b, Seely 1979, Holm and Scholz 1980).

The environmental gradient across the dune-field influences the abundance and species diversity not only of tenebrionids, but also thysanura, other ant species, dung beetles and possibly other arthropods (Seely,

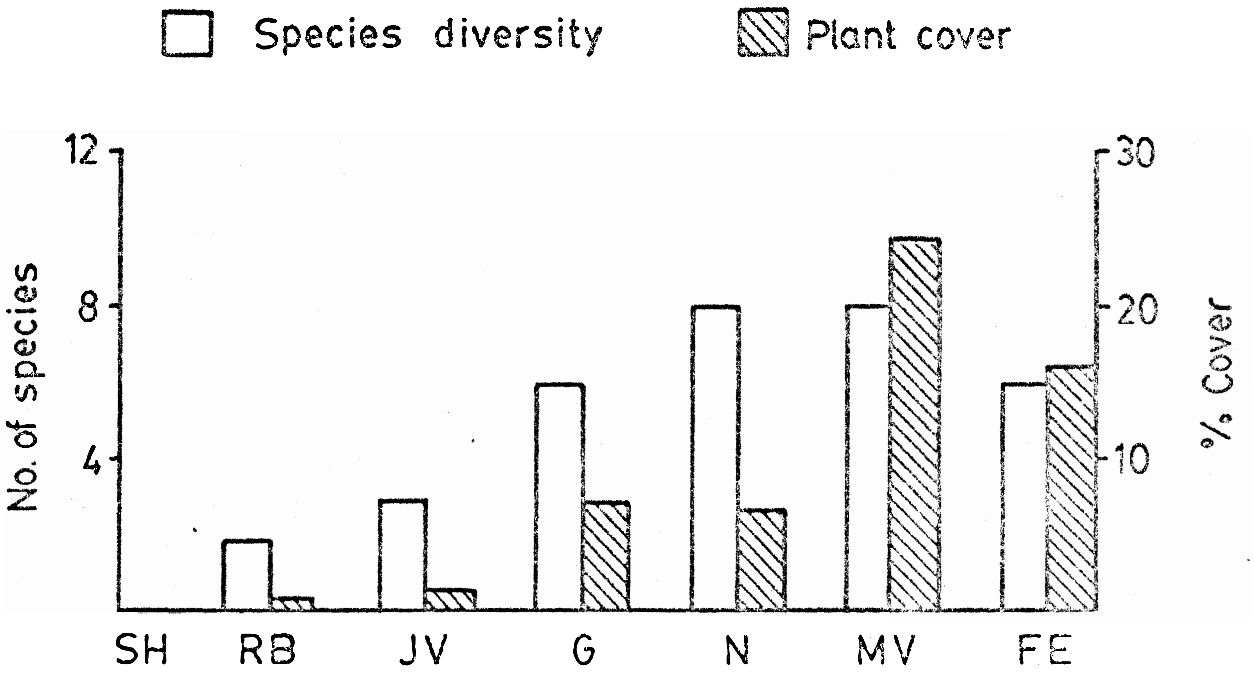


Fig. 1.4 Increase in the number of plant species and percentage vegetation cover on the dunes of the central Namib Desert (Seely, unpublished).

pers. comm.). It was felt, therefore, that a study of this common dune species, *Camponotus detritus*, across the gradient would help to further our understanding of its ecology and its role in the Namib dune ecosystem.

Section Two

PROCEDURE

2.1 Natural History and Behaviour

For a two year period (August 1980 - August 1982) regular observations were made on the behaviour of *Camponotus detritus* in the field. Data on life cycle patterns were obtained from nest excavations (Section 2.3.1) and pupae were removed to the laboratory where eclosion and behaviour of young workers (callows) were observed.

Following the only nuptial flight observed during this period, six newly inseminated queens were removed to the laboratory in order to record egg laying and subsequent development of the brood. They were housed in masonite boxes and kept under conditions of room temperature and humidity. Each box was divided into a nest area (150 x 100 x 50 mm) and foraging area (350 x 150 x 50 mm) with a 10 x 10 mm aperture connecting the two. A layer of sand (5 mm) was provided on the floor. Since ants are unable to see red light (Wilson 1971) a piece of glass covered with red cellophane was placed over the nest area. The walls of the foraging area were painted with polytetrafluoroethylene (FLUON), a highly slippery substance used to prevent the ants from escaping. Water was provided daily in the form of damp cottonwool, sugar water was similarly given every two days and dead arthropods once per week.

2.2 Food

Direct observations were made on the foraging behaviour of ants in the field and the proportion of workers returning to the nest with food or other objects was determined. To prove that the ants were collecting honeydew from scale insects, 50 stems of *Stipagrostis sabulicola* were injected with Robertsons red food colouring. To prevent ants sucking the plant juices directly from the wound, the hole was sealed off with tape. One hundred and fifty ants found tending scale insects above the point of injection were then collected and their crops dissected to ascertain if any of the dye had been ingested.

To determine other components of the ant's diet, one hundred workers (30 of which were carrying detritus back to the nest in their jaws) were dissected and their crop contents examined under a light microscope.

2.3 Nests

2.3.1 Structure and Numbers of Individuals

Attempts were made to estimate the number of workers per nest non-destructively using the mark-recapture method (Begon 1979). Subsequent excavations of these nests, however, revealed that this method grossly underestimated numbers of workers and therefore nests were dug up completely. Excavations took place in the early morning when most workers were in the nest and relatively inactive. During the first seven excavations the sand and nest material was removed in roughly 50 mm layers and sifted through 2 mm mesh sieves. As the workers and alates emerged they were collected, while the brood was carefully removed and later both were counted. Notes were made on the internal structure of the nest as well as the position of the brood.

This method proved very time consuming, and later excavations were conducted as follows : ants and nest material were shovelled rapidly into sieves, sand was shaken out, and the ants, brood and debris were placed in plastic buckets with a ring of FLUON at the top. Ants and brood were later extracted from the debris and counted. The same evening or following morning they were released as near to the old nest as possible. A total of 36 nests was excavated using the two methods described.

2.3.2 Nest Temperatures

A thermocouple meter (Bailey BAT 4) was used to measure nest temperatures in the field. Thermocouples were inserted into the nests at varying depths from 100 - 150 mm and 150 - 300 mm (approximate depth of most nests), and temperatures recorded at hourly intervals during the day and two-hourly intervals at night. Simultaneously, temperatures of the bare sand, nest surface and air at 1 m were also recorded.

2.3.3 Nest Density and Dispersion, and Territory Size

Dispersion is a description of the distribution pattern of plants or animals in space and may be determined by various methods (Southwood 1978). At Gobabeb (midway across the dune-field) nest density and dispersion were estimated using two different methods. On a large scale (over an area of roughly 40 km^2) ten random one-hectare transects (Section 2.5.1) were used. Nest dispersion was determined using the variance : mean ratio in which dispersion is considered to be random when the variance equals the mean, regular (overdispersed) when the variance is less than the mean, and aggregated when the variance is greater than the mean.

Nest density and dispersion were also determined at Bannoch Burn, an area of 9,5 ha on the eastern plinth of a dune about 6 km southwest of Gobabeb (Fig. 2.3). The plinth, approximately 230 m from the slipface to the interdune valley, supports *Stipagrostis sabulicola* and *Trianthema hereroensis*. All living plants in this area were mapped and the location of each nest and each scale-hosting plant was noted. Changes in the position of nests were recorded over the period October 1980 to November 1982. Nest dispersion was determined using the nearest neighbour index (Clark and Evans 1954).

With this index the ratio

$$R = \frac{\bar{r}_A}{\bar{r}_E}$$

is determined, where

$\bar{r}_A$ = The mean observed distance between nearest neighbours and

$\bar{r}_E$ = The mean distance which would be expected if the population were randomly distributed.

$\bar{r}_E$ can be calculated from $\frac{1}{2\sqrt{p}}$ where p = density of nests in the population. In a random distribution R = 1. Under conditions of maximum aggregation R = 0 since all individuals occupy the same locus.

Under conditions of maximum spacing where individuals are distributed in an even, hexagonal pattern, R would be 2,1491. The significance of the departure of $\bar{r}_A$ from $\bar{r}_E$ i.e. the observed dispersion from randomness, may be tested using the formula

$$c = \frac{\bar{r}_A - \bar{r}_E}{\sigma \bar{r}_E}$$

where c is the standard variate of the normal curve and $\sigma \bar{r}_E$ is the standard error of $\bar{r}_E$

$$\sigma \bar{r}_E = \frac{0,26136}{\sqrt{Np}}$$

N = The number of measurements of distance made. The c values 1,96 and 2,58 respectively represent the 5 % and 1 % levels of significance.

As *C. detritus* workers are territorial and attack conspecifics from alien colonies, marked ants from one nest were placed near the entrance of a second nest in order to determine which nests at Bannoch Burn belonged to a single colony. Members of the same colony were accepted while members of a different colony were immediately attacked. Similarly, by taking ants from scale-infested plants and releasing them at nearby nests it was possible to establish which plants in the area belonged to each colony's territory. The territory size of two colonies at sites other than Bannoch Burn was determined by following individual ants to their foraging grounds, marking the plants and measuring the area.

2.4 Activity

The term "activity" refers to the state of moving of an animal. Most authors, when referring to ant activity, are referring to those ants entering or leaving the nest, usually along well-defined trails or tracks (De Bruyn and Kruk-De Bruin 1972, Sanders 1972, Whitford and Ettershank 1975). They equate this activity with foraging intensity. However, the term "activity" can be somewhat misleading, since ants involved in maintaining the nest are "active" yet are not foraging. Similarly, not all the *C. detritus* workers leaving the nest area go in search of food. Many may be going to a sister nest belonging to the same colony. When visible activity on the sand surface ceases, foragers may still be "active" on the scale-covered plants. For this reason I have divided "activity" into various components.

2.4.1 Surface Nest Maintenance

This term refers to those individuals which are involved in excavating the nest entrance, rearranging detritus on a pile above the nest or moving gravel from the base of the nest mound to the surface of the nest. Notes were made on this form of activity during observations on transit activity.

2.4.2 Transit Activity

This term refers to those individuals leaving the nest area altogether, or returning from a distance of at least 300 mm, whether it be to forage, to enter another nest belonging to the same colony or to collect building material for the nest. Forty daytime and twenty night observations were made at ten different nests over the period July 1979 to July 1982. A circle was drawn in the sand, or marked with string, around the nest entrance 200 - 300 mm from the hole. The number of ants crossing the line, whether on their way into or out of the nest, was counted over a five minute period every 15 or 30 minutes. If a nest had more than one entrance on opposite sides of the mound, a circle was drawn around the entire mound and divided into segments. Numbers of ants crossing the line were counted for one minute per segment, and the total from all the segments expressed as the number of ants active per minute during that observation period. The number of ants carrying material in their jaws was recorded and the behaviour of ants within the circle was also noted.

Micro-climatic data were recorded concomitantly : sand surface temperature was measured with either a Yellow Springs Instruments telethermistor probe or a thermocouple and a Bailey BAT 4; air humidity at 1,5 m with a sling psychrometer. During the last 15 observations, temperature of the air at ant body height (5 mm above the sand surface) was measured with a thermocouple and a Bailey BAT 4. For convenience, all wind speeds were recorded with a Lampbrecht wind totaliser at a height of 1 m. Since wind speed increases greatly with height, the wind speed which the ants experience at 5 mm above the ground would be less than that recorded by the wind totaliser. The simplest expression of the relationship between wind speed and height is

$$\log u = a \log z + \log u_1$$

where u = wind speed at height z (expressed in metres)

u_1 = wind speed at 1 m

a = a variable which depends on wind speed, temperature and ground surface (Geiger 1973 p. 117).

On five occasions simultaneous recordings of wind speed at 5 mm and 1 m were compared and a mean value of 0,114 calculated for "a". This value was used in the above equation to convert wind speed at 1 m to wind speed at 5 mm. All wind speeds presented in the Results have been thus converted to wind speed at 5 mm.

To compare activity patterns at various sites across the dune-field, observations were made on three nests each at Rooibank, Far East and Noctivaga during January/February 1982 and again at Rooibank and Far East in April 1982 (Fig. 1.1).

2.4.3 Honeydew Collection

The terms "honeydew collection", "tending" and "foraging" are used interchangeably in Section 6.2 to refer to those workers present on scale-infested plants. The number of workers present per unit area of plant was counted hourly during the day and every two hours at night, usually concurrently with transit activity observations. As movement of ants on the plant was slight it was possible to count the number of ants in a small area at one time. Night observations were made using a fluorescent torch. Air temperature at 0,5 m, sand surface temperature, wind speed and humidity were recorded as before. To determine the lengths of time which individual ants spent foraging, 40 and 17 ants were marked with a spot of Humbrol enamel paint on the thorax and their position noted every half hour for 29 and 48 hours respectively.

Differences between the number of ants collecting honeydew at night and during the day were tested using Students t-test. Correlations between the number of honeydew collectors and micro-climatic data were determined using the Product Moment correlation coefficient.

2.5 Environmental Gradient

To determine the effect of the environmental gradient on *C. detritus* abundance from west to east across the dune-field, six study areas were selected (Table 2.1 and Figs. 2.1 to 2.6).

2.5.1 Nest Density and Distribution

Since the vegetation on the dunes is patchily distributed and with it the ant nests, long narrow transects were selected in preference to smaller, square quadrants, so that a greater variety of vegetation associations would be included. In each area ten random transects 2 km by 5 m (1 ha) were examined in detail and the number of nests counted. Notes were made on the position of the nests on the dune, together with the orientation of the entrance and the type of plant in which the nest occurred. The number of plants in each transect which had *C. detritus* or any other ant species tending scale insects was also recorded. Nest dispersion was determined using the mean : variance ratio (Southwood 1978) (Section 2.3.3).

2.5.2 Number of Workers Per Hectare

At each site four to six nests were totally excavated (Section 2.3.1). In addition four nests were excavated at Elephant Valley, roughly midway between Noctivaga and Mniszechi's Vlei. Since the size of ant nests was

Table 2.1

Six study sites across the environmental gradient of the central Namib Dune-field.

Th = *Trianthema hereroensis*
Es = *Eragrostis spinosa*
Ss = *Stipagrostis sabulicola*
Sn = *S.* cf. *namaquensis*
Sl = *S. lutescens*
Sc = *S. ciliata*
Ag = *Asthenatherum glaucum*

Study Site	Rooibank	Jumbo Valley	Gobabeb	Noctivaga	Mniszechi's Vlei	Far East
Co-ordinates	23°10' S 14°35' E	23°30' S 14°52' E	23°32' S 15°04' E	23°43' S 15°14' E	23°43' S 15°29' E	23°46' S 15°47' E
Distance From Sea (km)	14	37	56	75	100	130
Mean Height of Dunes (m)	60 - 80	100 - 120	60 - 80	80 - 110	20 - 30	10 - 15
Mean Length of Slope (m)	[1] 1 000	[1] 1 600	[2] 200 - 300	[2] 200 - 300	[2] 50 - 100	[2] 50 - 100
Interdune Substrate	Sand	Sand	Gravel	Gravel	Sand	Sand
Interdune Vegetation	Th	Es	-	-	Sc	Sc
Dominant Slope Vegetation	Th	Th, Es	Th, Ss	Ss, Sn Ag	Ss, Sn Ag, Sl	Es, Ss Ag, Sl

1. From one crest to another, across the sandy interdune
2. From slipface base to edge of interdune

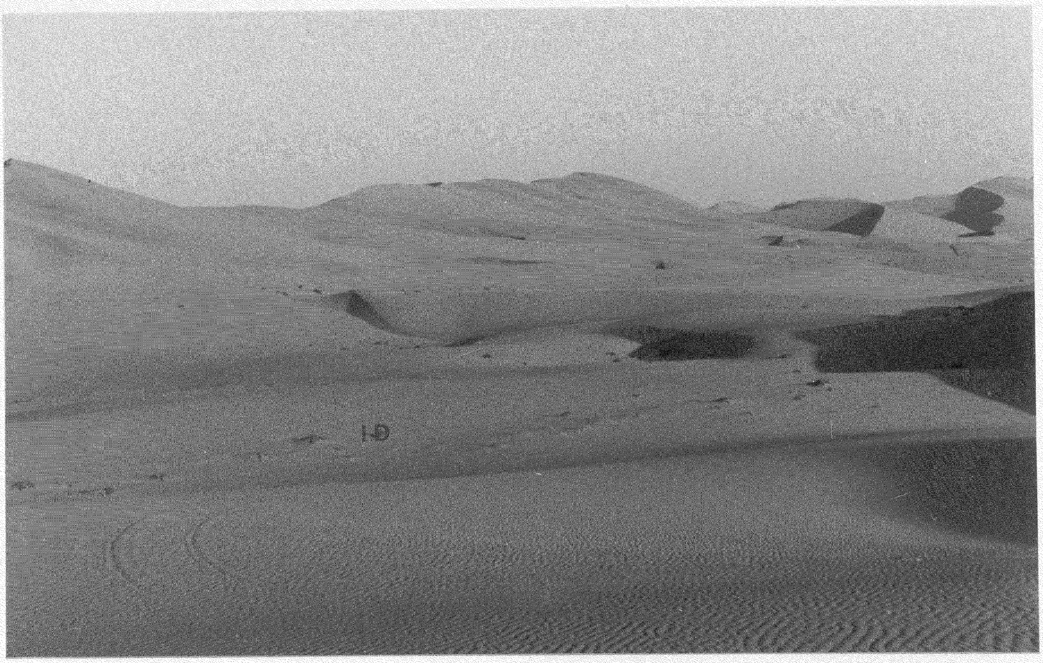


Fig. 2.1 Rooibank study site, showing lightly vegetated, sandy interdune (ID) valley.

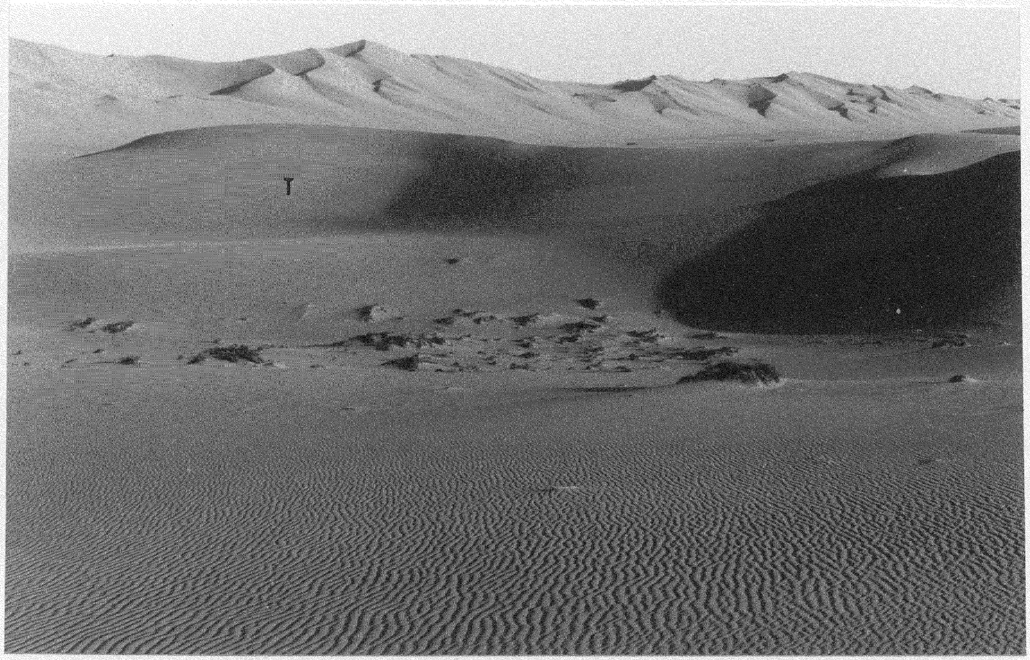


Fig. 2.2 Vegetation growing in a hollow to the north of a transverse dune (T) at Jumbo Valley.

Fig. 2.3 Bannoch Burn study site, Gobabeb. Note gravel interdune (ID) and vegetated dune plinth (P).

Fig. 2.4 Vegetated plinth (P) and gravel interdune (ID) of Noctivaga study site (Photo: L.Praetorius).

Fig. 2.5 Low dunes (D) and hollows (H) at Mniszechi's Vlei study site.

Fig. 2.6 Low dunes (D) and hollows (H) at the Far East study site. Gravel plain (GP) in left distance.

found to vary considerably, it was felt that density expressed as the number of workers ha^{-1} was a more meaningful value than the number of nests ha^{-1}. The size of nests was also found to vary depending on the species of plant under which it was constructed (Table 7.3). For this reason the density of nests in each study area was subdivided according to the proportion of nests constructed under each plant species. Each value was then multiplied by the mean number of workers found in nests of each plant species. (Mean values were obtained for all nests of a particular plant species across the dune-field, excluding Rooibank - see Table 7.3). The Wilcoxon test was used to determine significant differences between nest sizes.

For comparative purposes with other animals, biomass is more meaningful than number of individuals. Thus the mean biomass of *C. detritus* in each area was calculated by multiplying the number of workers of the three size categories by their mean weights.

2.5.3 Correlations of Ant Density With Environmental Variables

The density of *C. detritus* workers across the environmental gradient was correlated with environmental variables using Spearmans Rank correlation coefficient. Vegetation cover was determined in each area from transects along the upper, lower and mid-dunes on both the east and west plinths, as well as the sandy interdunes at Rooibank and Jumbo Valley. Only plants with green shoots were included : dead or dormant plants being excluded. The density of scale insect-hosting plants was estimated by adding the total cover of the three commonly infested species (*Trianthema hereroensis*, *Stipagrostis sabulicola* and *S.* cf. *namaquensis*) to a proportion of the cover of the less commonly infested species (50 % of *Eragrostis spinosa* and 20 % of *S. lutescens).*

A preliminary estimate of the numbers of the scale insect, *Aclerda namibensis*, per plant was obtained by multiplying the mean number of scale insects per node (N = 30) by the mean number of nodes per stem (N = 30) which in turn was multiplied by the mean number of stems per plant (N = 10). From this the abundance of scale insects per hectare could be estimated. The percentage of each plant species infested with scale insects was determined from the nest density transects (Section 2.5.1). Climatic data were obtained from the Desert Ecological Research Unit records at Gobabeb.

2.6 Ecophysiology

All laboratory experiments were carried out in the Department of Zoology, University of Cape Town. Ants were collected from the dunes in October 1981 and flown to Cape Town, where they were housed in plastic containers at 25 ± 3°C and maintained on a diet of sugar water.

2.6.1 Preferred Temperatures

A temperature gradient chamber was constructed after Kay (1978). The plexiglass chamber was 980 mm long, 5,5 mm wide and 4,8 mm high, with a removable lid and an aluminium floor. Brass rods under the floor extended beyond both ends of the chamber. One end of the rods was immersed in a water bath cooled by a refrigerated coil. The other end was buried in a container of dune sand heated on a hotplate. The chamber was placed in a masonite box insulated with vermiculite. With this apparatus a linear gradient of 18 - 50°C could be maintained. The chamber walls were lined with FLUON to prevent the ants escaping. The lid was covered with red cellophane and observations were made with the aid of a torch, which was found to be less disturbing to the ants than daylight. Lines were drawn on the lid, so that the number of ants per 50 mm could be counted. The floor was covered with 5 mm of dune sand. Thermocouples 2 mm above the sand surface, measured the temperature at 50 mm intervals along the approximate temperature range 29 - 44°C. Along the remainder of the chamber thermocouples were at 200 mm intervals. The entire apparatus was kept in a walk-in constant temperature room, with an ambient temperature of 22 ± 2°C and 30 ± 4 % rh.

At the start of all experiments groups of 20 ants were distributed evenly within the chamber and left to settle for an hour. As it was impossible to control the temperature gradient thermostatically, a certain amount of temperature change occurred. This caused the ants to move as their preferred temperature shifted. For this reason five observations were made per group at approximately hourly intervals and the mean number of ants per temperature interval calculated. Six such groups were examined on dry sand (rh 30 ± 5 %) and six groups on moist sand (rh 100 %). A few ants persisted in trying to escape from the cold end of the chamber. These were excluded from the calculations and only those ants in a resting position were considered.

To determine the temperature chosen by the workers for the brood, larvae and pupae were placed in the chamber with the ants. This procedure was replicated twice on moist sand and three times on dry sand.

2.6.2 Critical Maximum (CT_{max}) and Critical Minimum (CT_{min}) Temperatures

Each experiment was replicated with 30 ants using the method of Schumacher and Whitford (1974). Groups of 5 - 10 ants were placed in a 100 ml beaker immersed in a water bath. The beaker contained a 10 mm layer of dune sand, above which was a ring of FLUON. Thermocouples recorded the temperature on the sand surface and 10 mm above the sand. In order to keep the air in the beaker saturated the sand was dampened, a moist ball of cottonwool suspended in the beaker and a layer of plastic placed over the beaker.

CT_{max} : The water bath was heated at a rate of 1°C min^{-1}. As each ant reached its CT_{max} (regarded as that temperature at which the ants lost co-ordination) it was removed from the beaker. To determine whether high humidity affected CT_{max}, the experiment was repeated with the ants on dry sand, without cottonwool and plastic cover.

CT_{min} : The water bath was cooled with the aid of an immersion cooler at a rate of 0,07°C min^{-1}. CT_{min} was regarded as that temperature at which ants were incapable of righting themselves when turned onto their backs, even though they were still capable of movement.

Significant differences in preferred and critical temperatures were determined using Students t-test.

2.6.3 Long-Term Tolerance to Extreme Temperatures

Two groups of 20 ants were placed in 1 000 ml beakers. One beaker contained dry sand and the other moist sand. Because FLUON vapourizes at high temperatures and high humidity, and prolonged exposure to these fumes kills the ants, a gauze lid was placed 20 mm above the moist sand. Damp cottonwool and a plastic covering were used as for the previous experiment. The beakers were immersed in a water bath maintained at 45 ± 2°C for 24 hours, and the per cent mortality observed after 12 and 24 hours.

Long-term tolerance to low temperatures was examined in a similar manner on 30 ants left at -0,5 ± 1°C and 95 % rh for 24 hours.

2.6.4 Water Loss

In all experiments loss of body weight was assumed to reflect loss of body moisture. Prior to each experiment, ants were given access to water. Thirty ants (10 major, 10 media, 10 minor) were then placed in individual glass vials with perforated plastic tops, and weighed to the nearest 0,01 mg. Since ants are social and naturally exchange liquid food by trophallaxis, groups of 30 ants were also placed together in containers and desiccated simultaneously. Water loss at 35°C and 50 % rh was determined in a constant temperature and humidity room. For 0 % rh and 95 % rh a desiccator containing silica gel or a saturated K_2SO_4 solution respectively was placed in a constant temperature room at 25°C or 35°C. All experiments ran for four days and the live ants were weighed in their vials every 24 hours.

As many of the small workers died during the experimental period, water loss rates were only calculated for the first 24 hours. Long-term water loss rates were determined for those individuals which survived for four days. From these experiments the mortality rate under different conditions could also be determined.

All results were expressed as a percentage of the initial body weight. For comparison with work on other desert arthropods, however, rates of water loss were also converted to water loss per unit area of cuticle. Surface area was calculated using a standard formula (Edney 1977)

$$S = K.W^{0,66}$$

where S = surface area in mm^2

K = surface-weight relationship constant. The value of 7,5 as determined by Délye (1968) for Saharan ant species was used.

W = weight in mg.

For purposes of comparison with the work of Whitford, Kay and Schumacher (1975) on North American desert ants, an experiment similar to theirs was conducted over 24 hours. Twenty ants were placed in individual vials perforated at both ends and mounted at one end of a metal cylinder containing silica gel. Air pumped through a tube containing silica gel, into the metal cylinder, flowed over the ants and out of the cylinder, at a rate of flow adjusted to replace the air in each vial every minute. The ants were weighed before and after each exposure.

Significant differences in the rates of water loss for all experiments were determined using Students t-test.

RESULTS AND DISCUSSION

Section Three

NATURAL HISTORY AND BEHAVIOUR

3.1 Workers

Camponotus detritus workers are polymorphic with a continuous range in size from about 7 to 16 mm in length (head to tip of gaster)(Fig. 3.1). They are dark brick-red except for the gaster, which is black and covered in stiff, off-white hairs. On the dorsal surface of each gaster segment is a smooth, hairless area, giving it a partially striped appearance (Frontispiece). When the gaster is distended with food or liquid, thin, black lines become visible between the segments (Fig. 3.2). Although there are no distinct worker castes, for ease of data collection we divided workers into three size classes: major, media and minor (Table 3.1). The mean ratio of workers in the three classes was 1:1:7.

A typical feature of insect societies is polyethism, the division of labour among workers (Wilson 1971). Caste polyethism refers to task specialization as a result of worker polymorphism. In age polyethism, the task specialization of a worker changes with age; for example young workers remain in the nest and nurse the brood while the older workers spend more time outside the nest. Although *C. detritus* appeared to

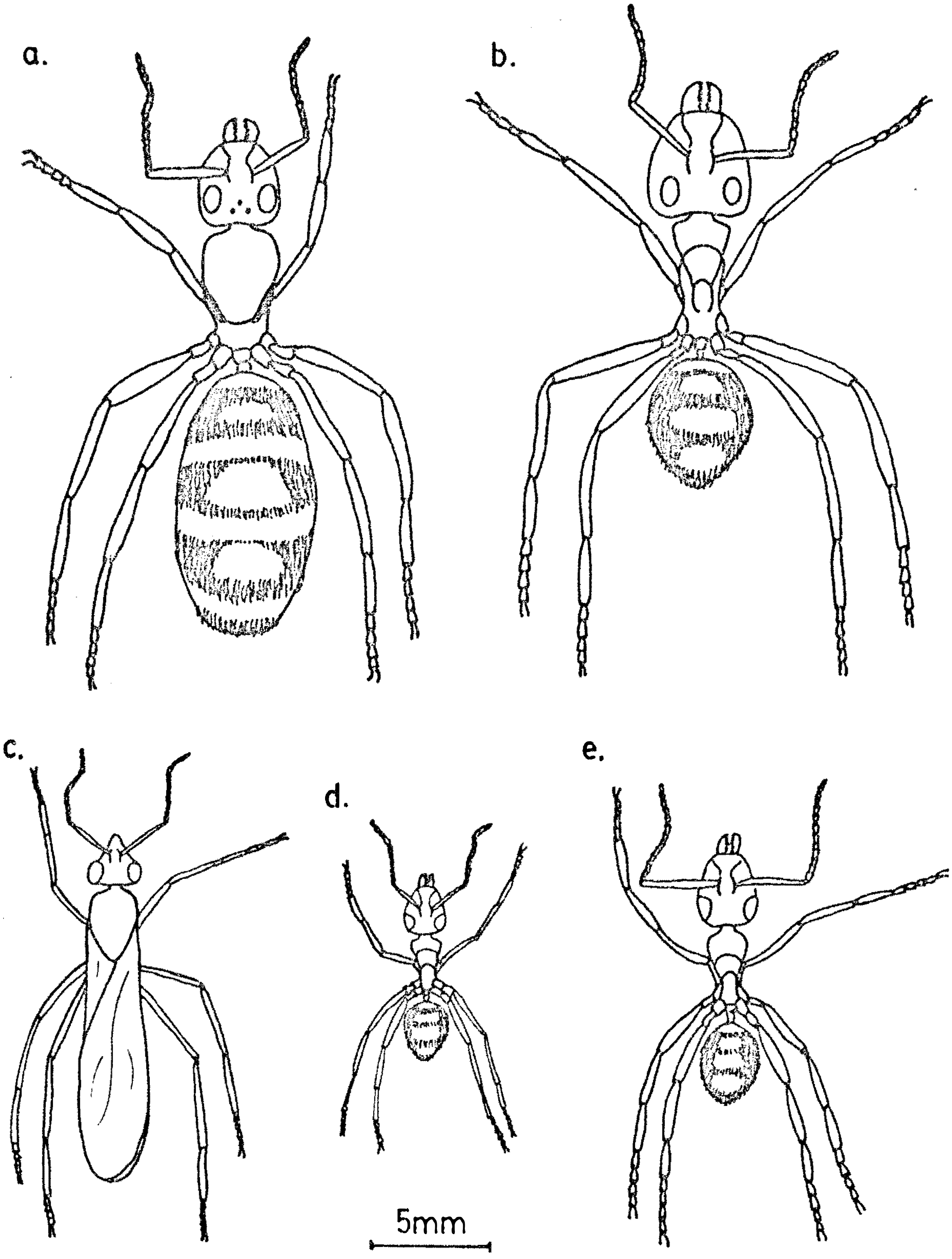


Fig. 3.1 Relative size of members of a *Camponotus detritus* colony.

a. Queen b. Major worker c. Male

d. First worker produced by newly inseminated queen.

e. Average minor worker.

Table 3.1

Mean lengths (head to tip of gaster), wet and dry weights of *Camponotus detritus* ants.
N.D. = No data

	Length (mm)			Wet Weight (mg)			Dry Weight (mg)		
	$\overline{X}$	S.E.	N	$\overline{X}$	S.E.	N	$\overline{X}$	S.E.	N
Major workers	14,33	0,13	30	69,15	1,14	35	25,82	0,69	30
Media workers	12,48	0,14	30	48,47	1,31	54	18,72	0,70	30
Minor workers	10,20	0,12	30	28,62	4,18	55	9,69	0,46	30
Alate males	10,59	0,12	30		N.D.		4,23	0,14	30
Alate females	18,87	0,11	30		N.D.		32,54	2,89	30

exhibit no strict polyethism, with workers of each size class performing most tasks, certain activities appeared to be performed primarily by one size class (Table 3.2). There was, for example, a predominance of major workers involved in colony defense, of media and minor workers in transporting, foraging and trail laying, and of minor workers in nest excavation. The smallest workers were seldom found outside the nest and were invariably associated with the brood.

This form of polyethism based on moderate polymorphism, where major workers are involved in fighting, small and medium workers in nest building and foraging and small workers in brood care, occurs among a number of *Camponotus* species from different habitats (Wilson 1971). In contrast, there are a few *Camponotus* species which have distinct soldier castes with morphological specializations (Wilson 1971).

3.2 Queens

Although identical to the workers in colouration, *C. detritus* queens are slightly longer than major workers, having smaller heads and larger gasters and thoraxes (Fig. 3.1). The gaster of a functionally laying queen is markedly distended and upon dissection reveals a mass of eggs with very little fat reserves (Fig. 3.3). Queens were found in only 10 out of 36 excavated nests. Two of these nests contained two queens each whereas one, the largest excavated and housing almost 20 000 individuals, contained eight dealate females. The remaining seven nests had only one queen each.

Table 3.2

Ratios of major: media: minor *Camponotus detritus* workers involved in various activities outside the nest.

N = total number observed

Activity	Major	Media	Minor	N
Foraging	1	1,5	10	1 000
Transporting Food or Nesting Materials to Nest	1	4,9	10	239
Transporting Brood or Adults Outside Nest	1	11	11	23
Transportee	0	1	19	20
Nest Excavation	1	2,7	19,3	69
Fighting	4,8	2,1	1	135
Trail Laying	1	1,3	3,7	54
Mean Ratio of All Workers (Data from Excavations)	1	1	7	108 000

Fig. 3.2 *Camponotus detritus* worker with distended gaster.

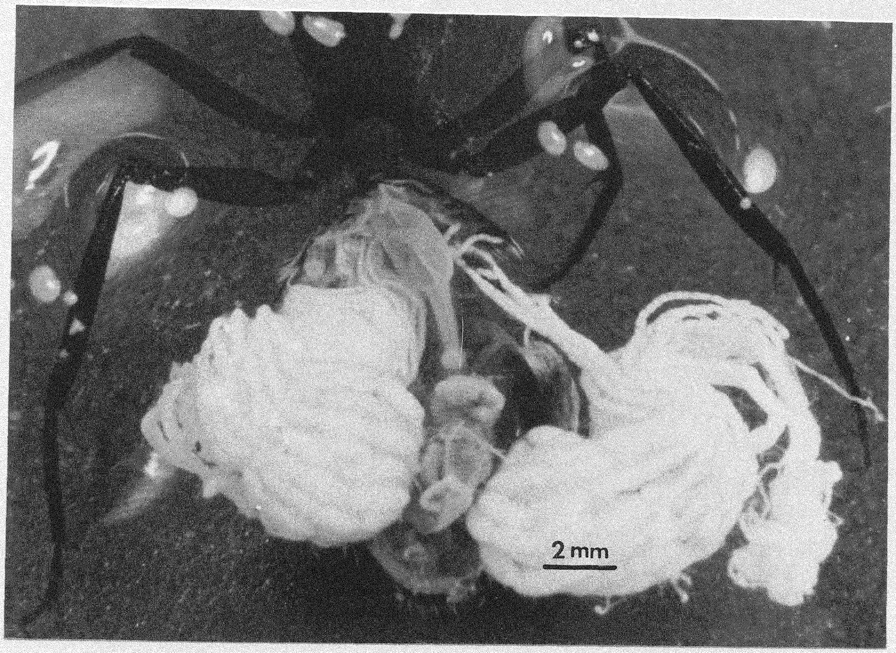


Fig. 3.3 *Camponotus detritus* queen dissected to show ovaries containing eggs (two large white structures) (Photo:L. Praetorius).

There are three possible explanations for the apparent absence of queens in *C. detritus* nests. The most obvious one is that excavations were incomplete and of insufficient depth to reveal the royal chambers. Chew (1959) cites the example of *Myrmecocystus melliger*, a species which Wheeler (1908 in Chew 1959) thought formed small colonies with shallow chambers. Later, Creighton and Crandall (1954 in Chew 1959) found a single small tunnel descending from the nest vertically through a layer of calcrete to a depth of about 16 feet. Here they found a royal chamber and hundreds of repletes which had not previously been recorded for this species. In the Namib dunes, *C. detritus* is only able to make nests among the roots of vegetation because there is nothing to bind the sand below root level. As most of our excavations went below this level with no further evidence of nest material, it seems unlikely that excavations were incomplete.

Another possibility is that the queen may have escaped, or been overlooked. This is unlikely as most of the ants in a nest were collected and later counted individually. Although the queen is similar to the workers in appearance, she is sufficiently different not to be mistaken for a worker.

A third explanation is that many *C. detritus* nests are queenless and workers either transport brood across from a nest without a queen or are able to lay eggs parthenogenically. Nest splitting has been witnessed in *C. detritus* (Section 5.5) where workers transport brood from one established nest to another. It is therefore probable that daughter nests are queenless and workers transport brood from the mother nest. Skaife (1961) found queens in only two nests out of fifty of the ubiquitous southern African species, *C. maculatus*, and four out of twelve nests of *C. werthi*. In both the above species as well as in *C. detritus*, queenless nests contained brood.

Hymenoptera have a haplodiploid form of sex determination in which unfertilized eggs produce haploid males while fertilized eggs produce diploid females. All workers are females which may or may not be sterile. It is possible among some species of ants for workers to lay female-producing eggs by a form of parthenogenesis known as thelytoky (Wilson 1971). These eggs may produce workers or reproductive females. Generally this is a deviation from the norm, but according to Ledoux (1949, 1950 in Wilson 1971) the African weaver ant, *Oecophylla longinoda*, exhibits a true alternation of generations. There appear to be no records of thelytoky among *Camponotus* however, but *Cataglyphis cursor*, a closely related species from the drier areas of France, has workers which are capable of producing females by thelytoky (Cagniant 1979, 1980). Queenless *C. cursor* colonies reared in the laboratory produced workers as well as alate males and females, but the total productivity was nearly half of what it was when a queen was present (Cagniant 1980).

Polygynous colonies are not unusual among some ant species (Wilson 1971) but seem to be uncommon in the genus *Camponotus* (Mintzer 1979). An exception is the weaver ant *Camponotus (Myrmobrachys) senex textor* which may have as many as twenty-three queens in one nest (Schremmer 1979). Large colonies of *C. herculeanus* and *C. ligniperda* often contain several queens which are intolerant of each other and maintain individual territories at different ends of the nest (Hölldobler 1962). *Camponotus detritus* queens from the same nest, in contrast, showed no signs of antagonism towards one another. Although eight females were found in the largest nest, neither of the nests in which two queens were found were particilarly large. It is, however, possible that only one queen was functionally laying and that the others were dealates which had not left the nest on a nuptial flight.

Perhaps, if conditions are unfavourable for a nuptial flight, females lose their wings and remain in the nest as a living food reserve (Crewe, pers. comm.). Workers of certain nocturnal, deserticolous *Camponotus* species have exceptionally well developed fat reserves which act as a food storage system for the colony (Emery 1898 in Wilson 1971). This condition, known as adipogastry, could exist among dealate *C. detritus* females. For example, on one occasion, after rainfall, nine dealate females together with workers emerged from a nest to drink moisture from the sand. Dissection of these females revealed very reduced ovaries, but large fat reserves. Some dealates might assume the role of workers, since they have been observed foraging with workers up to 15 m from the nest, but this was rather unusual.

It is suggested that *C. detritus* colonies are monogynous with brood being transported from the mother nest to queenless daughter nests by the workers. Variable numbers of dealate non-reproductive females may be associated with the colonies. The territorial behaviour of *C. detritus* substantiates this idea since monogyny is often associated with colony territoriality (Hölldobler and Wilson 1977).

3.3 Alate Reproductives

Virgin females of *C. detritus* resemble queens, but lack a distended gaster and have thin, membranous wings (Fig. 3.4), whereas males are morphologically very different, being much smaller and totally black (Fig. 3.5 and Table 3.1). A few alates were found in some nests excavated in April, May and June, but the majority were found in December (Table 3.3). Alates were observed outside nests in January, April, June and August, and nuptial flights occurred in April (Section 3.4). Presumably, as in other ant species (Wilson 1971), a colony must reach a certain state of maturity before alates are produced. Pricer (1908) estimated that colonies of *Camponotus pennsylvanicus* and *C. ferrugineus* require from three to six years to reach maturity.

No alates of *C. detritus* were found in September or October, but nests excavated in early October contained very large larvae and pupae, and in late October pupae of alate females. This suggests that sexual brood may be produced towards the end of winter and alates remain in the nest until conditions are favourable for a nuptial flight (Section 3.4). Failing this, alates possibly remain in the nest until the following winter. For instance, not all alates of *Myrmecocystus mexicanus* participate in the nuptial flight; some return to the colony afterwards (Conway 1980). Like *C. detritus*, alates of two southern African species, *C. maculatus* and *C. werthi* occur in the nest in autumn and winter (Skaife 1961).

Although both alate males and alate females taken from nests appeared to be negatively phototactic, moving to the darkest areas available, as

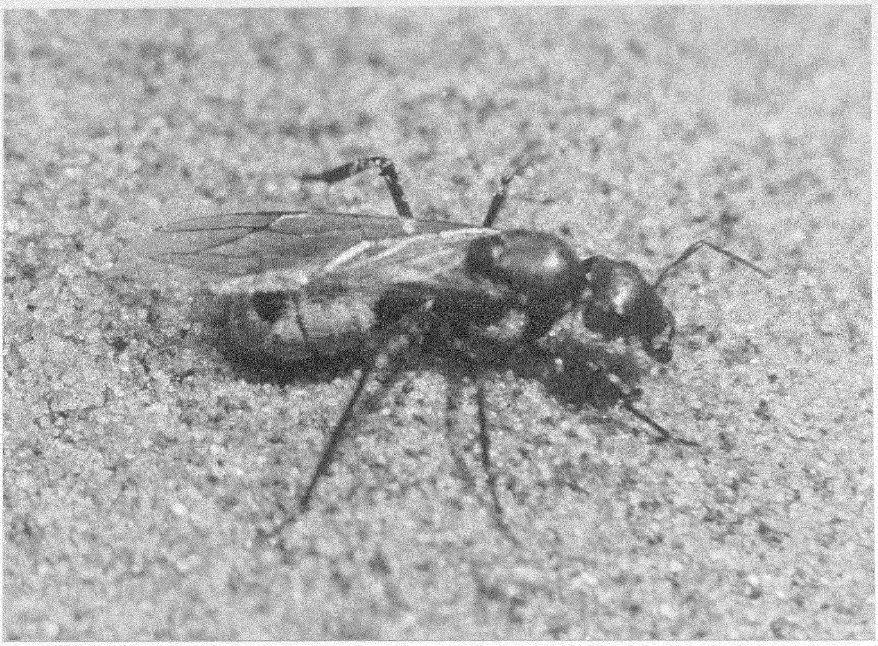


Fig. 3.4 Alate female *Camponotus detritus*.

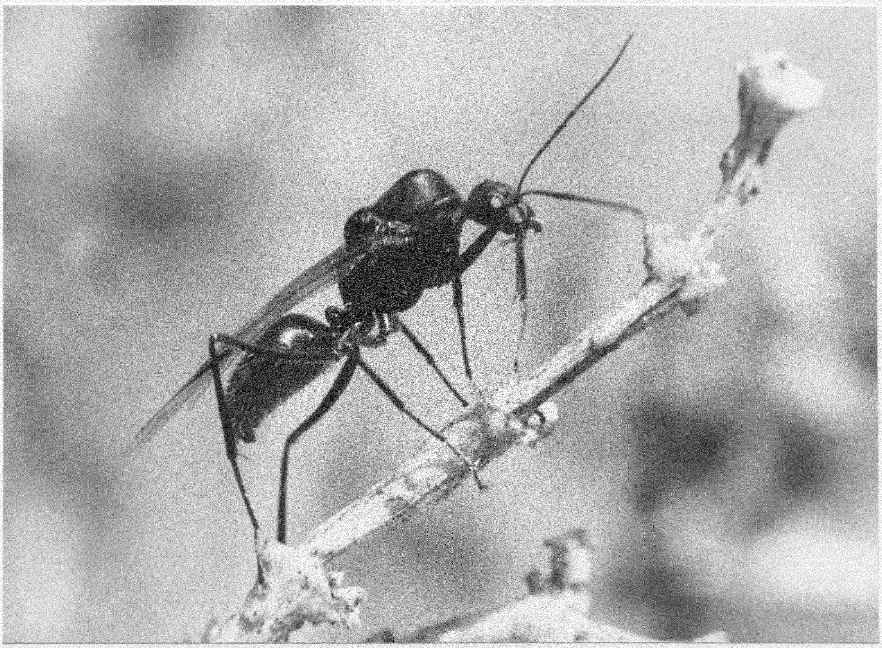


Fig. 3.5 Alate male *Camponotus detritus*.

Table 3.3

Seasonality of alate production in *Camponotus detritus* nests. Percentages are of the total number of adults per nest of all nests excavated.

Month	Males (%)		Females (%)		Number of nests	
	$\overline{x}$	S.D.	$\overline{x}$	S.D.	Housing alates	Excavated
January	0		0		0	4
April	present		present		1	2
May	0,9	0,9	0,2	0,3	4	7
June	1,3	1,9	0,1	0,1	3	4
July	0		0		0	1
September	0		0		0	4
October	0		0		0	11
December	0,4	0,9	24,2	8,6	5	5

mentioned previously they were occasionally observed outside the nest. Usually they remained near the nest entrance, but one alate female was seen walking 20 m away from the nest.

An example of this unusual ant behaviour was seen at a Gobabeb nest in April 1981, ten days after the nuptial flight which occurred at Mniszechi's Vlei (Section 3.4) (Gobabeb received no rainfall in April). At 07h00 one morning six alate males were seen outside the nest. From three to six remained outside until midday, after which they disappeared, reappearing in the late afternoon. A number had their heads in *Trianthema hereroensis* flowers as if foraging (Fig. 3.6). At night more than 20 were outside the nest. At all times while the males were present 100 to 200 workers were also near the nest entrance. Occasionally some attempted to carry or drag the males back into the nest (Section 3.11). This behaviour continued for at least five days and for three further days only one or two males came outside. We then simulated rainfall by pouring the equivalent of 4 mm water around the nest and within minutes about 30 males plus many workers emerged. The following day 20 males were again outside the nest. At no time were winged females present and, except for the few males at a sister nest belonging to the same colony, none of the other twelve nests in the area had males outside. Weather conditions during the period under discussion were not unusual. On the first day mean air temperature was 34°C during the day and 26°C at night. Humidity was low, 10% during the day and 17% at night. The wind in the morning averaged 23 km h^{-1} from the north-east until midday when it dropped and remained fairly calm for the rest of the day.

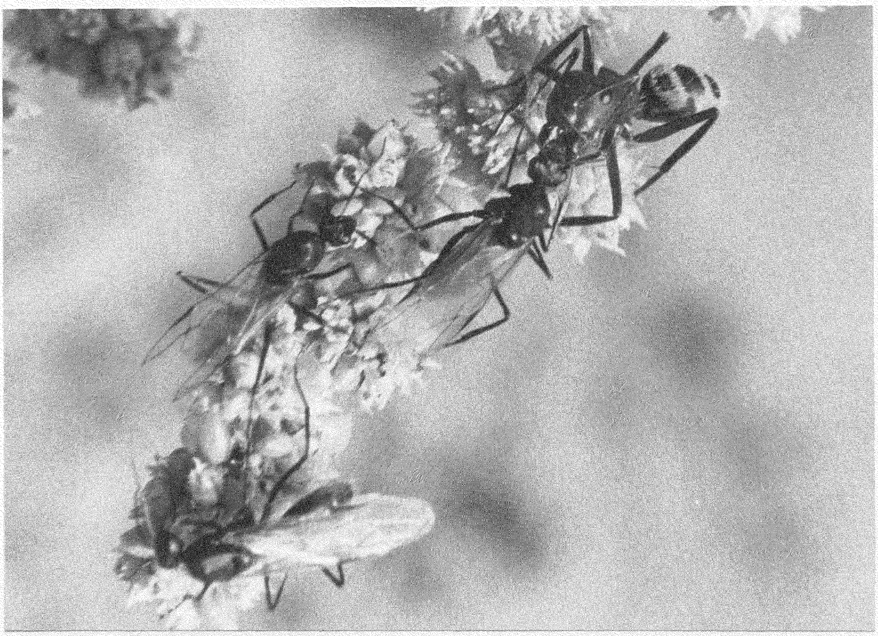


Fig. 3.6 *Camponotus detritus* males foraging on *Trianthema hereroensis*. Note trophallaxis between worker and male (top right hand corner).

Although foraging of alates appears to be unusual, winged reproductives of *Myrmecocystus mexicanus* were seen outside nest entrances a few days before or after nuptial flights (Conway 1980). Conway suggested that the appearance of reproductives outside the nest prior to swarming may be a result of increased restlessness at the hour of the nuptial flight due to a circadian rhythm in the sexuals. Since *C. detritus* workers were outside the nest most of the time, a similar circadian rhythm was unlikely to be affecting them, but some other form of endogenous rhythm could have been governing their behaviour. For instance, males of the American *C. herculeanus* and *C. ligniperda* remain in the adult phase for 9 to 10 months after eclosion until their nuptial flight early the following summer. Initially they are in an active "social phase", receiving food from workers and passing it on to others. Later they enter a "sexual phase" in which they feed very little and rely on their own tissue reserves. Simultaneously they change from being negatively to positively phototactic (Hölldobler 1964 in Wilson 1971). A similar change in *C. detritus* males may have caused them to leave the nest.

3.4 Nuptial Flight

Among social insects, mating often occurs during or immediately after the nuptial flight. Hundreds of males and females from different colonies meet and copulate either in the air or on the ground, after which, male ants die and the females shed their wings and begin a new colony (Wilson 1971) (Section 3.5).

Only one nuptial flight of *C. detritus* was witnessed. This occurred in the eastern dunes near the Mniszechi's Vlei study site. On the afternoon of 9 April 1981 a series of thunder-showers produced 3 mm of rainfall. The following day was sunny and at 10h00 we noticed hundreds of males at the top of the tallest grass stems above a nest, while females and workers were moving about outside the nest entrance. Half an hour later the males took to the air and by 10h45 the majority had left the grass clump. Many did not fly far, landing within 5 m of the nest. At 10h50 the females began climbing up the grass stems before flying away. Some fell off the grass and had to climb up again while others took off from the ground. By 11h15 the last female had flown. At this time the air temperature was approximately 33 - 35°C and the sand was still damp. No copulations of *C. detritus* were witnessed. Nuptial flights apparently occurred at other nests as well since throughout the rest of that day we found dealate females and dead males over a distance of about 5 km. Contrary to expectation few birds or lizards were seen collecting alates. The males became prey to other ant species and spiders while a number of the dealate females were attacked by other ants and conspecific workers.

3.5 Colony Foundation

Colony foundation may take on a number of forms in ants. Generally, among the more advanced ants claustral foundation occurs in which the new queen remains inside her initial cell and nourishes her first brood entirely from her own metabolized fat bodies and alary muscle tissue. Less commonly she may forage outside the new nest. Sometimes, more than one queen may found a colony together, a condition known as pleometrosis (Wilson 1971).

After the nuptial flight, *C. detritus* females were seen to be excavating holes in the damp sand at the base of vegetation. When taken to the laboratory, these females immediately sealed off the entrances to their nest boxes and, although food was placed outside, they did not forage. This behaviour suggests that *C. detritus* has a claustral form of colony foundation, similar to that of the seven American species of *Camponotus* studied by Mintzer (1979).

All seven *C. detritus* queens collected after their nuptial flight laid eggs which developed into pupae in the laboratory. Eggs took from 19 to 22 days to become larvae and a further 11 to 15 days to pupate. The exact length of time taken for workers to eclose is unknown, but was probably about 30 days. Only one queen successfully reared two workers (about 4 mm long) (Fig. 3.1). It is usual among ants for the first workers to be smaller than subsequent ones (Pricer 1908, Wilson 1971). The development time for the first brood was similar to that of other *Camponotus* species (Mintzer 1979). Among the seven species which he studied in the laboratory, the egg to larva period was 20 - 33 days, larva to pupa took 12 - 14 days and first workers took a further 17 - 28 days to eclose.

3.6 Brood

Although comparable data on other desert ant species were not found, the relationship between wet weight and length of *C. detritus* brood, excluding eggs, is shown in Fig. 3.7. This would correspond with the increase in wet weight with time. There was a slight drop in weight of brood of any one size as it metamorphozed from larvae to pupae containing adults prior to eclosion. This is to be expected since

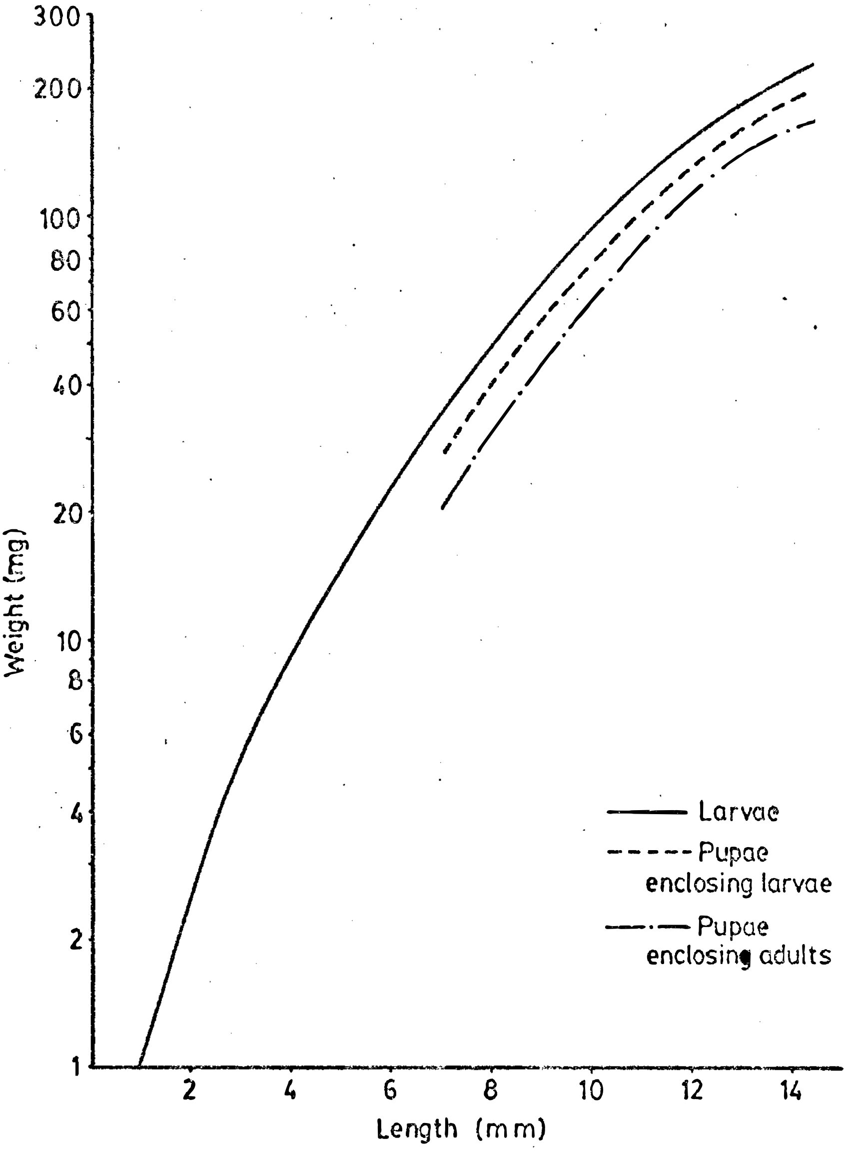


Fig. 3.7 Relationship between wet weight (expressed on a log. scale) and length of *Camponotus detritus* brood.

larvae cease feeding after pupation and live on stored fat reserves until eclosion. The mean wet weight of eggs was 0,43 ± 0,10 mg and length was 1,51 ± 0,07 mm. Dry weights of brood are shown in Table 3.4.

Unlike many temperate ant species which show marked seasonality in brood production (Wallwork 1970, Wilson 1971, Dartigues and Passera 1979), every *C. detritus* nest excavated contained brood at all stages of development. There was, however, great variability in the ratio of brood to workers and in the number of callows present per nest, which appeared to be correlated neither with season nor location of nests across the environmental gradient (Fig. 3.8). Similarly, the relative proportions of different developmental stages of the brood varied between nests in the same area, as indicated by the large standard errors in Table 3.5. The higher proportion of pupae found at Elephant Valley in January as compared with Rooibank, may have been a result of seasonal brood development, but the data are insufficient to be conclusive.

Other southern African ant species similarly show variation in the relative proportions of brood present throughout the year, but this is generally associated with climate (Broekhuysen 1948, Steyn 1954). Peak numbers of brood of *Camponotus maculatus* occur in midsummer and eclosion takes place in autumn (Skaife 1961). In contrast, the ratio of workers to larvae of the temperate species, *Myrmica ruginodus macrogyna* tends to be fairly constant (Brian 1950). The ratio of *C. detritus* workers to pupae varied from 1 : 0,02 to 1 0,58. Similarly workers : pupae ratios of the East African weaver ant, *Oecophyla longinoda*, varied from 1 : 0,03 to 1 : 0,87 (Way 1954). In contrast, the ratio within a single nest of

Table 3.4

Mean dry weights of *Camponotus detritus* brood.

Brood Stage	Dry Weight (mg) $\bar{x}$	S.E.	N
Larvae			
1 - 4 mm	1,22	0,09	35
5 - 8 mm	5,01	0,29	92
9 - 13 mm	16,15	0,52	50
Pupae Containing Larvae			
7 - 10 mm	8,96	0,57	50
10 - 14 mm	12,72	0,48	40
Pupae Containing Adults			
7 - 10 mm	4,60	0,28	100
11 - 14 mm	10,43	0,54	24

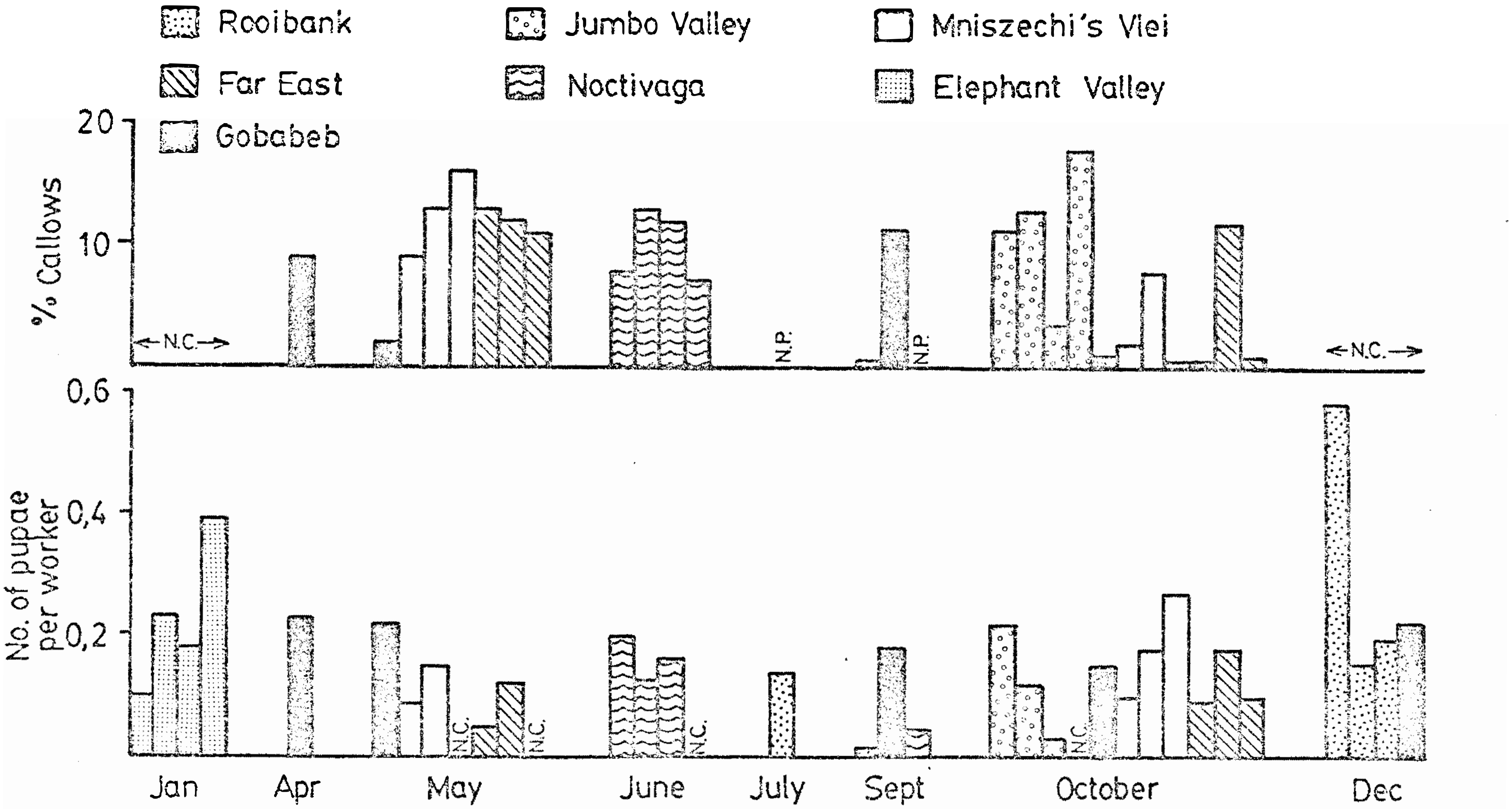


Fig. 3.8 Number of callows (newly eclosed workers) expressed as a percentage of the total number of workers (above) and number of pupae per worker (including callows) (below) of every *Camponotus detritus* nest excavated throughout the year. Various shadings represent the site at which each nest was excavated. N.P. = Not present. N.C. = Present but not counted.

Table 3.5

Proportions of different developmental stages of the brood from *Camponotus detritus* nest excavations. Percentages are of the total biomass (dry weight) of the brood, excluding eggs.

Brood Stage	Rooibank (14 km inland) December 1980		Elephant Valley (87 km inland) January 1981	
	(%) $\bar{x}$	S.E.	(%) $\bar{x}$	S.E.
Larvae				
0 - 4 mm	20	7	11	6
5 - 8 mm	29	3	22	7
9 mm	8	4	4	1
Pupae				
10 mm with larva	10	2	21	4
10 mm with adult	12	6	15	5
10 mm with larva	8	6	12	2
10 mm with adult	13	4	15	6
Total Larvae	58	7	38	11
Total Pupae	42	7	62	11
Number of Nests Excavated	4		4	

the tropical *Camponotus solon* was 1 : 0,84.

It would appear therefore, that other factors besides season and climate, for example colony age or availability of food, affect brood production in *C. detritus*. Further detailed study of the development of brood would provide valuable data on production in this dune species.

On one occasion at 02h00 I saw six large pupae lying on the surface of a detritus accumulation on a large nest. Many workers were moving about outside the nest. Whitford, Depree and Johnson (1980) observed similar behaviour in *Novomessor albisetosus* when larvae and pupae were carried to the surface during the evening. They proposed that the nest microclimate may be conducive to the growth of micro-organisms and that exposure of the brood to lower temperatures and humidity on the surface may inhibit this growth. The particular night in question at Gobabeb was a warm, dry night (26°C surface temperature, 8 % rh).

3.7 Callows

Young *C. detritus* workers which eclosed in the laboratory were yellow with white gaster hairs. As the cuticle gradually darkened the gaster hairs became off-white, until after about 20 days the ants were the same colour as mature adults. In general, ants which are black when mature have drab or yellowish callows while those which are bright red have sulphur yellow or orange callows (Wheeler 1910).

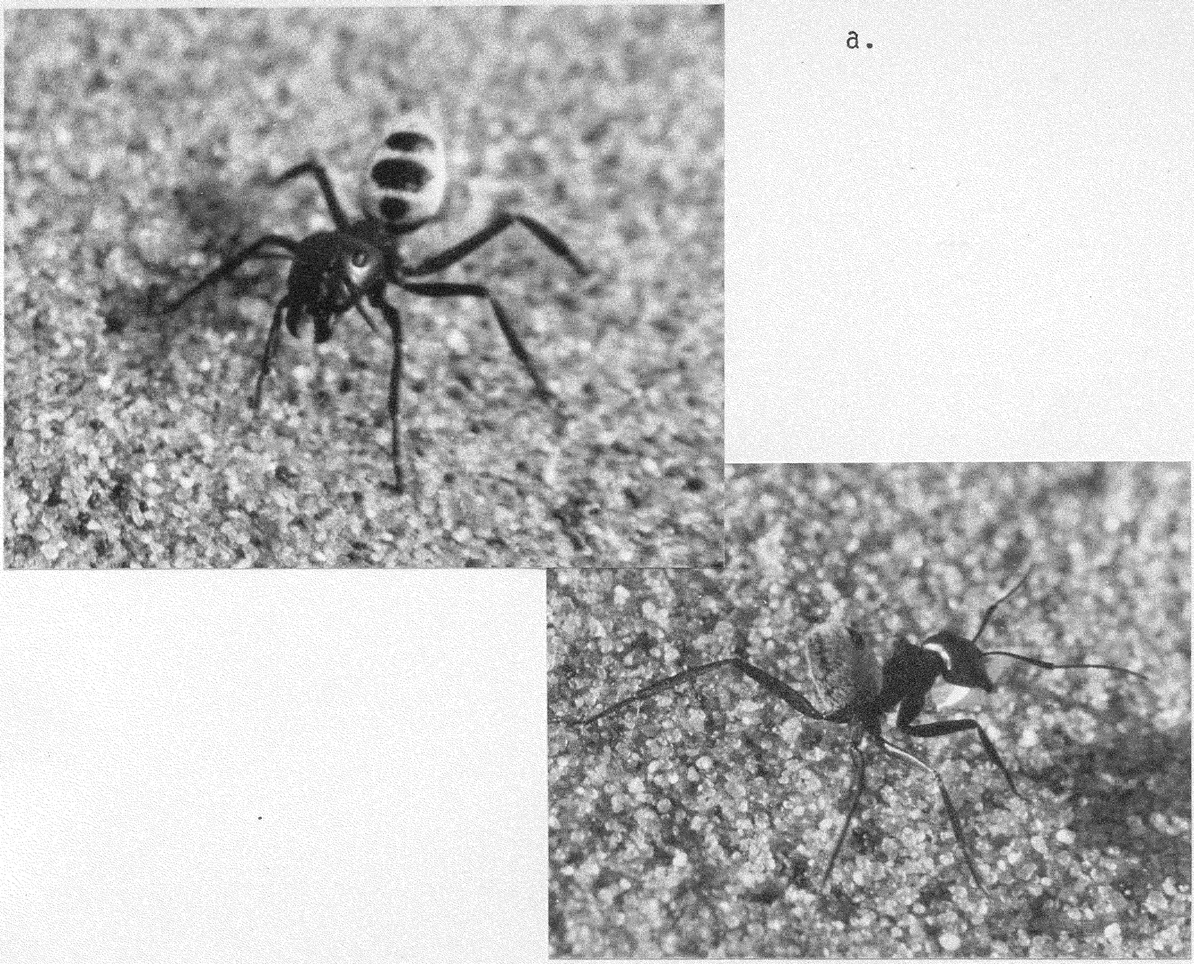
In the laboratory, *C. detritus* callows exhibited a negative phototactic response. The length of time which they spent inside the nest assisting the older workers with brood care was not established. In the field, workers which were lighter red than most, and therefore probably 15 - 20 days old, sometimes appeared and remained near the nest entrance, retreating inside at the slightest disturbance.

3.8 Aggressive Behaviour

The typical alarm response of *C. detritus* workers was to first face the source of alarm with jaws open and gaster raised above the level of the rest of the body (Fig. 3.9a). Continued provocation caused them either to bite the intruder or to tuck the gaster underneath the thorax and spray formic acid on the intruder. Often both actions were performed simultaneously although the response of workers towards intruders varied (Fig. 3.9b). Major workers tended to attack more readily than minors, while the smallest minors usually retreated rapidly. All workers, as well as females, exhibited the same aggressive posture with raised gaster. Males, in contrast, did not exhibit any aggression. Dobrzańska (1959 in Wilson 1971) showed that the aggressiveness of ants was strongly correlated with proximity of workers to their nest, which in turn was associated with their age. This seemed to be the case also among *C. detritus* workers.

3.9 Territoriality

Many species of social insects are known to defend the area immediately around their nests (Wheeler 1910,Brian 1965, Wilson 1971). Defense of food sites apparently evolved when ants began to utilise persistant carbohydrate food sources (Wilson 1971), but spread to include other



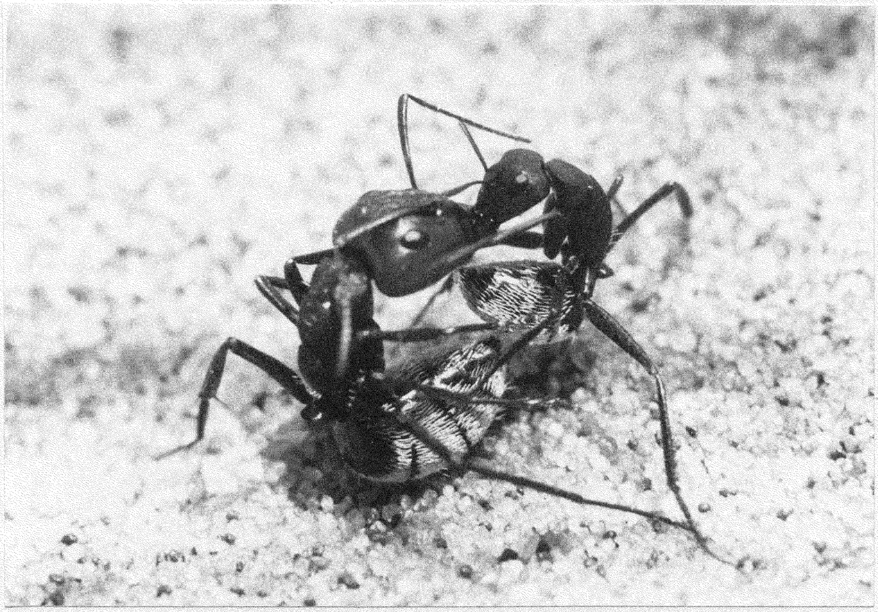


Fig. 3.9 a. Aggressive posture of *Camponotus detritus* workers.
b. Two fighting workers. Note that the gaster is tucked underneath the body to spray formic acid (Photo: E. McClain).

food sources as well (Wilson 1971, Hölldobler 1974, 1976). Among social insects the establishment and maintenance of territories is based upon a division of labour and a complex communication system. Whereas a solitary animal can only be in one place at one time doing one thing, members of a colony can be in many places doing many things simultaneously (Hölldobler and Lumsden 1980). Territorial behaviour varies among species depending on the nature of the food sources and normal behaviour patterns of the colony (Hölldobler and Lumsden 1980).

Camponotus detritus appeared to be a territorial species, defending the nest and foraging sites against conspecifics. Colonies comprised from one to four nests, with constant movement of ants between sister nests (Table 3.6). Territory size varied considerably, probably as a function of the size of the colony and the abundance of scale insects present (Fig. 3.10 and Table 3.6). Nests were seldom situated in the middle of territories and "foreign" nests were sometimes closer together than sister nests belonging to the same colony. The plants hosting scale insects which were included in a territory were not necessarily those closest to the nest. For example, nest S was 170 m from its furthest foraging grounds while a plant only 25 m from the nest was utilized by a neighbouring colony. The factors determining possession of plants are probably a combination of time (the first workers to find an unexploited food source take possession of it) and aggression.

Foraging areas of most ant species are seldom circular with a nest in the centre (Brian 1955, Hölldobler 1971, Stradling 1978, Skinner 1980a). They tend to be rather irregular in shape depending on the distribution of food resources in the territory, with territorities of neighbouring

Table 3.6

Camponotus detritus territories in the dunes near Gobabeb.

A = Mean distance between nests of the same colony.

B = Nearest nest of a "foreign" colony to any nest of the colony under consideration.

C = The greatest distance between a nest and a scale insect-hosting plant within one territory.

D = The nearest distances from a nest of the colony under consideration to a scale-hosting plant of a neighbouring territory.

All distances in metres. ? = Unknown.

Territories	Territory size (ha)	Number of nests	A		B	C	D
			x	S.E.			
Marmaduke's March Sept 1980	5,5	3	170,7	96,9	32	185	32
South Kahani April 1980	2,1	3	121,7	39,5	?	155	?
Bannoch Burn Feb 1982:							
KB Territory	0,6	3	18,3	5,5	35	82	38
CD Territory	0,5	1	-	-	75	35	75
SE Territory	1,5	1	-	-	75	170	25

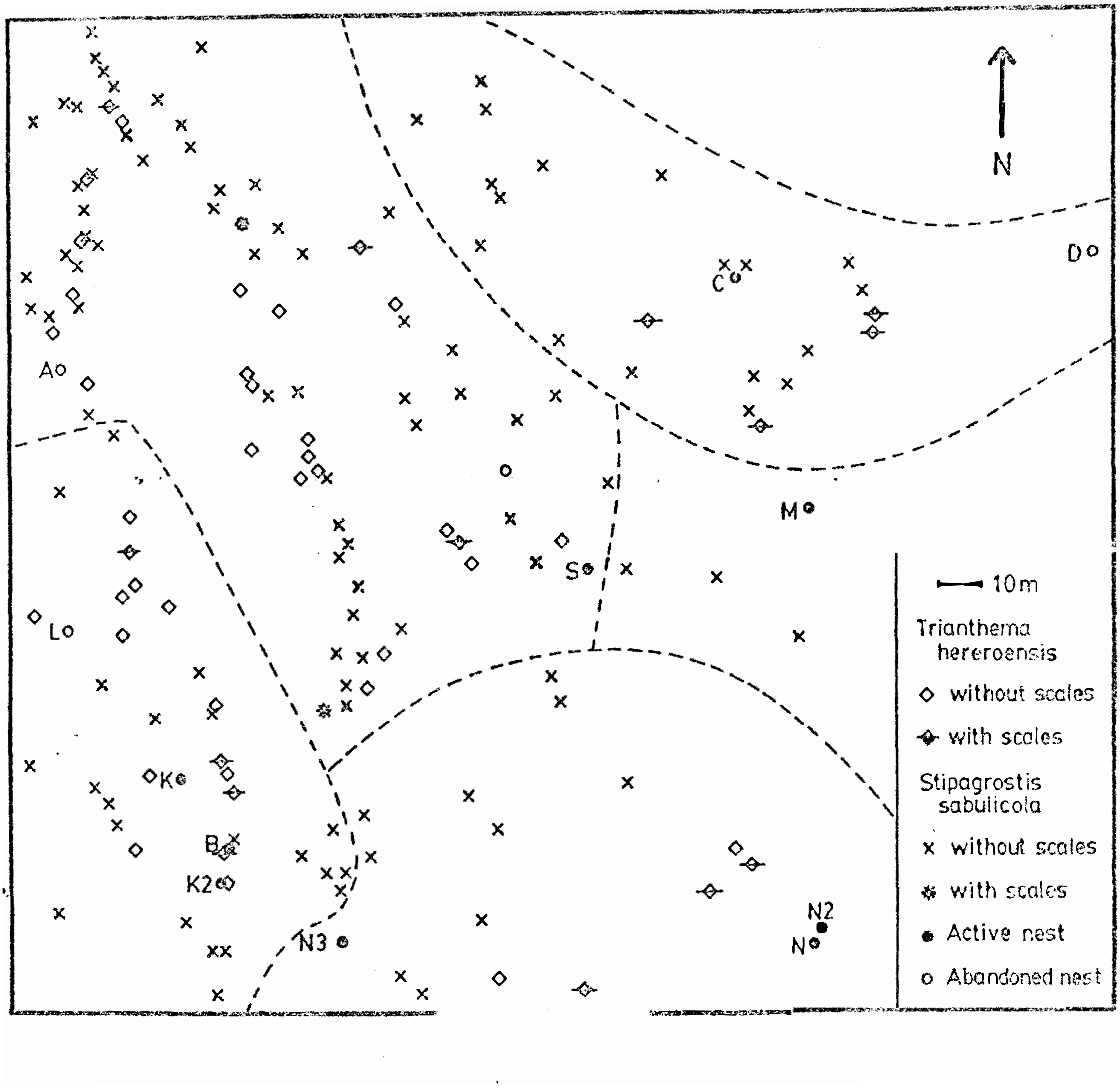


Fig. 3.10 Territories (outlines indicated by dotted lines) of *Camponotus detritus* colonies at Bannoch Burn, Gobabeb in February 1982 showing nests (designated by letters as used in text) and all live plants (*T. hereroensis* and *S. sabulicola)*, with or without scale insects.

colonies fitting together into a mosaic. Bernstein and Gobbel(1979) found that the size of the foraging area of desert harvester ants was negatively correlated with food density.

If conspecifics from "foreign" *C. detritus* colonies encountered one another they usually made brief antennal contact, while both exhibited the aggressive, gaster-raised posture. Following this, one ant either retreated or attacked, usually the latter. Generally two or three other nearby workers joined in and the intruder was dismembered.(Fig. 3.11). No defensive recruitment was ever witnessed but there were sometimes large conflicts involving up to fifty ants, invariably occurring near a nest or food source.

Camponotus detritus exhibited two aspects of territoriality common to most ant species. Firstly, although defended territories were persistant throughout the life of the colony, they changed in size and shape as scale-infested plants sometimes died and the ants were forced to search for new foraging grounds. Secondly, hostility was most intense between alien colonies of the same species, becoming progressively less the greater the taxonomic difference between species (Wilson 1971). *Camponotus detritus* workers were highly aggressive towards "foreign" conspecifics and attacked *C. mystaceus* and *C. maculatus* workers, but showed no hostility towards ants of other genera.

Territorial fighting has been observed in various *Camponotus* species (Wilson 1971). One East African species has a defense recruitment system whereby hundreds of workers are recruited when scout ants patrolling the territory encounter intruders (Hölldobler and Lumsden 1980).

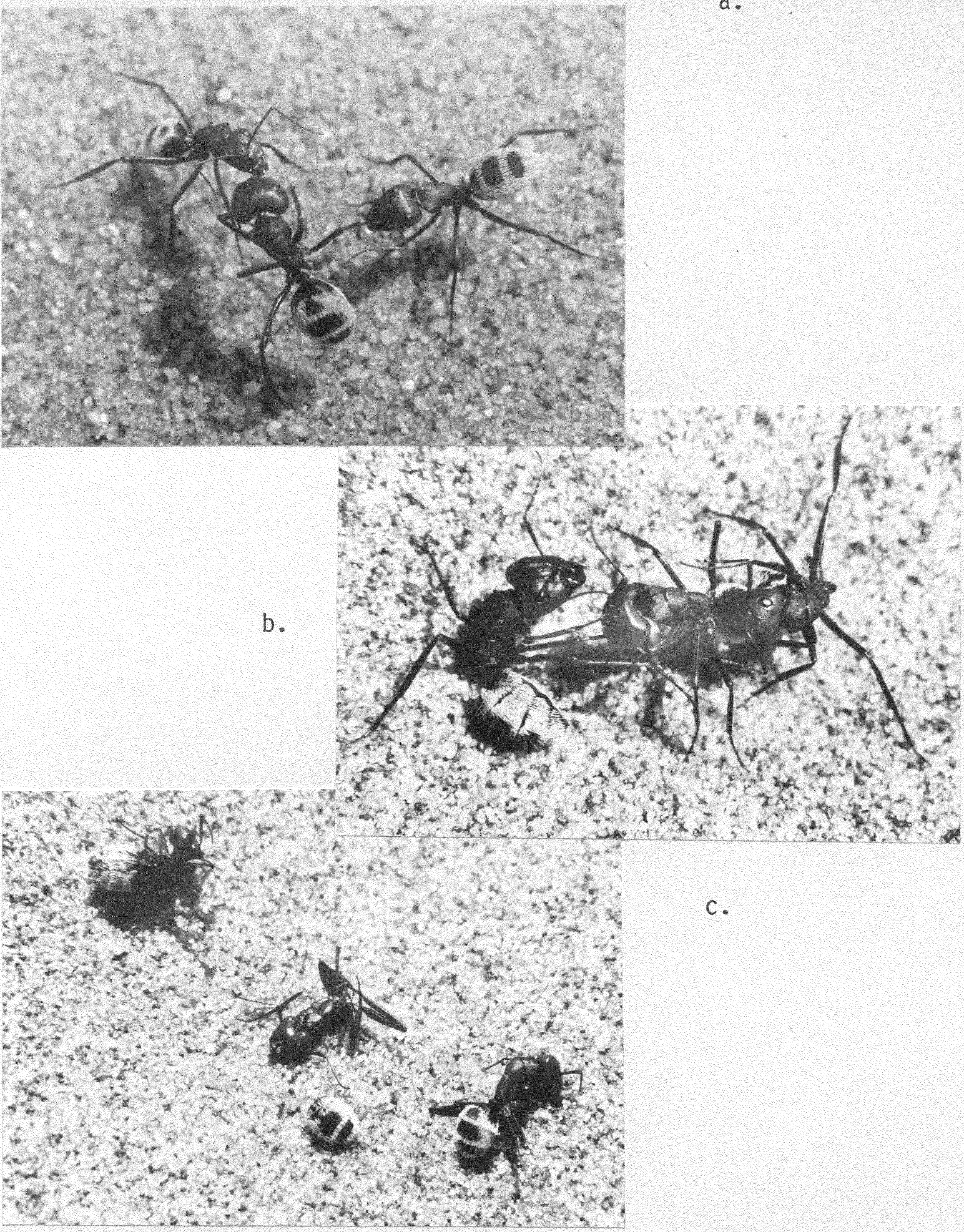


Fig. 3.11 Fighting between *Camponotus detritus* workers.

a. Two workers pulling on an "alien".

b. Worker on the right biting through the petiole of centre worker. Left and right-hand workers from the same colony.

c. The result of a fight.

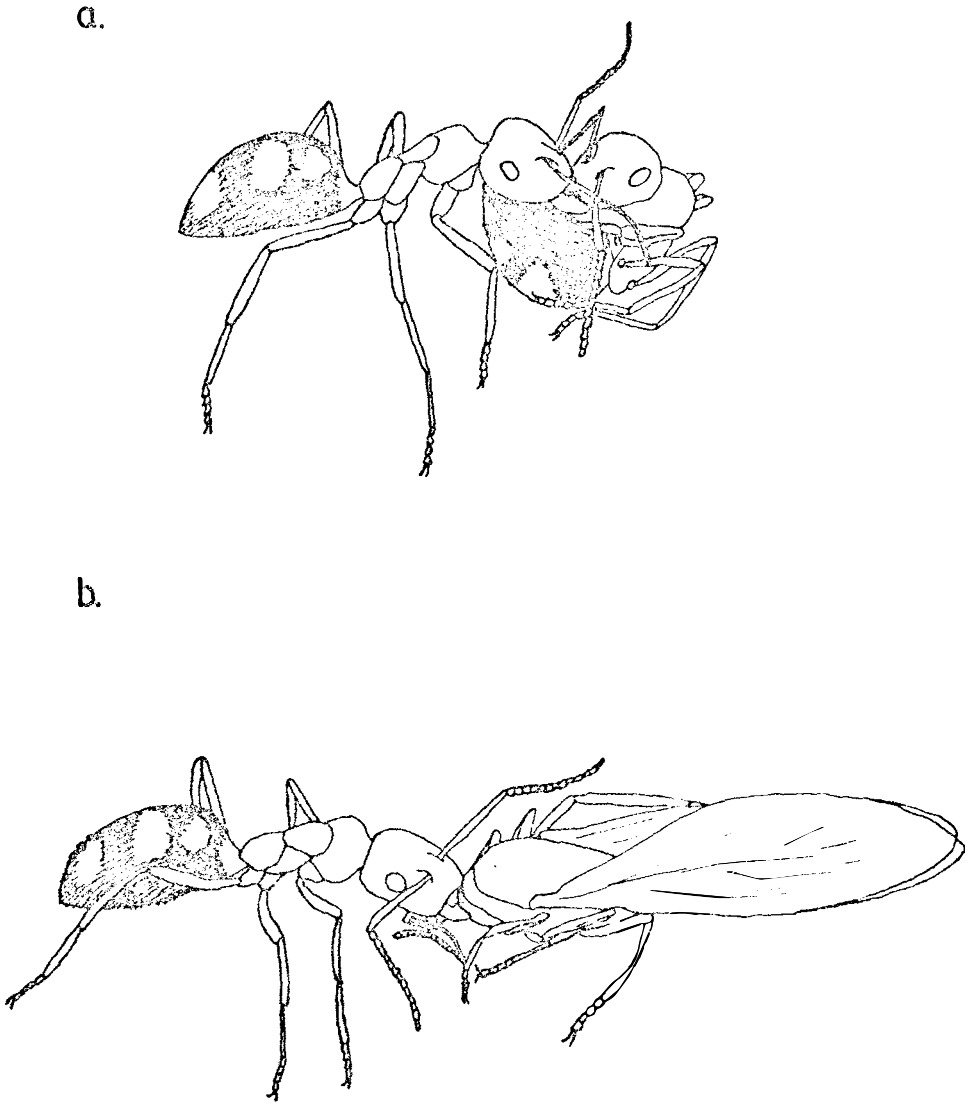


Fig. 3.12 Adult transport in *Camponotus detritus*

a. One worker (left) transporting another.

b. A worker (left) transporting a male.

3.12 Trophallaxis

Trophallaxis is the exchange of alimentary liquid between colony members. The frequency of trophallaxis is variable among ant species and seems to increase with the relative amount of liquid in the natural diet (Wilson 1971). The crops of most ant species which feed on nectar or honeydew are capable of considerable distention (Wilson 1971). As Wilson (1971) describes it "the crops of all the workers taken together serve as a 'social stomach' from which the colony as a whole draws nourishment". Frequently observed among *C. detritus* workers and between workers and reproductives (Fig. 3.6), trophallaxis occurred while ants were in the nest, on plants or on the sand surface. The gasters of *C. detritus* were capable of marked distention, noticeable by the black rings around the gaster as previously described (Fig. 3.2). Unlike the Australian ant, *C. inflatus*, and the desert ants of the genus *Myrmecocystus*, no replete caste was found. In the latter species the gasters of certain major workers become distended with liquid to such an extent that the ants cannot walk and are obliged to remain in the nest as a living food container or "honeypot" (Wilson 1971).

3.13 Nest Cleaning

Like all social insects (Wilson 1971), *C. detritus* workers removed dead individuals, pupal cases and other waste material from their nest. Unlike some species, they had no specific rubbish pile, but simply walked 0,5 to 1 m away from the nest and deposited the items. In an environmemt such as the Namib where fairly strong winds are common, discarded material is rapidly blown away. Pupal cases were also found packed into blind ends of tunnels or incorporated into the detritus lining of the nest.

3.14 Orientation

Ants orientate by various means such as the use of visual cues, polarized light, angle of the sun's rays, anemomenotaxis or the strength of the wind, and by laying pheromone trails (Wilson 1971, Harkness and Wehner 1977, Wehner and Räber 1979). *Camponotus detritus* did not appear to use pheromone trails for orientation. The movement of sand would probably rapidly destroy pheromone trails (Section 3.15). The only workers observed to be laying trails were those recruiting nestmates to new food or nest sites (Section 3.15). The majority of workers moved singly across the sand, and none of these single ants were ever observed laying a trail. Nor did all workers follow the same path, although they all moved in the same general direction.

Since *C. detritus* workers were never observed walking across the sand at night, it is possible that they use a combination of visual cues and the sun's rays. Visual cues are unlikely to be their only form of navigation since landmarks are sparse in the dunes and individual ants may walk across 20 to 40 m of bare sand in search of food. In the eastern dunes, where the sand is coarser and more stable, trails formed by the mechanical action of many feet across the same stretch of sand were evident (Fig. 3.13). These may be used as a secondary visual cue but are unlikely to be important for orientation since they are absent in the west and central dunes.

Orientation to polarized light occurs among several *Camponotus* species (Wilson 1971). *Cataglyphis bicolor* of the Tunisian desert usually uses the pattern of polarized light for its orientation but on moonless nights it reacts anemomenotactically. Visual cues are only used over short distances around the nest (Duelli 1972 and Wehner and Flatt 1972 in Cloudsley-Thompson 1975).

3.15 Recruitment and Tandem Running

One of the unique features about social insects is their ability to assemble workers for combined efforts in food collection, nest construction, defense or migration. Wilson (1971) has defined recruitment as "communication that brings nestmates to some point in space where work is required". Recruitment may take on various forms in different species, but is basically of two types. Firstly, ants may be transported physically with no chemical communication being involved. Secondly, a more efficient form of recruitment, since it generally involves more than two ants, is the use of trail pheromones.

Both methods of recruitment appear to be employed by *C. detritus*, adult transport to new nest sites (Section 3.11) and group recruitment either to new nest sites or new food sources. Occasionally a worker ant was observed leaving the nest dragging its gaster along the ground, presumably secreting a pheromone, followed by one to twenty other workers in a highly excited state (Fig. 3.14). Every so often the leader stopped and remained perfectly still until touched by the ant behind. The followers did not remain in an orderly line behind the leader, but constantly changed places with one another, making brief

Fig. 3.13 *Camponotus detritus* path in the sand after rain, Mniszechi's Vlei.

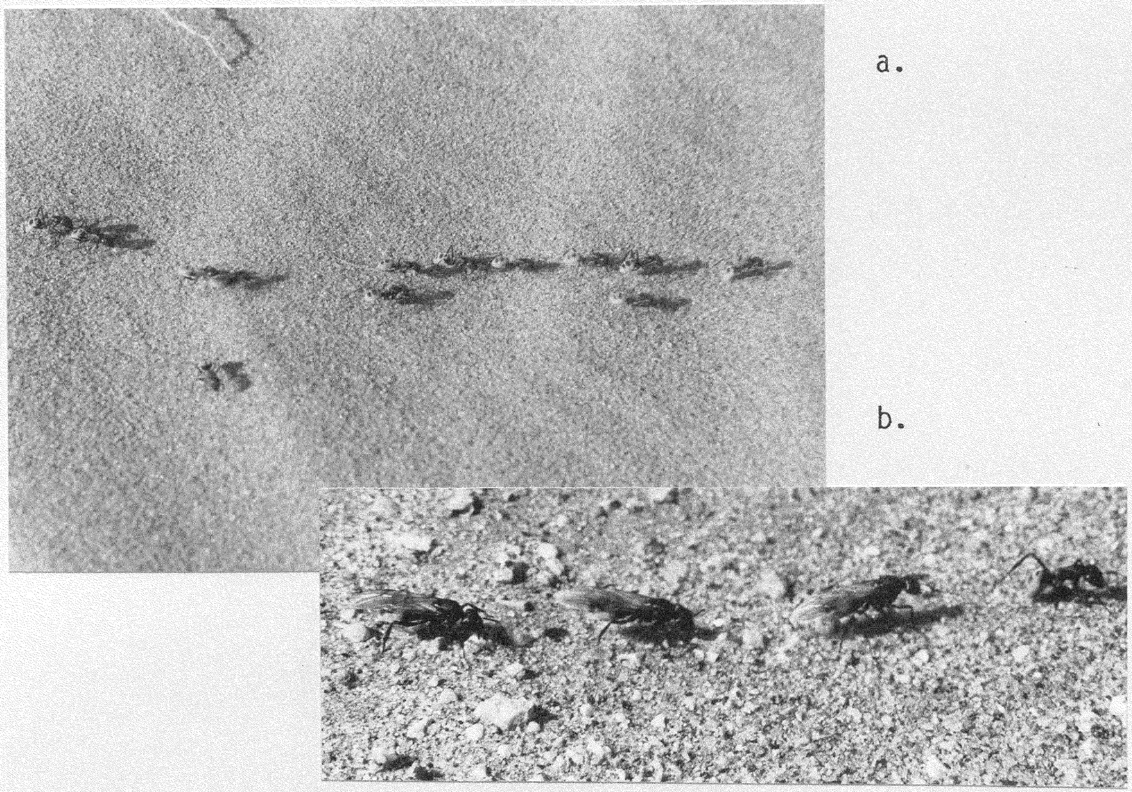


Fig. 3.14 Group recruitment in *Camponotus detritus*.

a. Leader (right) dragging its gaster along the sand, followed by workers.

b. Unusual observation made after completion of thesis. Worker (right) followed by alate females.

circles away from the group, or stopping to make antennal contact with ants passing in the opposite direction. Periodically the leader stopped and cleaned the tip of its gaster. Consequently progress of ants in such groups was slower than that of single ants. Often individuals left the group and others joined it with the result that by the time the group reached its destination it was frequently half the size it was when it started.

The pheromone secreted by the leader apparently kept the followers in a state of excitement and appeared to be extremely short-lived, because the degree of excitement of the followers diminished the further they were from the leader. It was always the ants at the end of the line which left the group before reaching their destination. Furthermore, strong winds appeared to dissipate the chemical, presumably by moving the sand. For example, during one fairly windy day, six major workers, led by a media were blown momentarily off-course by a gust of wind. Thereafter, only the ant immediately behind the leader continued to follow it. The others appeared to lose the trail and ran about in different directions before they finally returned to the nest.

Wilson (1971) has shown that there is a gradual improvement in chemical recruitment techniques among the Formicidae. Examples of each form can be found within the genus *Camponotus*, but most species, including *C. detritus*, seem to be at an intermediate stage. The most primitive form, tandem running, is shown by *C. sericeus* (Hölldobler, Möglich and Maschwitz 1974). One individual closely follows and maintains frequent antennal contact with the leader. A pheromone trail, which acts as an orientation cue, is discharged from the hindgut of the leader.

Scout ants of *C. socius* leave chemical markers around newly discovered food sources and return to the nest laying a trail which has a long-lasting orientation signal but no recruitment effect on the nestmates (Hölldobler 1971). Inside the nest the recruiting ant performs a "waggle" motor display which can alert and stimulate up to 30 nestmates to follow it. The ant then returns to the food source following the trail, still dragging its gaster. The hindgut secretion,now mixed with formic acid, keeps the followers excited. *Camponotus paria, C. compressus* (Hingston 1929 in Wilson 1971) and *C. beebei* (Wilson 1965) apparently display a form of recruitment similar to that of *C. detritus*. The most sophisticated form is mass recruitment, shown by *C. pennsylvanicus*, where the trail laid to the nest by scout ants is sufficient stimulation for other workers to follow it to the food source, even in the absence of the trail laying ant (Traniello 1977).

3.16 Interaction With Other Species

3.16.1 Ants

Camponotus olivieri For*is a small ,black species of which only one colony has been found to date in the dunes. This was in the large *C. detritus* nest mentioned previously. Each species had its own brood, workers and alates, but it was not possible to tell whether the brood of the two species was kept separately or together. It is possible that this was a form of compound nest, in which two or more species live close to each other but keep their brood separate.

Among ants a diverse array of social parasitism occurs from plesiobiosis in which vastly different species nest very closely to one another but engage in little or no direct communication, to inquilinism in which the parasitic species spends its entire life cycle in the nest of the host species (Wilson 1971). The genus *Camponotus* appears to be relatively immune to social parasitism (Wilson 1971) but a few cases may be cited. Trophic parasitism and trail sharing has been observed in *C. lateralis* (Goetsch 1953 in Wilson 1971) and *C. beebei* (Wilson 1965). Parabiosis occurs between *C. femoratus* and *Crematogaster limata parabiotica* where the two species nest together, but house their brood separately. They share common trails and foraging grounds and workers have even been observed regurgitating food to one another (Wheeler 1921 in Wilson 1971). The relationship of the parasite *C. universitatus* and its host *C. aethiops* is thought to be a form of inquilinism (Bernard 1968 in Wilson 1971).

Crematogaster sp. (cf. *melanogaster*)*, a small species occurring in the dunes east of Gobabeb, appeared to be the major potential competitor of *C. detritus* for honeydew. Although it was observed tending the gall-forming scale insects, *Membrania* sp., which *C. detritus* also tends on *Stipagrostis* cf. *namaquensis*, the two species have not been seen foraging together on the same plant.

The small harvester species, *Tetramorium jordani* Sant*, occurring in the dunes east of Gobabeb, appeared to have little interaction with *C. detritus*. When *C. detritus* workers encountered *T. jordani* workers outside the nest they ignored them. However, once I noticed a media

* Specimens lodged at the Desert Ecological Research Unit

C. detritus worker with its head in the entrance to a *T. jordani* nest, digging at the loose sand. When a *T. jordani* worker appeared and sprayed it, the *C. detritus* worker rubbed its mouthparts on the sand and then lunged at the *T. jordani* worker with its jaws open, but did not appear to make contact with the latter. This was repeated a few times until a second media *C. detritus* worker arrived. The performance was then repeated by both ants. After 20 minutes the *C. detritus* workers left the *T. jordani* nest. A possible explanation for this behaviour could be that *C. detritus* workers might have been trying to obtain moisture from the damp sand which the *T. jordani* workers were bringing up to the surface, since similar behaviour has also been noticed at termite nests.

3.16.2 Termites

On three occasions I have seen *C. detritus* workers with their mouthparts on the damp sand around the entrances to a *Hodotermes mossambicus* nest, and sometimes digging at the nest entrance (Fig. 3.15.). The ants did not appear to actively prey on the termites as *H. mossambicus* nests were often situated in very close proximity to *C. detritus* nests (within 1 m) and I have seen termites actually taking detritus from the pile above a *C. detritus* nest. The ants made no attempt to interfere and when an ant encountered a termite, the former gave way although in most instances the ant was larger than the termite. On another occasion, however, it was noticed that there were aggressive encounters between ants and termites, sometimes leading to the injury of the termites which were then carried to the ant nest. Murray (1981) also observed *C. detritus* workers carrying pieces of termite to their nests. These were probably dead termites which foragers had found. One observation was recorded of a *C. detritus* worker chewing on the anal region of a *Psammotermes allocerus* worker. It then dropped the termite and moved off. Apart from this, no interactions between these two species have been seen.

3.16.3 Spiders

The salticid, *Cosmophasis* sp., closely mimics *C. detritus* (Fig. 3.16). Being about 9 mm long, it is the size of the smallest *C. detritus* workers. Its legs and prosoma are brick-red with a slight purple tinge and the opisthosoma is off-white with black markings, similar to that of the ant. When moving, the spider's two front legs are held above its head, resembling a pair of antennae. It has only been found from Noctivaga eastwards. One individual was found in a *C. detritus* nest, two in cocoons among grass leaves and two were seen on a *Stipagrostis sabulicola* where numerous *C. detritus* workers were foraging. Each of the spiders darted rapidly towards a feeding ant, but backed away equally rapidly when the ant moved. After a while each spider had an ant in its jaws. Presumably the spider only sucks the body fluids from the ants since the bodies of the ants were later discarded.

3.16.4 Vertebrates

Camponotus detritus appeared to be avoided to a large extent by vertebrate predators, probably because of the unpalatable formic acid which workers secrete. On a few occasions, however, we witnessed the Karoo lark, *Certhilauda albescens*, eating *C. detritus* workers. Willoughby (1971) also mentions the presence of "large ants that swarm in the dunes around the clumps of *S. sabulicola*" in the stomachs of Karoo larks.

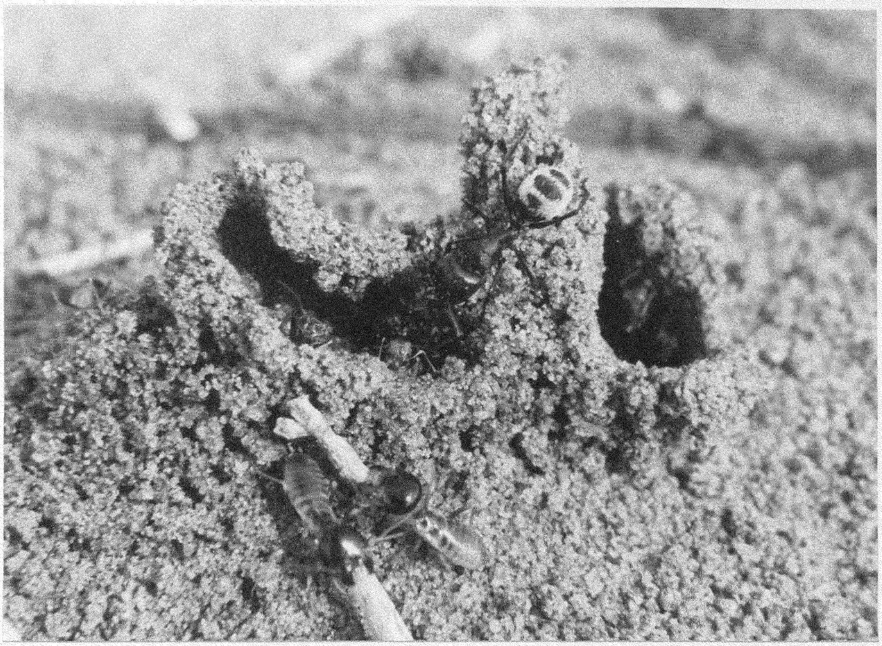


Fig. 3.15 A *Camponotus detritus* worker at entrance to a *Hodotermes mossambicus* nest.

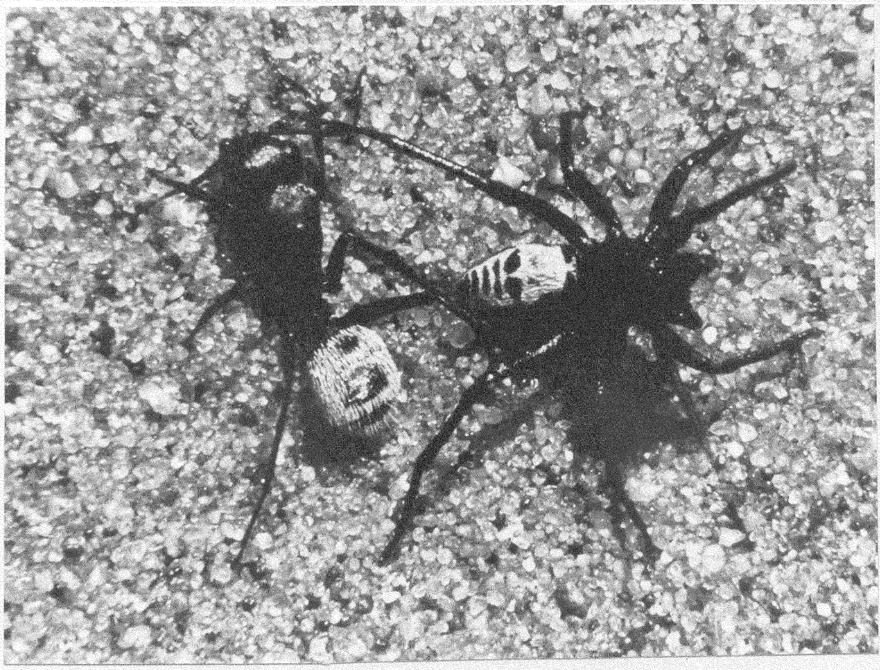


Fig. 3.16 Model and mimic : *Camponotus detritus* (left) and *Cosmophasis* sp.

I once found a partially uncovered *C. detritus* nest around which were many Ludwigs bustard, *Neotis ludwigii,* and Karoo lark tracks. Presumably the former had opened up the nest and the latter had used the opportunity to collect brood. The nest, however, was not totally destroyed by the birds.

The dune lizard, *Meroles cuneirostris,* preys on *C. detritus* (Robinson and Cunningham 1978, Murray 1981). Murray (1981) observed these lizards robbing *C. detritus* ants of food items, notably termites. The lizard would dart out at the ant, causing it to drop its burden, which the lizard then retrieved. Louw and Holm (1972) found " dune ants" (*C. detritus* (Louw, pers. comm.)) in the stomachs of the sand-diving lizard, *Aporosaura anchietae*.

Another ant nest was found open in a few places and surrounded by small canine footprints, either Cape fox, *Vulpes chama,* or Bat-eared fox, *Otocyon megalotis*, although the animal concerned did not appear to have done much damage to the nest.

Section Four

FOOD AND FORAGING BEHAVIOUR

4.1 Food

The major food of *Camponotus detritus* appeared to be the honeydew secretions of scale insects (Coccoidea) (Table 4.1 and Fig. 4.1), although workers were also observed carrying dead arthropods back to the nest or eating the flesh of larger dead animals when encountered (Fig. 4.2). Very rarely were they seen taking live prey. On a few occasions, when termites, *Hodotermes mossambicus*, were active near a *C. detritus* nest, an aggressive encounter between the two species led to the injury of a termite by an ant, after which the injured termite was carried back to the ant nest. The ants did not, however, appear to be actively preying on the termites and in most cases allowed the termites to pass by unmolested (Section 3.16.2). On another occasion, when an experiment was being performed in the dunes on the decomposition of an Oryx carcass by maggots, *C. detritus* workers were observed to be attacking the maggots as they migrated across the sand, and transporting them to the nest (Fig. 4.3).

No quantitative data were obtained on the relative proportions of honeydew and animal material returned to the nest but information on visible (solid) material was recorded and quantified. Out of more than 9 000 workers observed entering the nest only 3,4 % carried visible material in their jaws. Most of the identifiable material returned to

Table 4.1

Honeydew-producing scale insects (Hemiptera : Coccoidea) of the central Namib dune-field and their host plants.

Family	Species	Host Plant	
Aclerdidae	*Aclerda namibensis* Ben-Dov.	*Stipagrostis sabulicola*	1
		S. cf. *namaquensis*	1
		S. lutescens	3
		Eragrostis spinosa	2
Coccidae	*Membranaria* sp.	*S.* cf. *namaquensis*	1
		S. lutescens	3
Pseudococcidae	*Trionymus* sp. 1	*S.* cf. *namaquensis*	2
	Trionymus sp. 2	*S.* cf. *namaquensis*	3
Eriococcidae	*Eriococcus* sp.	*Trianthema hereroensis*	1
Margarodidae	New Species	*T. hereroensis*	2

1 : Commonly infested

2 : Occasionally infested

3 : Rarely infested

Fig. 4.1 *Camponotus detritus* workers tending scale insects (marked by arrows).

a. *Aclerda namibensis* on *Stipagrostis sabulicola*.

b. *Eriococcus* sp. on *Trianthema hereroensis*.

c. *Membranaria* sp. on *Stipagrostis* cf. *namaquensis*.

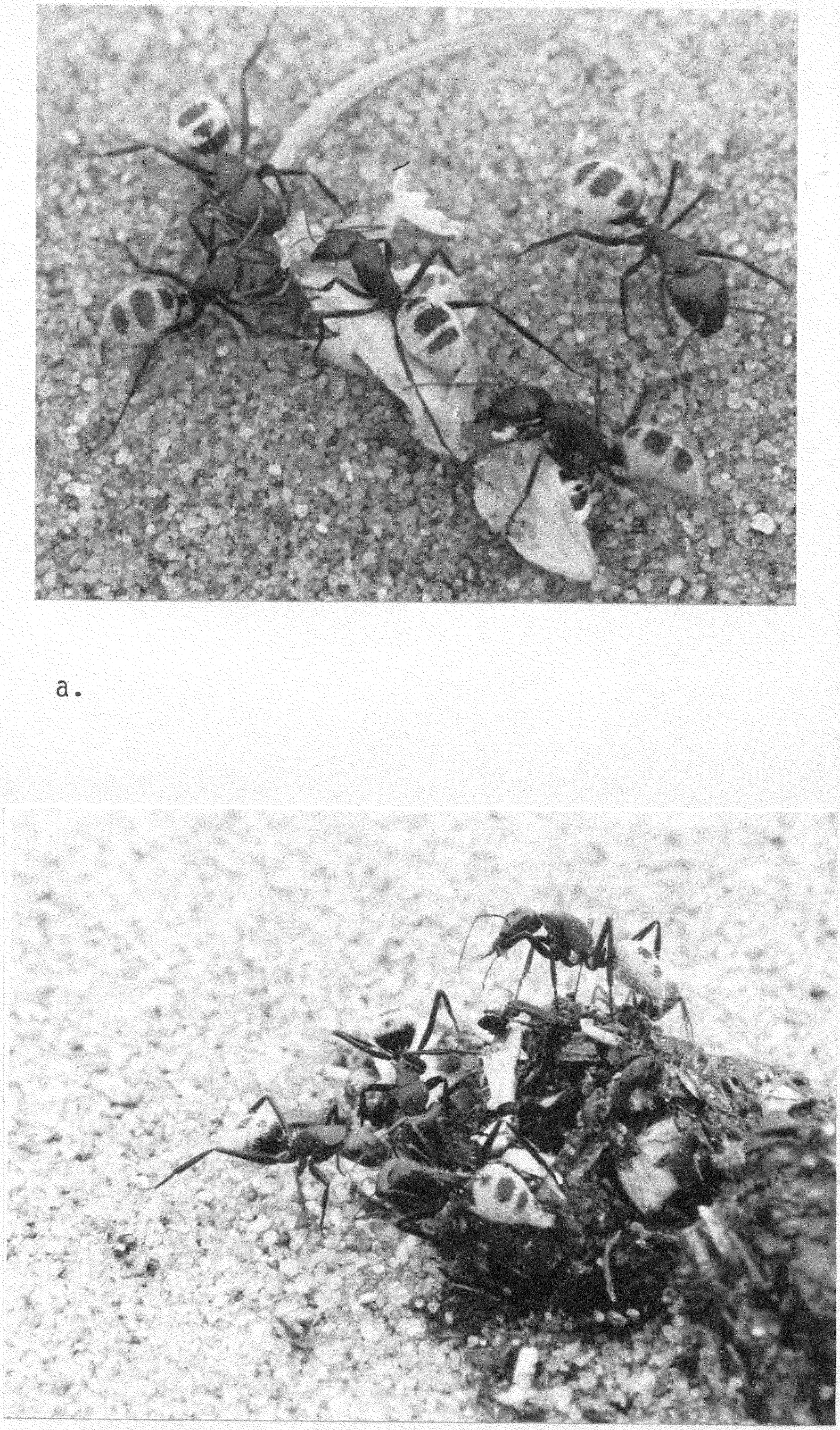


Fig. 4.2 *Camponotus detritus* workers scavenging.
a. Eating a dead lizard *(Palmatogecko rangeii)*.
b. Foraging on a jackal scat.

the nest was building material (Table 4.2). Numerous workers were seen walking to and from plants hosting scale insects and it was assumed that many of these returned to the nest with food in their crops (Section 3.12). Chew (1977) noted that returning workers of the omnivorous *Iridomyrmex humilis* weighed 27 % more than outbound foragers, although they rarely carried visible food. Similarly, Holt (1955 in Chew 1977) found that 81 % of *Formica rufa* workers returned to the nest with ingested food. Only 7,8 % of the returning *C. detritus* workers, however, had markedly distended gasters which seems to suggest that *C. detritus* workers are inefficient foragers. Whitford, Depree, Hamilton and Ettershank (1981) found that only about 20 % of the foragers of the harvester species *Pheidole* and *Pogonomyrmex* returned to the nest with visible food and they suggested that the other workers had satiated their appetites away from the nest, thereby decreasing their drive to return with food. This seems strange behaviour for a social insect, but may possibly also occur with *C. detritus* workers.

Wherever live scale insects were found, *C. detritus* workers were also present. Twenty per cent of a total of 150 ants collected from plants which had been injected with red dye were found to have dye in their crops. Ants were also observed with their heads in the flowers of *Trianthema hereroensis,* presumably collecting nectar (Fig. 4.4), but unlike honeydew collection, nectar collection only occurred during the day. Workers were never observed carrying seeds to the nest (Table 4.2).

From 14 to 26 % of the material returned to the nest was bird or lizard faeces. These faeces may have been taken for building material, but unlike gravel and detritus, which were also used for external nest

Table 4.2

Material transported to the nest by *Camponotus detritus* workers.

A = Identifiable material returned to the nest during transit activity observations

B = Observations made on other occasions.

Material	A (%)	B (%)
Detritus	44,2	25,7
Bird / Lizard Faeces	25,8	14,1
Sand Aggregations	17,4	26,3
C. detritus Workers	8,4	1,3
C. detritus Brood	1,6	0,6
Dead *C. detritus*	0,5	0
Dead Arthropods:		
Flies	0	3,8
Beetles	0	3,8
Spiders	0	1,3
Commicus	0,5	0,6
Solifuges	0,5	0,6
Moths	0	0,6
Total no. of Dead Arthropods	1,0	10,7
Total no. Objects identified	190	156

Fig. 4.3 A major *Camponotus detritus* worker carrying a maggot.

Fig. 4.4 A minor *Camponotus detritus* worker with its mouthparts inside a *Trianthema hereroensis* flower.

construction, bird droppings were only found inside the nests, often in piles at the end of tunnels. Similarly, rat and bat droppings were returned to the nest by *Veromessor pergandei* (Tevis 1958 in Sudd 1967), and were also found in the nests of *Cataglyphis halophila*. The latter were thought to utilize these faeces as a food source (Bernard 1960).

Since the rumens of cattle are known to contain bacteria capable of synthesizing amino acids from urea (Schmidt-Nielsen 1975), perhaps the crops of *C. detritus* contain similar symbiotic bacteria which allow the uric acid of the bird faeces to be utilized. In fact Mahdihassan (1977) states that the oriental species of *Camponotus* contain intercellular symbiotic bacteria in their intestines, but he gives no evidence to support his statement. *Camponotus detritus* workers have also been seen breaking sand hardened by Oryx urine into small peices and carrying them to the nest. Again these may simply be useful for nest construction or they may provide a source of nitrogen for the ants. Mahdihassan (1977) found *C. compressus* in Pakistan collecting human urine and suggested that it was the nitrogen in the urea which attracted the ants. However, as Sevastopulo (1978) pointed out, it may not have been the urea but the sugar in the urine. This is very likely as the reaction of ants offered urea powder was indecisive and uric acid was completely ignored (Mahdihassan 1977). Human urine also attracted *C. detritus*, but this may have been more for the water than the sugar/nitrogen content. Bird droppings and hardened gemsbok urine are unlikely to attract the ants as a source of sugar or water. Thus although it is not possible to be conclusive it seems feasible that faeces may be attractive as a food source, and an interesting sequel to the present study would be to search for evidence of symbiotic intestinal bacteria in *C. detritus*.

Moreover, in view of the variable amount and composition of amino acids in honeydew, the major food source of *C. detritus,* this type of study would be well justified.

Holm and Scholtz (1980) described *C. detritus* as a detritivore, but gave no evidence for this. Of one hundred workers' crops which were dissected during the present study (30 ants had detritus in their jaws when caught) none contained recognisable plant material. Fifty-five per cent of the crops contained a mass of amorphous brown material, while 45 % had a clear semi-fluid. The amorphous brown material may have been digested cellulose, but presumably some of the crops would have contained undigested material of a recognisable form as well. In the laboratory, ants were seen carrying detritus into the artificial nests and placing it in piles in the corners, but were never observed chewing it. It seems more likely, therefore that detritus is only used for nest construction and not for food.

No food stores were found in *C. detritus* nests (apart from the piles of bird droppings previously described). Neither was *C. detritus* found to have a replete caste, and only ten per cent of the workers dissected contained fat deposits. This is unusual for a desert species. Harvesters all have large stores of grain and many other species either store honeydew in repletes or workers have large fat deposits (Wilson 1971). The lack of food stores in *C. detritus* nests suggests that all food returned to the nest is utilized immediately and that the availability of food throughout the year is sufficient to meet the needs of the colony.

Most ant species are omnivorous and opportunistic, combining predation and scavenging with collection of plant foods (Carroll and Janzen 1973, Stradling 1978), but the importance of a particular food in the diet appears to vary according to season and locality (Way 1963, Burns 1973). In the Sahara Desert, however, many ant species are specialized feeders (Bernard 1951, Délye 1968). Similarly, the majority of North American desert ant species are seed harvesters (Chew 1977, Davidson 1977a & b, Whitford 1978b, Bernstein 1979a).

The symbiotic relationship between ants and homopterans has long been known (Wheeler 1910, Wilson 1971) and has been reviewed by Nixon (1951) and Way (1963). Dependence on honeydew as a food source is greatest among the Camponotinae and Dolichoderinae, and for genera such as *Lasius*, *Formica* and *Iridomyrmex* honeydew constitutes the major part of the diet (Nixon 1951). Ants of the genus *Camponotus* are generally very catholic in their choice of food (Ayre 1963 in Sanders 1970). Although many are honeydew feeders (Sanders 1970, Burns 1973, Lévieux 1975, Chew 1977, Mahdihassan 1977) most take insects and often plant juices as well (Sanders 1970, Lévieux 1975, Lévieux and Louis 1975). The common Indian ant, *C. compressus*, tends aphids which it protects against predators (Bose and Ray 1975). The Saharan species, *C. thoracicus*, besides collecting honeydew and insects, takes nectar from flowers and buds and collects the gum of *Acacias* (Délye 1968). Unlike *C. detritus*, workers of this species have well developed fat deposits which may constitute 30 % of the fresh weight. *Camponotus inflatus* of the Australian deserts has a replete caste in which honeydew is stored for seasons of low honeydew production (Wilson 1971).

Earlier workers considered honeydew to be pure carbohydrate and supposed that a supplementary protein source must be necessary for so called "honeydew feeding" ants (Auclair 1963, Way 1963). Although most honeydew feeding ants do supplement their diet with insects, there are some species which appear to be obligate honeydew feeders (Nixon 1951, Auclair 1963) and must therefore obtain sufficient essential amino acids from their diet. Subsequent research has shown that honeydew is a mixture of sugars, amino acids, amides, minerals, salts, and B-vitamins (Auclair 1963, Way 1963). The amount and composition of amino acids and sugars varies according to the species of host plant, its age, the part of the plant on which the homopteran is feeding and the length of time that it feeds (Way 1963). Twenty-two free amino acids comprising 13,2 % of the dry weight were found in the honeydew of *Aulocorthrum circumflexum*. These included all the essential amino acids known to be needed by animals (Maltais and Auclair 1952). At least five amino acids absent from the plant sap have been reported to occur in certain honeydews (Gray 1952 in Auclair 1963, Salama and Rizk 1969). Thus it is possible for ants to obtain all the essential amino acids from their diet, depending on the species of homopterans and host plants. The amino acids in the honeydew collected by *Formica polyctena* in European forests are adequate for maintaining normal living and reproducing ant colonies (Gösswald 1958 in Way 1963). Hagan (1958) has also shown that fruit flies can survive and reproduce on honeydew alone.

Seasonal fluctuations in honeydew composition are known to occur, which reflect changes in the phloem content ingested by homopterans (Auclair 1963). Lamb (1959 in Auclair 1963) reported that honeydew collected in summer, when plants were actively growing, contained five times the amount of amino acids that were found in winter, when the plants were dormant. On plants crowded with aphids the total amino acid content of honeydew dropped by 10 to 50 % as compared with uncrowded plants. Nothing is known about the chemical composition of honeydew in the Namib nor of the activity or seasonality of the homopterans present. It seems unlikely, however, that *C. detritus* obtains sufficient nitrogen from the honeydew since the ants appeared to require additional nitrogen in the form of dead arthropods and possibly bird faeces. Nevertheless the honeydew secreted by homopterans in the Namib appeared to provide sufficient nutrients to supply the basic requirements of these ants. The lack of stores and the presence of ants tending scale insects all year round suggests a lack of seasonality for the homopterans feeding on the plants. This suggestion is further supported by the absence of marked seasonal climatic changes in the Namib and the occurrence of fog which sustains the perennial vegetation throughout the year.

Often ants supplement their honeydew diet by actually preying on the homopterans (Way 1963, Wilson 1971, Skinner 1980b), but this behaviour was not observed among *C. detritus*. It is well known that ants deter the predators and parasites of homopterans (Nixon 1951, Way 1963, Burns 1973) and although this has not been observed for *C. detritus*, it is likely to occur since the ants are in constant attendance on the coccoids. Nevertheless, the degree of parasitism of scale insects in the Namib seems high as indicated by the frequent occurrence of emergence holes on the bodies of the scale insects. It has been claimed that ants "herd" aphids and coccoids moving them to more favourable sites when conditions deteriorate, although there is some controversy as to the actual "purpose" of ants carrying homopterans (Nixon 1951, Way 1963, Wilson 1971). No movement of scale insects by *C. detritus* workers was observed during this study.

4.2 Water

Since *C. detritus* was found to have a predominantly liquid diet it is possible that its water requirements are largely satisfied thereby. Nevertheless, ants were observed collecting rain and fog water off the sand or the vegetation (Fig. 4.5). The weight increase of ants fed on sugar water after five days of dehydration, ranged from 48,7 ± 8,2 % of post dehydration weight in media workers, through 51,6 ± 2,7 % in major workers to 83,9 ± 7,8 % in minor workers (means and standard errors). In each case ants had clearly distended gasters. These results indicate that *C. detritus* workers are able to take up a large amount of liquid and transport it to the nest.

Uptake of fog water by ants is known to occur among Saharan species (Délye 1968) and *Monomorium subopacum* drinks dew from stones (Broza 1979). In the Namib Desert fog water forms a very important source of moisture, not only for the animals, some of which exhibit behavioural adaptations allowing them to utilize fog moisture, but also for plants (Louw 1972, Hamilton and Seely 1976, Seely *et al.* 1977, Seely 1979, Louw and Seely 1980).

4.3 Foraging Behaviour

Most *C. detritus* workers were observed to leave the nest singly and walk toward plants hosting scale insects. Less frequently groups of ants

Fig. 4.5 *Camponotus detritus* workers drinking rainwater from the sand. Some have slightly distended gasters.

were observed walking from the nest to the food plants (Section 3.15). Recruitment to new or temporary food sources was observed far more often than to well-used foraging grounds. Once on the plants, the ants gently tapped the scale insects with their antennae and placed their mouthparts near the anal region of the coccoids. They were also observed to eat the honeydew residue directly from the plant surface, and I have seen them biting and tearing away leaf sheaths in order to reach scale insects. Often single ants were found on plants apparently not hosting scale insects, presumably searching for any new food source.

Virtually no co-operative carrying behaviour was observed among these ants. Usually, if a food item or piece of detritus was too large for a single ant to carry it would abandon the item. I once observed an ant bite a fairly long twig in half and carry one half back to the nest. On another occasion six major workers attempted to carry a dead beetle much larger than themselves *(Onymacris laeviceps)* to the nest. As each pulled in an opposing direction no overall progress was made.

Most of the foraging was done by minor workers (Table 3.2) with the exception of the maggot incident described previously (Section 4.1). Here, major workers attacked and carried the maggots to the nest, presumably because the maggots were too large for the minor workers to carry.

Section Five

NESTS

5.1 Structure

Nest architecture among ants is almost as diverse as the ants themselves (Wheeler 1910, Wilson 1971). However, there appears to be very little diversity of nest structure among desert ants. For example, most of the Saharan species have fairly simple nests in the ground consisting of galleries and chambers penetrating to a depth of about 1 m (Délye 1968). Similarly, *C. detritus* nests are simple structures excavated between roots of perennial vegetation, either living or dead (Fig. 5.1a). In some cases the aerial parts of the plant have disappeared leaving a hardened mound around the roots in which the nest is situated (Fig. 5.1b). Unlike certain ant and termite species, they appear to be unable to build a nest in loose sand and rely on the roots to provide a framework for the nest. Exceptions are one nest found in an old termitarium (Fig. 5.1c) and others excavated in silt or clay deposits in the Kuiseb River and Tsondab Vlei.

Externally, most nests had one or two entrance holes although some had more. The majority of nests opened to the east with the fewest opening to the south (Fig. 5.2). Nest orientation was negatively associated with percentage frequency of wind direction throughout the year, although there was not statistically significant correlation. Some had entrances on different sides of the nest. About half had an accumulation

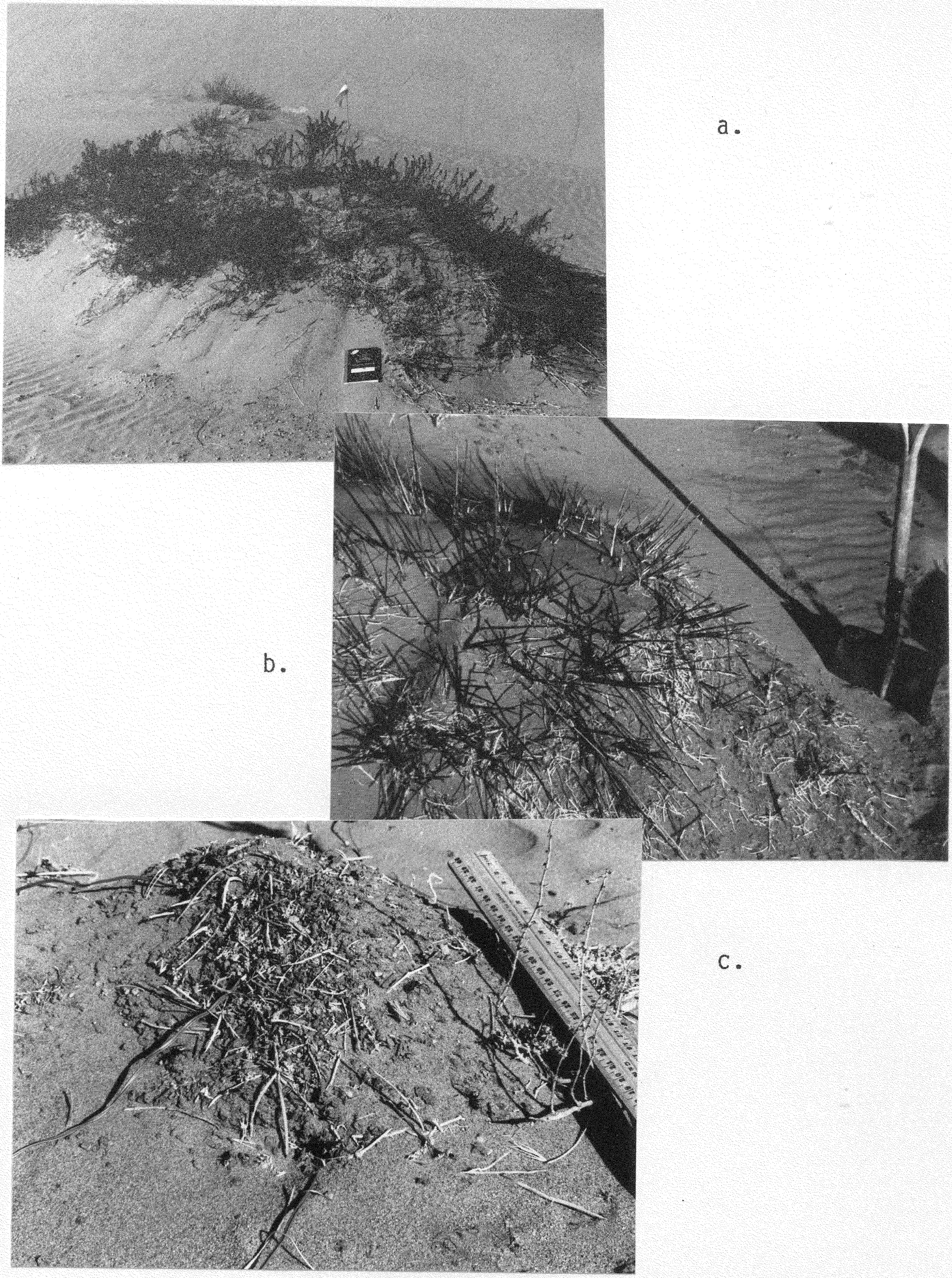


Fig. 5.1 Nests of *Camponotus detritus* in the central Namib Desert.

a. Under a dead *Trianthema hereroensis*.

b. Between the roots of a dead *Stipagrostis* sp.

c. In an old termitarium.

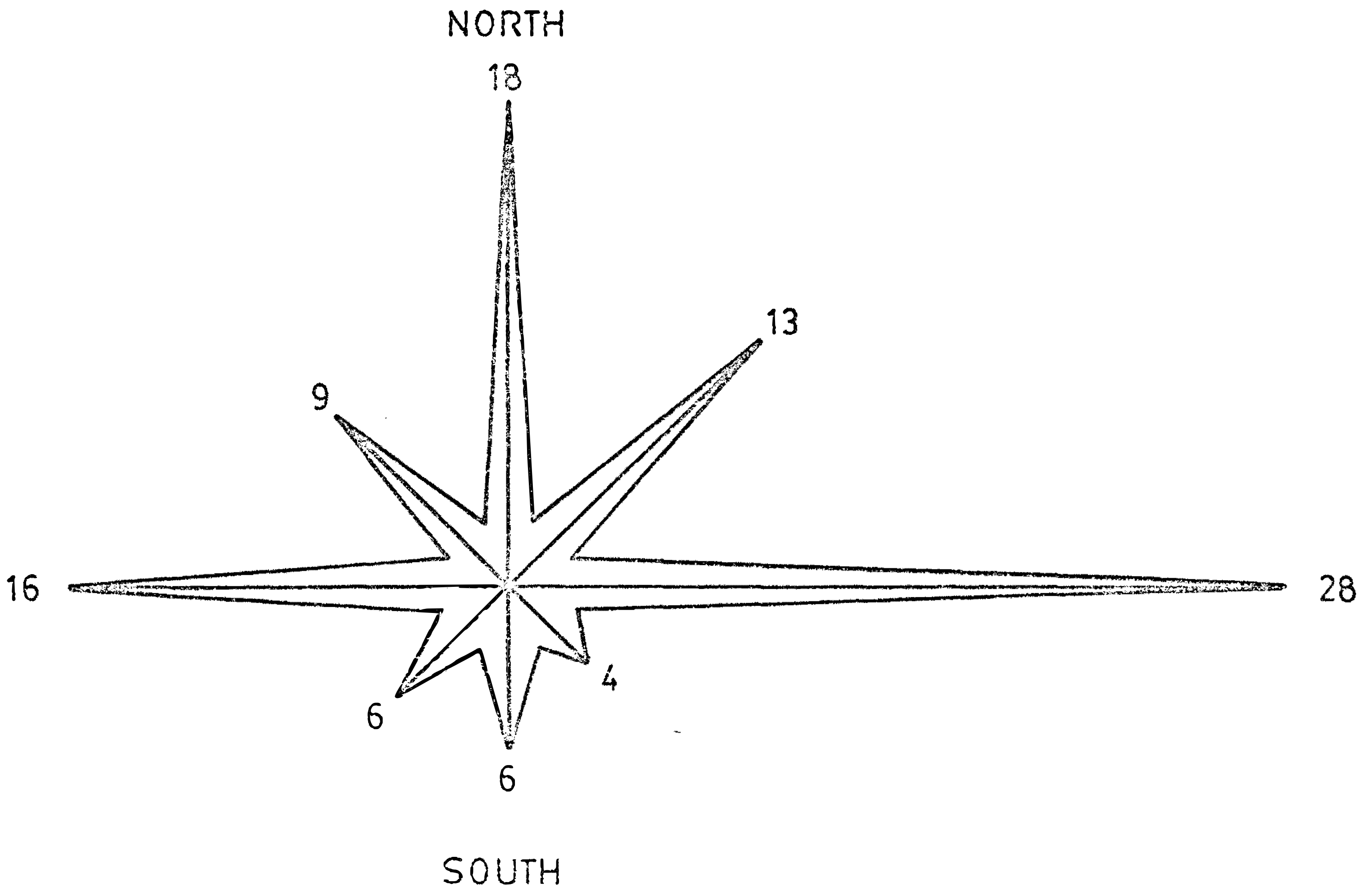
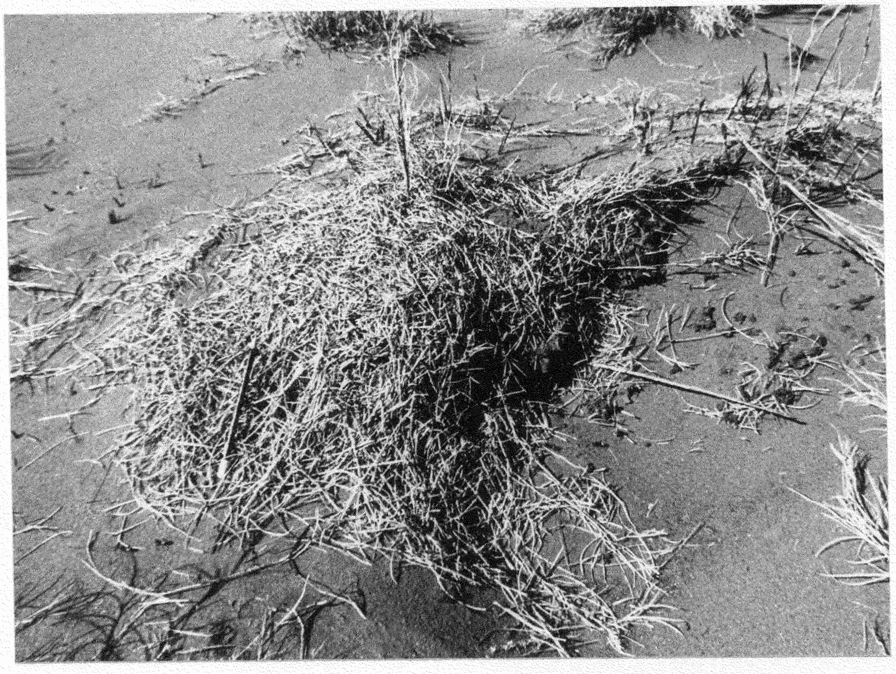


Fig. 5.2 Orientation of *Camponotus detritus* nest entrances. Each value is a percentage of the total number (110) of nests observed throughout a two year period.

of detritus either above the entire nest or just over the entrance (Fig. 5.3), but there was no correlation between the degree of exposure of the nest to the sun and the presence of a detritus pile (Table 5.1). Some of the completely exposed nests, situated at the base of the dunes near the interdune valley, were covered in fine quartz gravel (Fig. 5.4).

Internally the nest consisted of many interconnecting passages of variable length ranging from 9 - 22 mm in diameter(Fig. 5.5a), with occasional wide chambers of 30 - 80 mm in diameter. In some nests the walls of the passages and chambers were lined with a pliable viscous substance which hardened to form rigid tunnels. Since this was only found in a few (10 %) of the nests, it was assumed that the substance was provided by the environment rather than by the ants themselves. Most of the nests simply comprised a series of closely packed galleries and chambers in the sand, lined with detritus and bird droppings. Sometimes the upper chambers were made entirely of detritus with no sand at all. Chambers usually started at a depth of 100 mm and rarely exceeded 400 mm. Passages occasionally ramified, if the mound in which the nest was made was sufficiently large. No specific "royal chamber" in which the queen resides was ever found, and brood of all stages of development was found in the passages as well as the chambers (Fig. 5.5b). No food stores were ever found.

Although it appears to be uncommon among desert ants (Délye 1968), the habit of piling detritus or gravel on nests is not unique to *C. detritus*. Many species of mound builders thatch their nests with bits of leaves and stems, or pile gravel or pieces of charcoal on the nest (Wheeler 1910, Wilson 1971).



a.

b.

Fig. 5.3 Detritus accumulations above *Camponotus detritus* nests.

a. Over the whole nest (note pencil on left side of detritus).

b. Over the entrance only.

Table 5.1

Percentage of *Camponotus detritus* nests covered either by an accumulation of detritus or gravel. Total number of nests = 111.

	Nests Exposed to Sun	Nests Shaded by Vegetation	Total
Detritus Accumulation Present	23,4	33,3	56,7
Gravel Present	4,4	0	4,4
Neither Present	20,7	18,2	38,9
Total	48,5	57,5	100

Table 5.2

Camponotus detritus nest temperatures in summer (Nov - Feb) and winter (May - Aug) at two different depths.

Depth	Nest Temperatures (°C)						
Summer	Max	S.D.	Min	S.D.	Mean	S.D.	N
100 - 150 mm	38,0	2,3	25,6	3,9	32,0	2,2	9
150 - 300 mm	34,5	3,7	28,8	3,4	32,0	3,3	4
Winter							
100 - 150 mm	24,2	4,7	14,4	5,4	19,6	4,7	5
150 - 300 mm	26,4	3,2	19,4	3,6	23,0	3,4	8

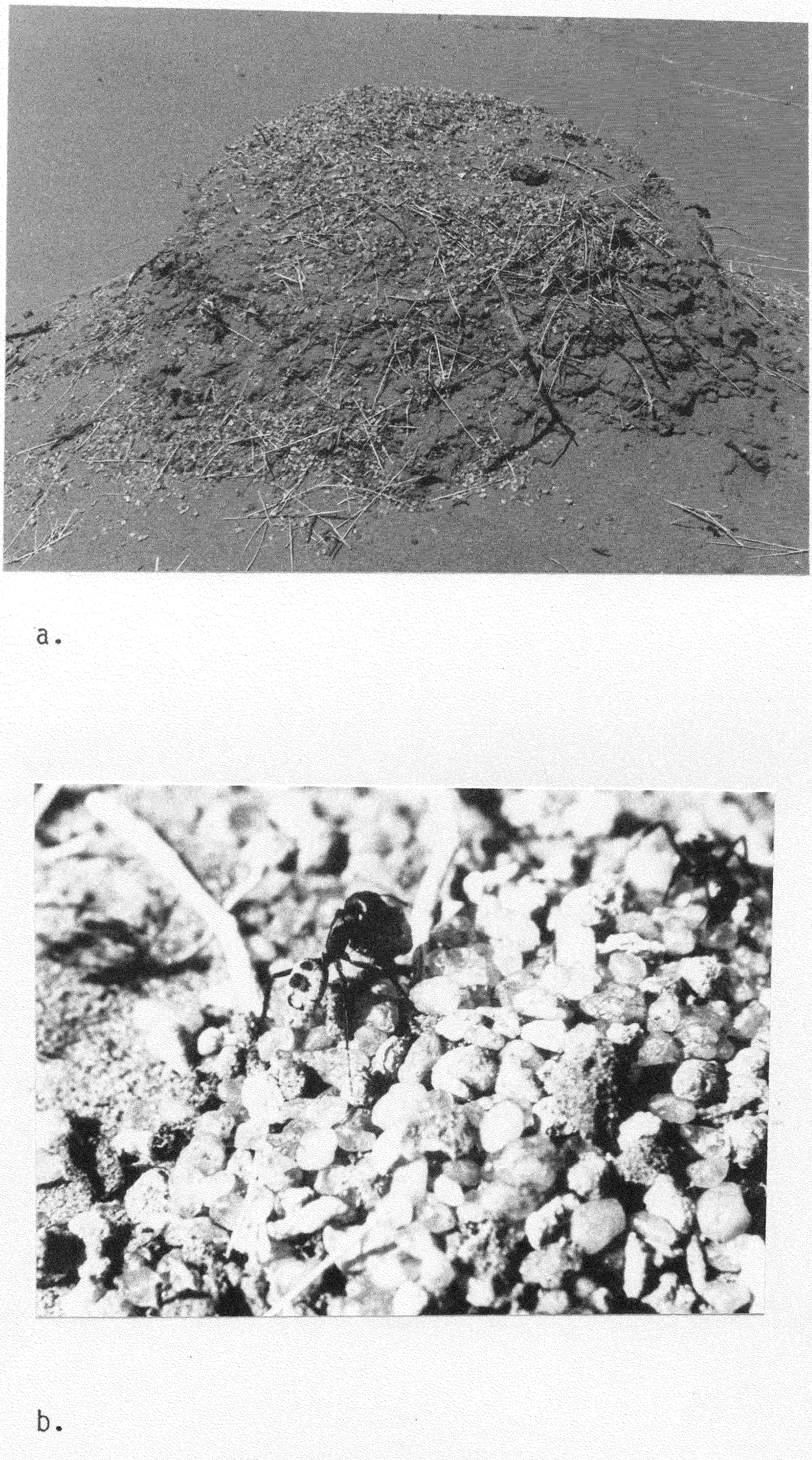
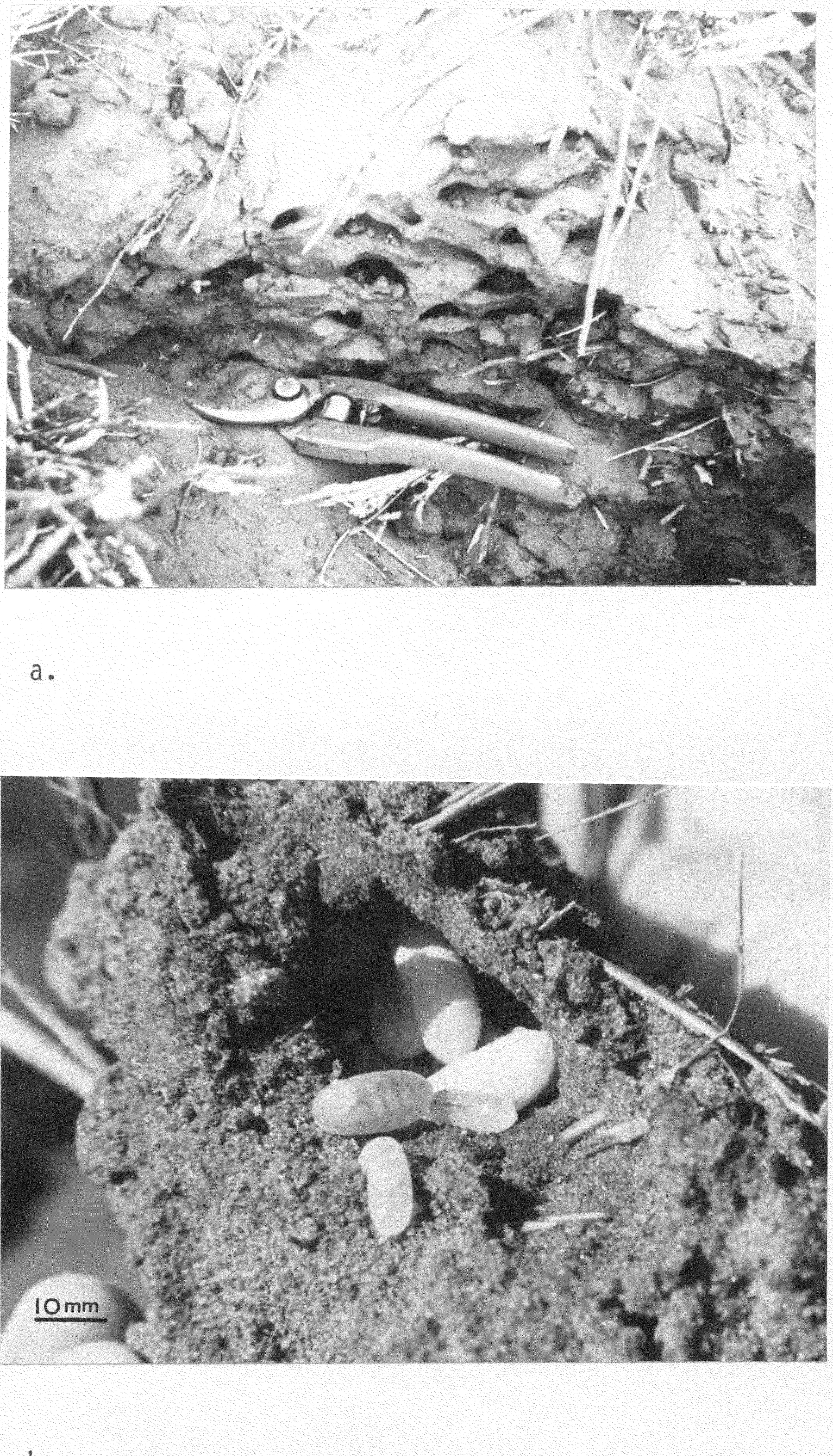


Fig. 5.4 Quartz gravel on *Camponotus detritus* nests.
a. Nest covered with gravel.
b. Worker placing gravel on the nest.



a.

b.

Fig. 5.5 Internal structure of a *Camponotus detritus* nest.

a. Partially excavated nest showing passages.

b. Chamber housing brood.

Members of the genus *Camponotus* are generally known as carpenter ants due to their habit of nesting in trees or dead wood in more mesic environments (Wheeler 1910, Wilson 1971). *Camponotus herculeanus* and *C. noveboracensis* nests consist of a series of vertical galleries hollowed out in tree trunks while underground entrance tunnels lined with wood chippings run through the moss and litter of the forest floor (Sanders 1964). *Camponotus fallax* inhabits the solid wood of hickory, pine or oak twigs 30 - 40 mm in diameter (Wheeler 1910). Not all *Camponotus* species are carpenters, however. *Camponotus senex* uses larval silk to construct tent-like arboreal nests among the leaves of the American forests (Schremmer 1979). The tropical species *C. femoratus* builds spherical nests made of particles of earth suspended around the branches of trees (Ule 1905 in Wheeler 1910). *Camponotus inaequalis* from Cuba has been found nesting in dried bean-pods, while colonies of *C. nearcticus* occur in pine cones (Wheeler 1910). *Camponotus thoracicus* nests, excavated in the limestone soils of the Sahara, form a fairly superficial horizontal network, with occasional galleries reaching a depth of 600 mm (Délye 1968). They often have a pile of gravel at the nest entrance, with which the workers of this nocturnal species close the nest entrance during the day. In the Namib, *C. fulvopilosus* excavates nests in calcrete on the gravel plains while *C. mystaceus* and *C. maculatus* construct nests in the sand dunes.

5.2 Number of Adults Per Nest

The number of workers per nest varied considerably across the dune-field from only 218 to as many as 15 670 (Section 7.2), with a mean nest size of all 36 nests excavated of 3 404 ± 510 S.E. workers. Numbers of alates per nest varied similarly (Section 3.3). The largest nest housed, including alates, a total of 19 827 adults. This variability is probably due to a number of factors, such as nest age, location of nest, availability of food and proximity of rival colonies. It is known that ant colonies must reach a certain state of maturity (size) before they can produce reproductives (Pricer 1908, Wheeler 1910, Wilson 1971). However, the smallest *C. detritus* nest excavated, housing 218 workers, also contained 100 alate females, thus its small size was not associated with immaturity.

Colony expansion, which occurs commonly among *C. detritus* (Section 5.5), may be responsible for small, yet fully reproductive nests since brood is transported by the workers from the mother nest (which is generally much larger) to a daughter nest. As *C. detritus* colonies often comprised more than one nest, total colony size would also be variable. The large nest housing 15 670 workers had a sister/daughter nest and together the colony had 20 038 workers.

This marked variation in nest size also occurs among other *Camponotus* species. Immature nests of the temperate species *C. pennsylvanicus* and *C. ferrugineus* housed from three to thirty workers, while reproductive colonies had from 327 to 3 212 workers and up to 400 reproductives (Pricer 1908). Nests of *C. herculeanus*, a boreal species, had from 500 to 3 000 workers, whereas a single nest of *C. noveboracensis* held 7 500 workers (Sanders 1970). Single nests of the tropical species *C. papua*, *C. confusus*, *C. vitreus* (Wilson 1959) and *C. solon* (Lévieux 1975) housed 300, 200, more than 4 000 and 3 800 workers respectively.

In general, nests of Saharan ants appear to be small, for instance, *C. thoracicus* nests only contained 500 - 600 workers while the nests of *Cataglyphis* species varied from 60 - 2 000 depending on species and habitat (Délye 1968). It would seem therefore, that a large range in nest size is not unusual, but that *C. detritus* does have larger nests than most other *Camponotus* species. Factors responsible for large nest size of *C. detritus* may be lack of interspecific competition, as well as the favourable climate for breeding throughout the year and constant food supply which occur in the Namib dune-field.

5.3. Nest Temperature

For the majority of ants, nest thermoregulation is achieved by nesting in a generally favourable, long-lived microhabitat and then adjusting brood temperature by moving the brood within the nest. Thus species inhabiting tropical rain forests tend to live in trees or rotting wood on the ground, whereas desert species generally nest deep underground (Délye 1968, Whitford, Johnson and Ramirez 1976, Seeley and Heinrich 1981). Metabolic heat production by workers, as well as the decomposition of organic matter by microbes, is know to increase the temperature within some ant nests (Coenen-Stass, Schaarschmidt and Lamprecht 1980, Seeley and Heinrich 1981). These forms of heat production appeared to have little or no effect on the temperature of *C. detritus* nests since temperatures measured in the sand outside nests were similar to those measured simultaneously inside. As expected, daily fluctuations in *C. detritus* nest temperatures were greatest near the surface, decreasing with depth (Fig. 5.6). The thermal gradient within the nest, however, was never very great at any particular time of day. Although the

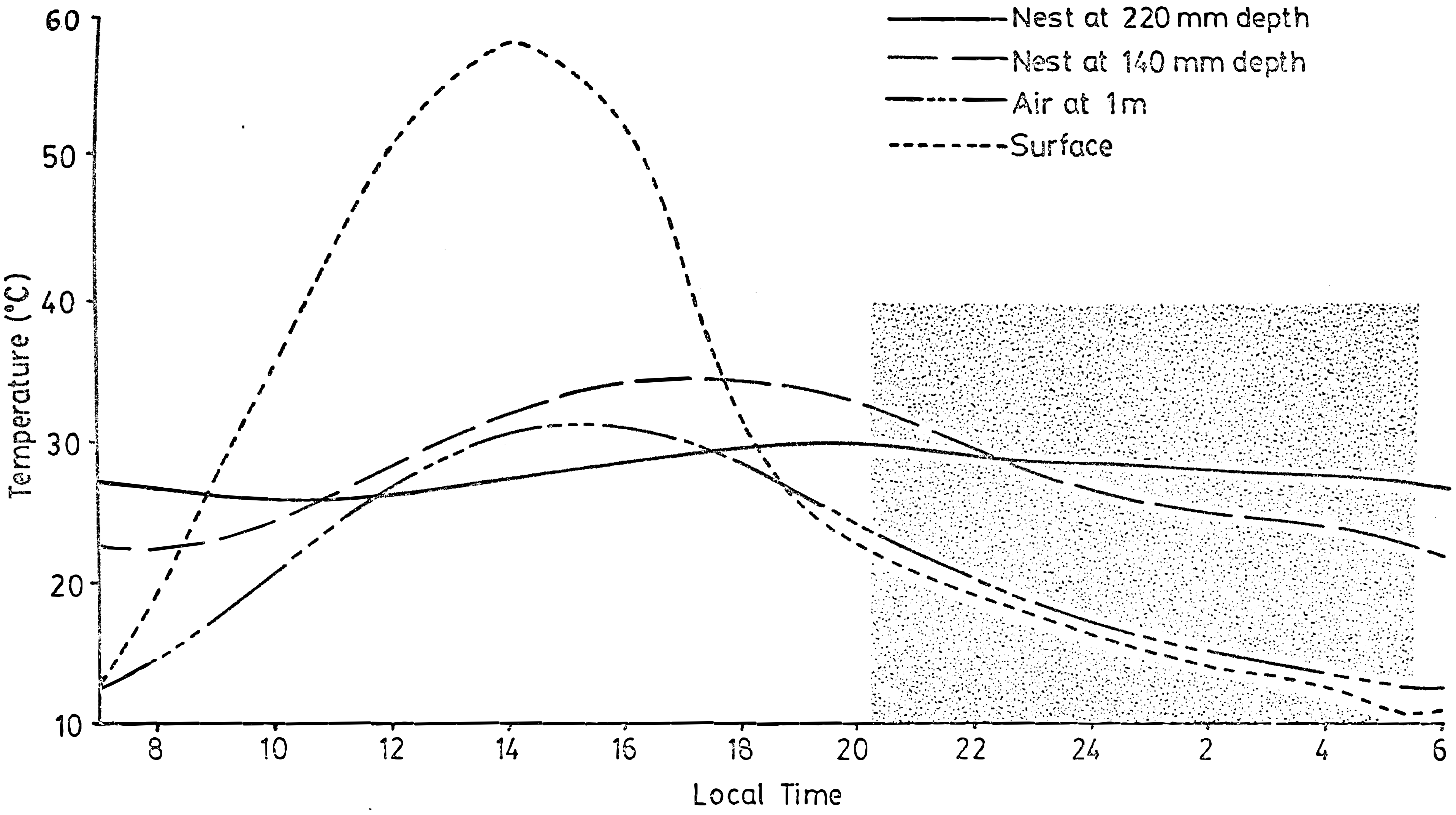


Fig. 5.6 Daily temperature fluctuations in a *Camponotus detritus* nest measured on 6 Jan 1981, together with the temperatures of the adjacent level sand surface and air at 1 m. Local time precedes sun time by one hour.

preferred temperature for the brood was 32°C (Section 8.1), it is apparently not essential that the brood be maintained at that temperature, since brood were found throughout the nest.

Many ant species move the brood around inside the nest throughout the day as internal temperatures fluctuate (Wilson 1971, Seeley and Heinrich 1981). Unlike most other ant species, *C. detritus* did not exhibit different temperature preferences for different developmental stages of the brood. Larvae and pupae of all stages were found in the same chambers. This differs markedly from a species like *Formica polyctena* which has four preferred temperatures for different stages of the brood (Ceusters 1977 in Seeley and Heinrich 1981). In contrast to *C. detritus* these mound building ants are able to create thermal gradients within their nests which are greater than those occurring in the surrounding sand, thereby providing more opportunity for temperature selection by the workers (Brandt 1980).

Table 5.2 shows mean nest temperatures for *C. detritus* in summer and winter. Mean summer nest temperature corresponded with the temperature chosen by the workers for the brood in the laboratory (Section 8.1). Since temperature is known to affect the rate of brood development in other ant species (Wheeler 1910), the lower nest temperatures experienced by *C. detritus* in winter may retard brood development, yet do not cause production to cease (Section 3.6).

Délye (1968) assumed nest temperatures of Saharan ants to be the same as the surrounding sand. Since fluctuations in soil and air temperatures measured in the Sahara were virtually the same as those found in the

Namib, and since *C. thoracicus*, like *C. detritus*, has many superficial nest chambers, it probably experiences similar nest temperatures to those experienced by *C. detritus*. *Cataglyphis bicolor*, a species of the arid regions of Greece, the Near and Middle East and North Africa, nests at a depth of 200 - 500 mm and has a nest temperature range of 25 - 35°C (Harkness and Wehner 1977), which is similar to *C. detritus*. The mean nest temperature of the tropical species *C. acvapimensis* is 26 - 27°C with a daily and annual fluctuation of 2°C. This is obtained by seasonally shifting the position of the nest in the soil about a mean depth of 250 mm (Lévieux 1972). Among the *Camponotus* species of the boreal forests, by comparison, nest temperature rises 16°C above normal during larval development (Sanders 1972).

5.4 Density and Dispersion

Density of ant nests is generally limited by the availability of either nest sites or food reserves while nest dispersion, or the pattern of distribution of ant nests, often indicates the degree of interaction between adjacent colonies (Brian 1965). Since intraspecific competition leads to territorial aggression which tends to space nests out as far from each other as possible, many ant species show a regular (over-dispersed) pattern (Waloff and Blackith 1962, Brian 1965, Bernstein and Gobbel 1979, Skinner 1980a).

At Gobabeb, nest density varied considerably from 0 to 5 nests per hectare. Overall density, estimated from ten one-hectare transects covering an area of roughly 40 km^2, was 2,2 nests ha^{-1}, with a variance of 2,9 (determined in March 1981). The variance : mean ratio test of dispersion (Southwood 1978) suggests that the overall nest dispersion in the Gobabeb dunes is aggregated. This contagion could be a result of the extremely patchy distribution of vegetation on the dunes, and localized scale insect-infestation of the plants.

When the density and dispersion of nests in one particular, vegetated area, namely Bannoch Burn (Fig. 5.7), was considered, the pattern was somewhat different (Table 5.3). In March 1981 nest density was 1,47 per hectare and in March 1982 it was 1,26. The nearest neighbour index R (Clark and Evans 1954) was calculated to be 1,58 for March 1982 (significant at $P_<$ 0,01), indicating a tendency towards a regular (overdispersed) pattern of nest distribution. This in turn implies a certain amount of intraspecific competition. Although *C. detritus* nests are restricted to the base of vegetation, usually where a pile of sand has accumulated, there were more potential nest sites at Bannoch Burn than were occupied by ants, thus competition for nest sites is unlikely to occur. In contrast, all scale-infested plants had foragers collecting honeydew, which suggests that intraspecific competition among *C. detritus* colonies is for food. The fact that *C. detritus* workers are territorial and defend their foraging grounds further substantiates this observation.

Thus two distinct patterns of nest dispersion were observed in the dunes at Gobabeb. On a large scale, nests were aggregated due to the clumped distribution of vegetation, whereas within areas of healthy vegetation, intraspecific competition appears to result in overdispersion. The major factors which affect the choice of nest site by the ants have been discussed in Section 7.1.

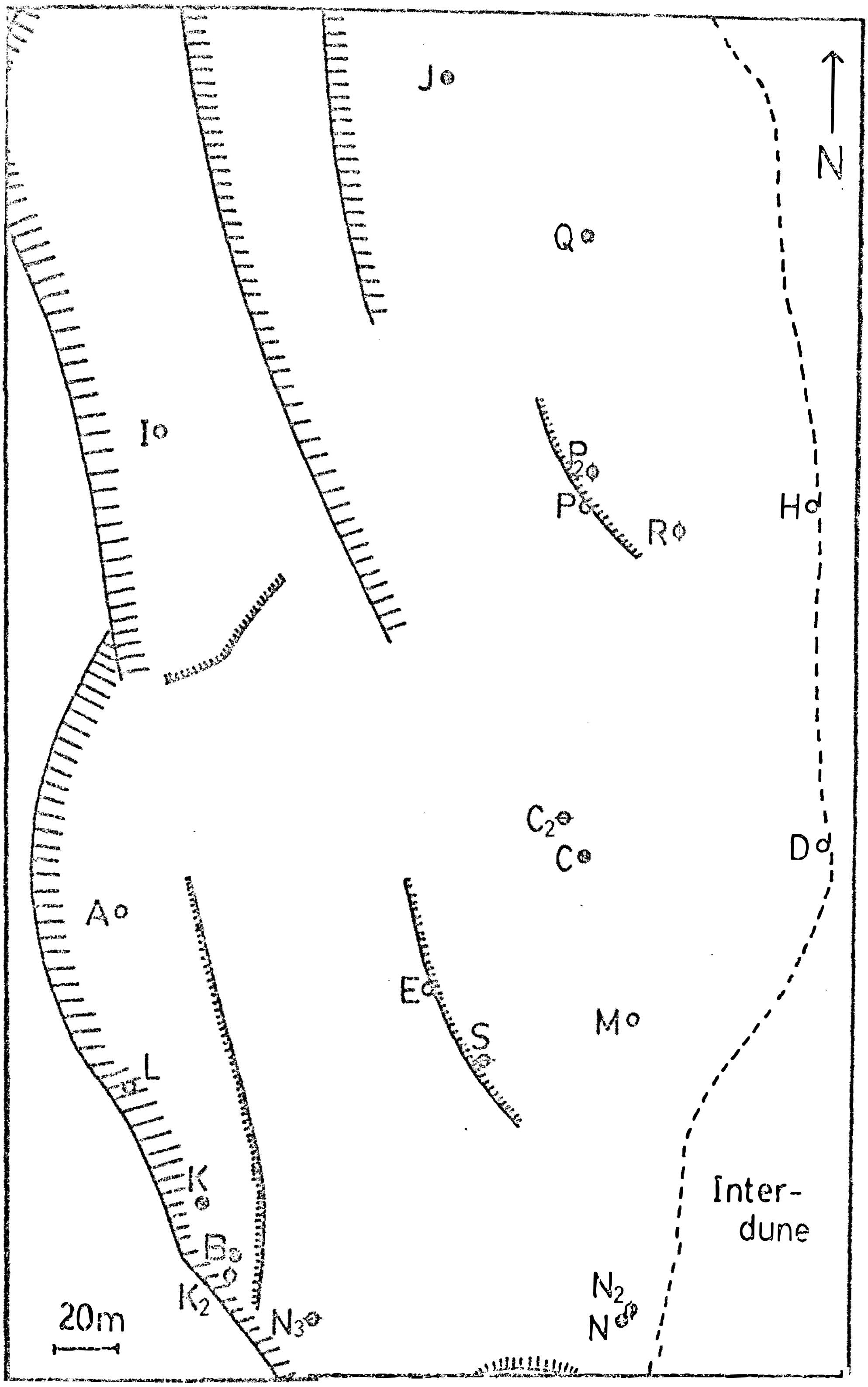


Fig. 5.7 Schematic map of Bannoch Burn, Gobabeb, showing changes in nest positions over two years. Total area: 9,5 ha. Nest symbols as in Fig. 3.10. ⊙ Nest present from Oct 1980 to Oct 1982

○ Nest present in Oct 1980 but not in Oct 1982

⊖ Nest present in Oct 1982 but not in Oct 1980

ϕ Nest present some time between Oct 1980 and Oct 1982

Wide hatching shows slipfaces and narrow shows steep slopes.

Table 5.3

Changes in *Camponotus detritus* nest density and distribution over an area of 9,5 ha at Bannoch Burn, Gobabeb.

Date	Total Nests	Nest Density (ha^{-1})	New Nest Opened	Old Nest Abandoned	Number of Nests			
					Upper Slope	Mid Slope	Lower Slope	Temporarily Inactive
Oct 1980	14	1,47	-	-	5	5	4	-
Feb 1981	14	1,47	2	2	5	5	4	1
June 1981	13	1,37	1	2	5	6	2	4
Sept 1981	13	1,37	0	0*	5	6	2	1
Feb 1982	12	1,26	3	4	5	3	4	0
July 1982	11	1,16	1	2*	4	4	3	2
Nov 1982	8	0,84	0	3	3	3	2	-

* Two additional nests declining in numbers of foragers.

No apparent seasonal change in *C. detritus* territory size occurred, but in June/July of both 1981 and 1982 four nests at Bannoch Burn were either totally or partially inactive. In all cases the inactive nests were small. The larger nests, in contrast, were active all year round. This differs from temperate ant species such as *Formica polyctena* and *F. rufa* which are totally inactive in winter, exhibiting territorial aggression and a gradual increase in territory size from spring to summer (Mabelis 1979, Skinner 1980a).

Maximum nest density depends upon factors which regulate the size of the foraging area which in turn are related to food availability (Bernstein and Gobbel 1979). Over the two year study period the total number of *C. detritus* nests at Bannoch Burn decreased from 14 to 8 (Table 5.3). This was probably related to the death of six scale-infested plants and the partial death of another five similar plants. Ten nests closed completely and another seven were opened (Section 5.5). Contrary to these results, Bernstein and Gobbel (1979) found very little change in nest positions over a six year period in the Mojave Desert.

The density of ant nests also varies considerably depending on the size of the ants, the size of the colonies and the habitats in which they occur. The maximum density in the Gobabeb dunes was 5 nests ha^{-1}. Similarly, total nest density of all ant species in the Saharan dunes near Bêni Abbês was 6,5, but the maximum nest density of any single ant species was 1,47 (Délye 1968). In the comparatively well-vegetated Mojave and Great Basin deserts, however, total nest density of all species present ranged from 61 to 448 ha^{-1} (Bernstein and Gobbel 1979). Among species of the genus *Camponotus* there is also great variability.

The density of *C. thoracicus* in the Sahara varies from 0,3 to 1,7 ha^{-1} depending on the habitat (Délye 1968). *Camponotus vicinus* of the North American deserts ranges from 15 to 37 nests ha^{-1} (Bernstein and Gobbel 1979). The arboreal *C. solon* of tropical Africa has a very low density of 1 or 2 nests ha^{-1} (Lévieux 1975), while the terrestrial, tropical *C. acvapimensis* has a density of 160 - 400 nests ha^{-1} (Lévieux 1977). Although nest density gives no indication of the total biomass of ants in an area, the figures given above show the low density of *C. detritus* compared with species of other habitats. This is to be expected in a species inhabiting a very arid and poorly vegetated area.

5.5 Colony Expansion and Nest Relocation

When conditions become unfavourable in an ant nest, or when the existing nest becomes too small, nest relocation or nest splitting may occur (Wilson 1971, Möglich and Hölldobler 1974, Mabelis 1979). The less elaborate the nest structure the more likely ants are to move. Thus the simple construction of *C. detritus* nests appears to be an adaptive feature of a species which nests in a rather unstable substrate, namely shifting dune sand. Nest splitting, where the mother nest is retained, but a daughter nest is started within the colony's territory, as well as nest relocation, where external factors render a nest uninhabitable and force the inhabitants to move to a new site, have both been witnessed on occasions at Bannoch Burn (Fig. 5.7 and 3.10).

In October 1980 nest N, the only nest in territory N, appeared to be large, with constant activity between it and foraging plant O, a healthy *T. hereroensis* heavily infested with scale insects. At the beginning of

1981 a new nest had been established in an adjacent dead *S. sabulicola* (N2). Gradually plant O began to die and the number of scale insects present decreased. The ants started to move southwards in search of new foraging grounds and by the end of 1981 nest N2 had closed again and far fewer ants were foraging on plant O. By February 1982 plant O was virtually dead, with only 10 scale insects on it and very few ants foraging. Nest N appeared to have decreased in size and activity while new nests had been established at N3 and N4 (± 200 m further south).

Similar changes occurred in other territories. Territory KB originally contained four nests in October 1980 : A, B, L and K. By November 1980 nest L, which had been in a dead *T. hereroensis* at the base of a slipface, had become completely covered in sand and no longer existed. The inhabitants of the nest presumably moved to one of the other nests. By January 1981 a new nest had been started in *T. hereroensis* K2, a healthy plant with numerous scale insects. Nest A was under a scale-infested *T. hereroensis* which gradually died, resulting in nest A becoming less active, until by January 1982 it was no longer occupied, and territory KB now only contained nests K, K2 and B. The few scale insects still present on plant A were taken over by colony SE. Initially colony SE had only one large, very active nest, E, which later was covered over by the advance of a small dune from the south-west. The ants presumably moved out of nest E into a new nest S. In February 1982 nest S was still the only nest in the territory.

A change of nest site due to the advance of a dune was actually witnessed. In October 1980 nest P was an active nest situated in a dead *T. hereroensis* with entrances on the southern and northern sides. By

5 December 1980 the small dune to the south had completely covered the southern entrance and a new entrance had been made on the east. By 26 December sand had covered the southern aspect and the top of the nest and was pouring into the northern entrance. Fifty or more large and medium workers were seen clearing away the encroaching sand while groups of 12 - 25 workers of all sizes moved across the sand to a large dead *T. hereroensis* 20 m away, where they had started to excavate a new nest. For the next week there was constant activity between nest P and the new nest, P2. Larvae, pupae, eggs and adults were transported by the workers to the new nest site, as many as 27 ants leaving nest P per minute. Activity had slowed down considerably between the two nests by 2 January 1981, but a few ants were still digging at the old nest entrance. There was, however, a great deal of activity and excavation at the new nest. By 29 January nest P was completely covered with sand and there was no sign of activity. Nest P2 remained active until August 1981, when the number of ants seen there had become very few. By January 1982 there was no longer a nest at P2, but a new nest had been started about 30 m to the east (R).

The encroachment of sand dunes is not the only hazard to which *C. detritus* nests are exposed. Strong south-east winds once completely undermined a nest situated on the top south-east corner of a large *S. sabulicola* mound, and brood was moved by the workers to a nearby sister nest. These observations serve to illustrate the dynamic nature of nest dispersion in the shifting dune sea.

Nest moving is known to occur in other *Camponotus* species for example, *C. sericeus* (Möglich and Hölldobler 1974). *Camponotus festinatus* avoids predation by the army ants, *Neivamyrmex nigrescens*, by complete evacuation of the nest. Brood, queens and workers are transported or climb up into the vegetation, away from the army ants which only raid along the ground (LaMon and Topoff 1981). Nest splitting occurs commonly in *Formica polyctena*. Like *C. detritus*, daughter nests in this species are sometimes short-lived (less than one year). Gradually, contact between mother and daughter nests diminishes until the two nests become separate colonies showing intercolonial aggression (Mabelis 1979). This gradual separation of related nests into two colonies may occur in *C. detritus*. For example, in one area constant activity was observed between nests 1 and 2 and between nests 3 and 4, but never any movement between the two pairs of nests. When ants from nest 2 were taken to nest 3 or vice versa, however, no hostility was observed. It is possible that nests 2 and 3 were related but that contact between the two had virtually ceased. With time, aggression may develop between the two colonies.

Section Six

ACTIVITY

6.1 Transit Activity

Transit activity (when individuals leave the nest area and move away to some other destination, or when they return to the nest area) was never observed at night but was very conspicuous during the day. This activity pattern was either bimodal or unimodal depending on the time of year. During the summer months, November to February (mean maximum surface temperature 61°C (Seely and Stuart 1976)), activity peaks occurred during the morning and afternoon with a cessation of activity during the hottest part of the day (Fig. 6.1). Sometimes, when heavy fog during the morning prevented midday surface temperatures from exceeding about 50°C, activity continued through midday; nevertheless the pattern remained bimodal. During the cooler months, May to August (mean maximum surface temperature 44,2°C (Seely and Stuart 1976)) transit activity was generally unimodal with no marked activity peaks and no midday cessation of activity (Fig. 6.2). Occasionally, when surface temperatures approached 50°C following a period of hot East Winds, a bimodal activity pattern with decreased midday activity was again observed. Activity patterns during the intervening months, March, April, September and October, varied depending on the midday surface temperatures.

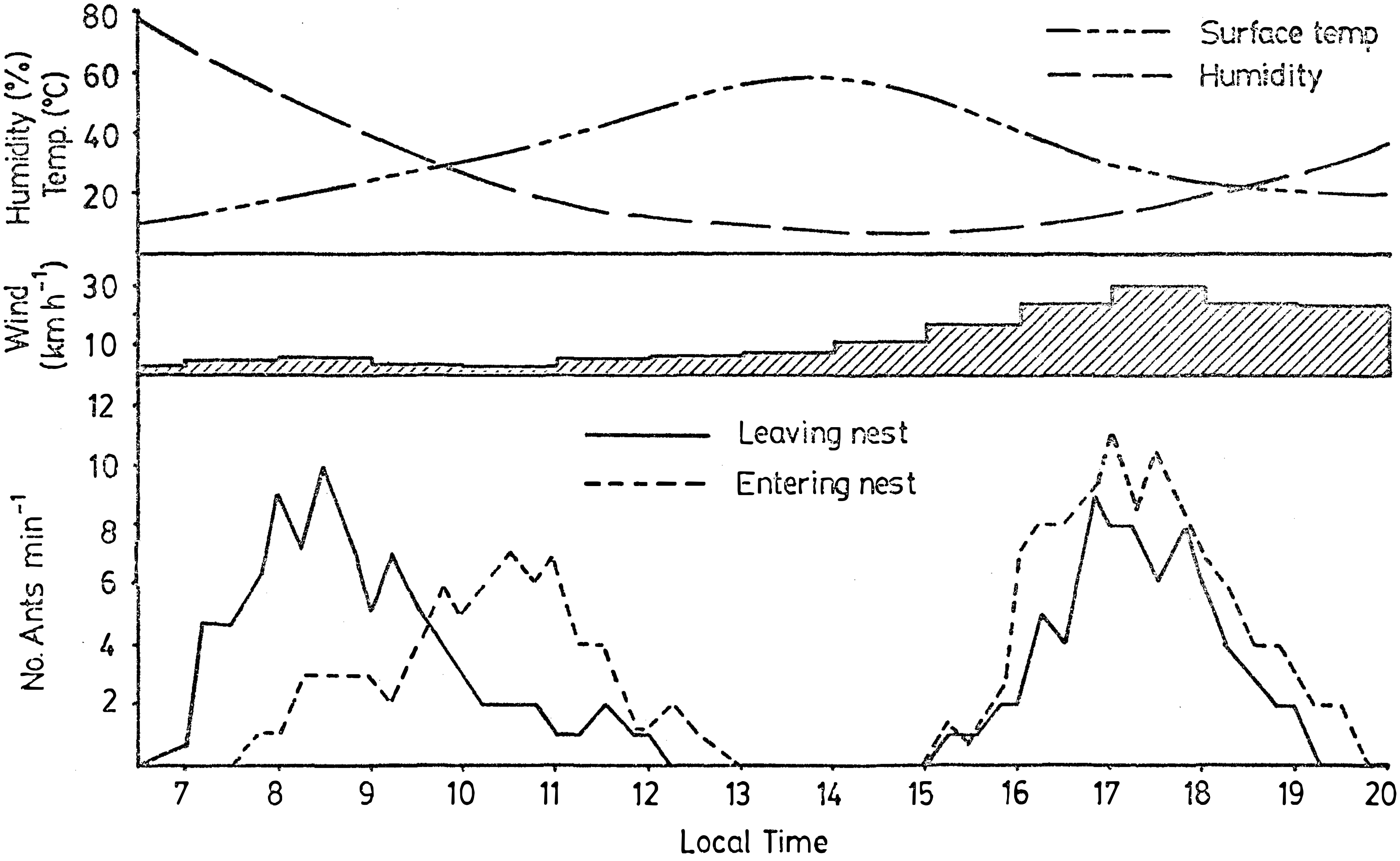


Fig. 6.1 The effect of micro-climate on transit activity in summer observed at a *Camponotus detritus* nest on 7 Nov 1980. Local time precedes sun time by one hour.

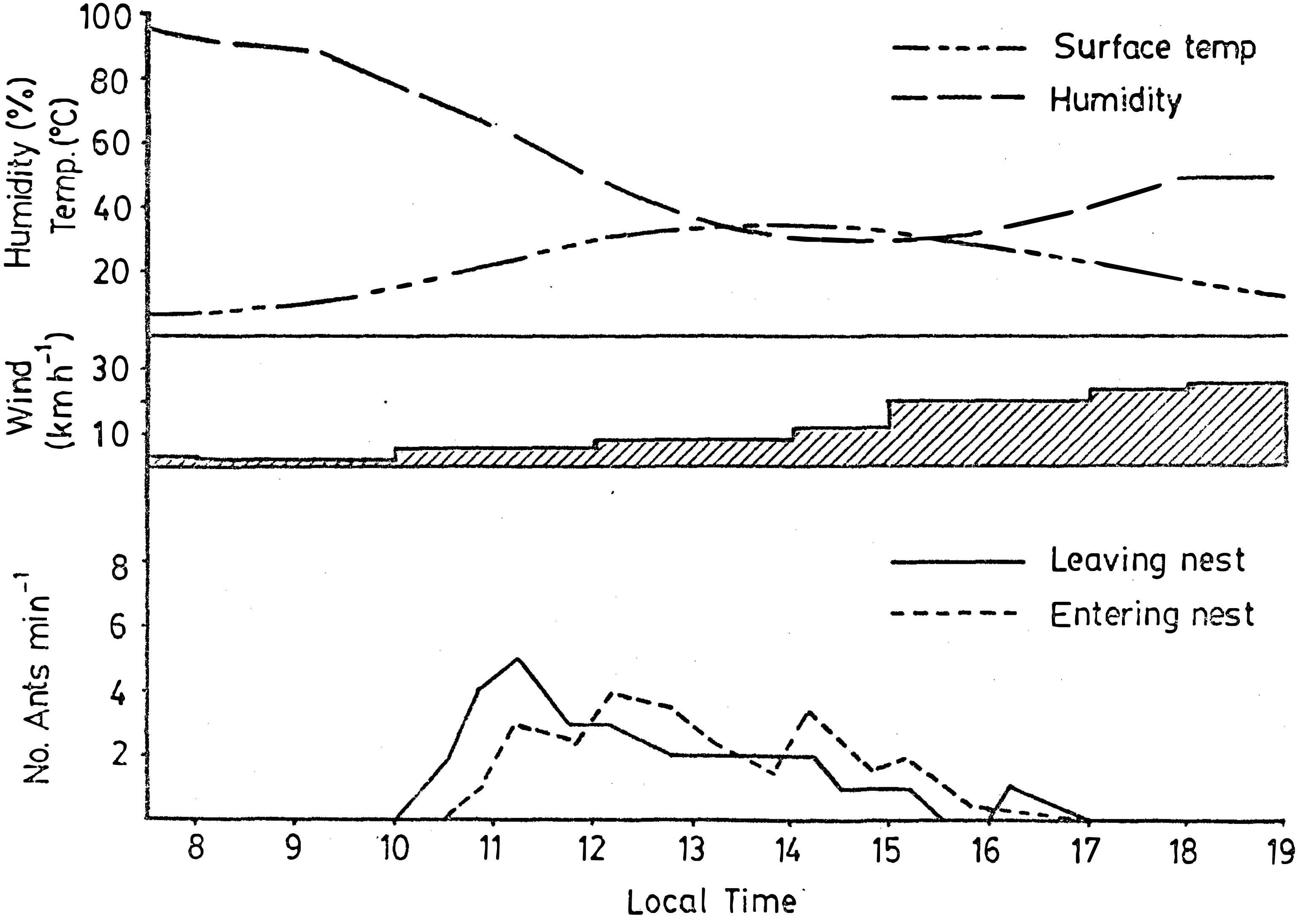


Fig. 6.2 The effect of micro-climate on transit activity in winter observed at a *Camponotus detritus* nest on 29 June 1981. Local time precedes sun time by one hour.

A bimodal pattern of diurnal activity occurs among many ant species from vastly differing habitats. For example, *Camponotus vividus* of tropical African forests (Lévieux 1977), *Formica polyctena* from Europe (De Bruyn and Kruk-De Bruin 1972), desert harvester ants (Whitford, Johnson and Ramirez 1976, Whitford *et al.* 1980) and various species from the gravel plains of the Namib Desert (Marsh, pers. comm.) exhibit this activity pattern. Some diurnal ant species only exhibit a single peak in foraging activity during all seasons, for example *C. acvapimensis* and *C. compressiscapus* of the tropical savannah (Lévieux 1977) and *C. herculeanus, C. noveboracensis* and *C. pennsylvanicus* of the boreal forests in Canada (Sanders 1972). Not all *Camponotus* species are diurnal, however. Many are nocturnal, exhibiting peak activity at different times of the night (Lévieux 1977), for example *C. maculatus* and *C. mystaceus* which also occur in the Namib.

6.1.1 Initiation of Transit Activity

Table 6.1 summarizes the micro-climatic data recorded at the start of transit activity. Light and temperature appeared to be the major factors responsible for initiation of activity. Although the mean surface temperature at the start of activity in summer was 16°C, activity never commenced before first light, even on occasions when pre-dawn surface temperatures were above 20°C. Often ants were observed standing outside the nest entrance, or rearranging detritus above the nest before dawn, but they only left the nest area when it became light. In contrast, winter activity often began an hour or two after sunrise when the mean surface temperature was 10°C. During the warm East Wind periods, however, when both air and surface temperatures were higher,

Table 6.1

Micro-climatic conditions prevailing at the start of *Camponotus detritus* transit activity.

Season	Time of Sunrise (Range)	Time Activity Commences (Range)	N	Surface Temp. (°C) $\bar{x}$	S.D.	N	Ambient rh (%) $\bar{x}$	S.D.	N	Nest Temp. (°C) $\bar{x}$	S.D.	N
Summer Nov - Feb	06h12 - 06h45	06h00 - 07h30	12	15,9	2,8	8	81,6	9,8	11	26,5	4,5	12
Intervening Months Mar, Apr, Sept, Oct	06h45 - 07h15	07h00 - 08h00	11	15,2	1,9	9	75,2	23	11	-	-	-
Winter May - Aug												
East Wind	07h15 - 07h40	07h00 - 08h30	6	17,5	4,6	6	10,7	2,9	6	25,3	1,5	3
Non-East Wind	07h15 - 07h40	08h15 - 09h30	11	10,3	3,1	10	68,1	29,3	11	15,7	2,2	6

winter activity began at sunrise. The presence of low fog appeared to have no effect upon transit activity except when surface temperatures were below about 10 - 15°C, at which point activity was delayed.

The large standard deviation in relative humidity at the start of transit activity suggests that there is no causal effect between humidity and onset of transit activity. For example, activity commenced during a fog when humidity was as high as 90 - 100% and during an East Wind when humidity was only 10%.

6.1.2 Termination of Transit Activity

The micro-climatic data recorded at the termination of transit activity are shown in Table 6.2. Both in summer and winter, surface temperatures at the end of transit activity were 10 - 11°C higher than those at the start of activity. This may be purely coincidental, since surface temperatures at sunset are usually higher than they are at sunrise and the onset of darkness may be the only causal factor for terminating activity. However in winter, activity always ceased either before or at sunset, and not at the onset of total darkness as in summer. An exception to this was activity during East Wind periods, when winter activity sometimes terminated with darkness, and surface temperatures were about 28°C. This again suggests that temperature, as well as light, controls the termination of activity, and is further substantiated by activity observed in summer at the Far East, which ceased at 18h30 (well before sunset) when surface temperature was 25°C. The inhibiting effect of darkness on transit activity was seen on very hot days when surface temperatures were above 30°C, yet all transit activity ceased by the

Table 6.2

Micro-climatic conditions prevailing at the termination of *Camponotus detritus* transit activity.

Season	Time of Sunset (Range)	Time Activity Ceases (Range)	N	Surface Temp. (°C)			Ambient rh (%)			Nest Temp. (°C)		
				$\bar{x}$	S.D.	N	$\bar{x}$	S.D.	N	$\bar{x}$	S.D.	N
Summer Nov - Feb	19h15 - 19h45	19h40 - 20h30	11	26,1	3,6	11	40,8	15,6	11	34,0	5,6	12
Intervening Months Mar, Apr, Sept, Oct.	18h45 - 19h15	17h00 - 19h30	9	26,1	2,5	9	32,8	19,6	11	-	-	-
Winter May - Aug												
East Wind	18h20 - 18h45	18h00 - 18h50	4	28,2	2,9	6	7,8	5,6	6	28,3	2,1	3
Non-East Wind	18h20 - 18h45	17h00 - 18h45	11	21,3	4,3	10	36,3	14,6	9	23,0	3,1	6

time darkness fell.

Darkness did not mean a total cessation of all activity, however. Surface nest maintenance continued throughout the night, both in summer and winter, when surface temperatures were above 10 - 15°C. Honeydew collection, too, continued throughout the night (Section 6.2).

It should be noted that mean nest temperatures at the start of transit activity in summer were similar to surface temperatures at the termination of activity. It is possible therefore, that a nest temperature of about 26°C in summer may have been the cue for ants to leave the nest and go out foraging, while the same surface temperature in the afternoon may have been the cue for transit activity to cease. In winter, however, nest temperatures in the morning were lower than surface temperatures at the finish of daily transit activity, thus there may not necessarily have been a link between morning nest temperatures and afternoon sand temperatures. Nest temperatures at the end of the day were always higher than surface temperatures, therefore in summer workers would have been returning to nest temperatures near their preferred temperatures (Section 8.1). As during the start of activity, humidity at the termination of activity was very variable and unlikely to have had a causal effect.

Light appears to be the controlling factor for activity of a number of ant species. This is particularly so for forest species such as the diurnal *Camponotus vividus* (Lévieux and Louis 1975) and the nocturnal *C. solon* (Lévieux 1975), which experience fairly constant temperatures and humidities. Among the Saharan species, temperature governs activity

(Délye 1968). *Pheidole* species of the North American deserts switch from crepuscular activity in summer to diurnal activity in winter, and Whitford *et al.* (1981) conclude that temperature is a more important activity cue to these species than light. Among other American desert ant species light, in conjunction with temperature, controls activity. Like *C. detritus,* temperature determines whether the ants are able to be active outside the nest, but light determines whether the activity takes the form of foraging or nest maintenance (Kay and Whitford 1978). Skinner (1980a) believes that the foraging intensity of *Formica rufa,* a temperate species, is related to nest temperature as well as surface temperature.

6.1.3 Midday Quiescence

Mean surface temperatures and humidities at the start and end of the period of midday inactivity are shown in Table 6.3. Both temperature and humidity were variable. On some occasions activity ceased when surface temperature was 40°C while on others a few individuals were active at 60°C. In general, it appeared that the ants were active at higher midday surface temperatures in summer than during the intervening months. Generally, no period of total inactivity occurred in winter, except sometimes when surface temperatures were above 40°C.

Saturation deficit, which is a measure of the dryness of the air, appeared to have little effect on the length of midday quiescence. This was in contrast to certain other ant species in which saturation deficit has a secondary effect to temperature on foraging activity (Schumacher and Whitford 1974, Whitford and Ettershank 1975, Fowler and Roberts 1980). It is likely, however, that a combination of factors,

Table 6.3

Micro-climatic conditions prevailing during the midday quiescence of *Camponotus detritus*.

	Summer Nov - Feb			Intervening Months Mar, Apr, Sep, Oct		
	$\bar{x}$	S.D.	N	$\bar{x}$	S.D.	N
Start of Quiescence						
Surface Temperature (°C)	55,8	5,2	11	46,6	5,6	5
Ambient Humidity (%)	29,5	8,8	10	17,8	6,9	5
Nest Temperature (°C)	29,8	5,9	11	-	-	-
End of Quiescence						
Surface Temperature (°C)	52,3	6,4	11	51,4	3,4	5
Ambient Humidity (%)	24,1	7,9	10	12,4	7,7	5
Nest Temperature (°C)	34,5	6,2	11	-	-	-
Length of Quiescence	Range			Range		
Days with Fog (h)	1,8 - 5,0		9	0 - 4,5		7
Days without Fog (h)	0 - 4,0		3	0 - 1,5		3

such as surface temperature, saturation deficit and wind speed, control the behaviour of *C. detritus* during the midday heat, with threshold temperatures being the major factor.

6.1.4 Peak Transit Activity

The time of peak transit activity varied considerably depending upon the prevailing micro-climatic conditions (Table 6.4). Although peak activity occurred over a fairly wide range of surface temperatures, activity patterns of neighbouring nests observed simultaneously were similar. Summer morning peaks always occurred at lower temperatures and higher humidities than afternoon peaks (Fig. 6.3). Sometimes in winter there were four or five small activity peaks, rather than one or two distinct peaks.

Many ant species exhibit a bimodal pattern of diurnal activity with a midday period of total inactivity when surface temperatures reach a certain threshold (Délye 1968, Lévieux 1977, Whitford *et al.* 1980, Whitford *et al.* 1981). Each species has its own characteristic range of temperatures over which activity occurs (Table 6.5). Individuals of *Cataglyphis bombycina* have been seen active at a surface temperature of 58°C (Délye 1968), while *Ocymyrmex barbiger* of the Namib is only active when temperatures are fairly high and has been observed moving across the sand at a surface temperature of 65°C (Marsh, pers. comm.). Like *C. detritus* however, most ants are exposed very briefly to surface temperatures above 50°C (Délye 1968, Whitford and Ettershank 1975, Kay and Whitford 1978).

Table 6.4

Micro-climatic conditions prevailing during *Camponotus detritus* activity peaks.

Season	Morning Peak						Afternoon Peak					
	Surface Temp. (°C)			Ambient rh (%)			Surface Temp. (°C)			Ambient rh (%)		
	$\overline{x}$	S.D.	N	$\overline{x}$	S.D.	N	$\overline{x}$	S.D.	N	$\overline{x}$	S.D.	N
Summer Nov - Feb	30,6	9,9	11	56,4	15,2	10	37,2	5,3	13	31,6	13,8	13
Intervening Months Mar, Apr, Sept, Oct	28,7	8,6	12	57,2	17,2	12	40,2	5,7	9	26,7	14,6	9
Winter May - Aug Non-East Wind	25,7	9,3	10	50,3	20,9	12	32,8	8,1	5	22,0	16,0	4

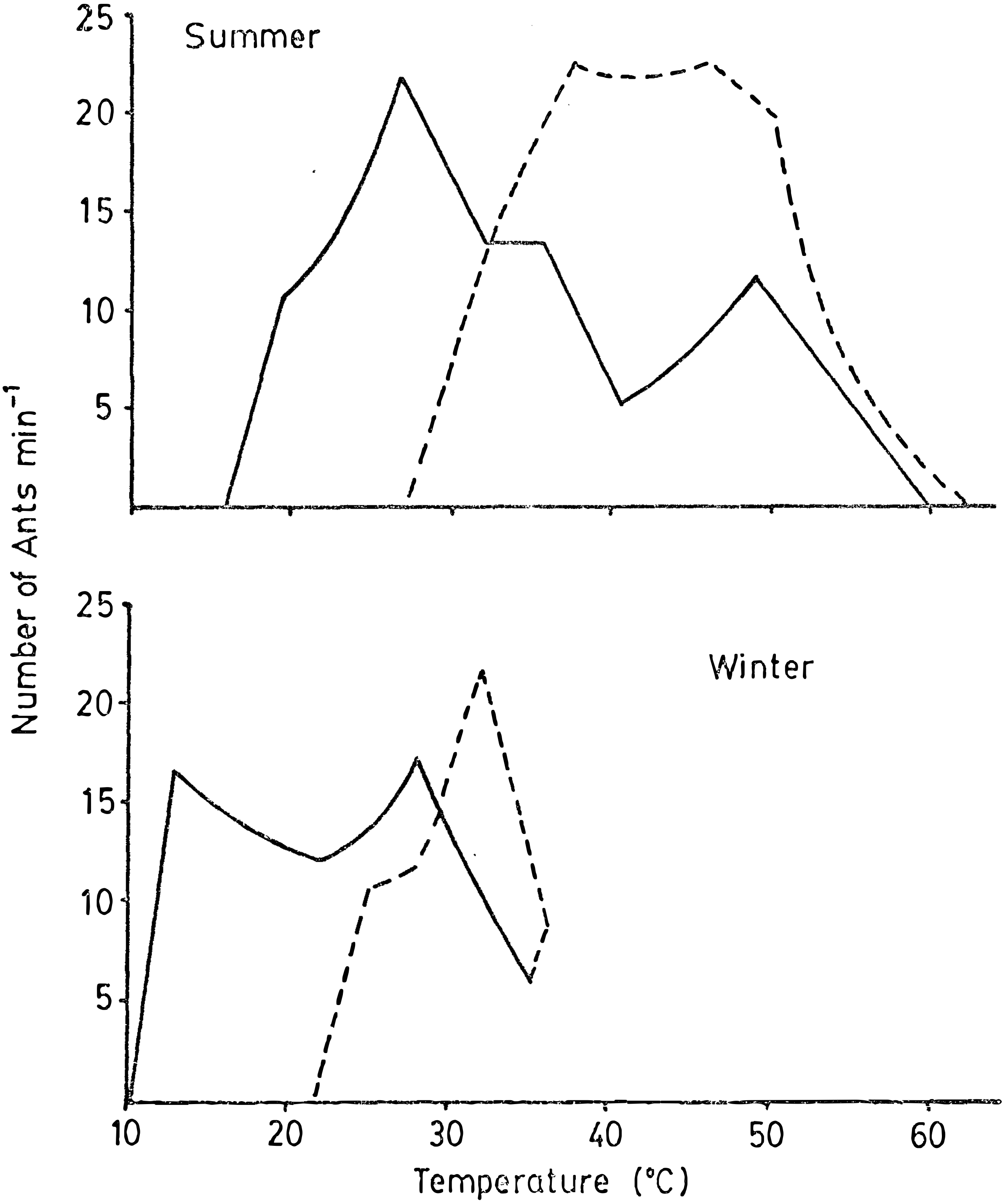


Fig. 6.3 An illustration of the difference between morning (sunrise to noon) (solid lines) and afternoon (noon to sunset) (broken lines) transit activity (ants entering and leaving the nest) as related to surface temperature.

Table 6.5

Range of surface temperatures over which some desert ant species are active.

Species	Range (°C)	
Diurnal		
Formica altipetens	4 - 47°	1
Tapinoma sessile	6 - 35°	1
Pogonomyrmex owyheei	13 - 42°	1
Pogonomyrmex occidentalis	27 - 54°	1
Pogonomyrmex californicus	32 - 54°	1
Myrmecocystus kennedei	36 - 57°	1
Veromessor pergandei	18 - 38°	1
Messor aegyptiacus	10 - 39°	2
Camponotus detritus	10 - 55°	3
Nocturnal		
Camponotus vicinus	2 - 23°	1
Myrmecocystus mexicanus	14 - 23°	1
Veromessor andrei	25 - 37°	1

1 : Bernstein 1979b 2 : Délye 1968 3 : Present study

6.1.5 Thermal Gradients

Myrmecologists studying terrestrial species generally only measure surface temperature (Whitford and Ettershank 1975, Whitford *et al.* 1981) as most ant species have short legs and their bodies are almost at ground level. Since *C. detritus* is a species with relatively long legs for an ant (length of tibia and tarsus 5,04 ± 0,58 mm, 20 workers of all sizes), the temperature to which an ant's body is exposed is the temperature of the air 5 mm above the ground. At night and in the early morning, air temperatures at 5 mm were the same as surface temperatures, but as surface temperature increased, a steep thermal gradient developed above the sand surface, until at midday in summer, temperatures at 5 mm were sometimes as much 10 - 15°C lower than surface temperatures (Fig. 6.4).

During midday in summer when surface temperatures were 50 - 55°C, the temperatures to which the ants' bodies were exposed were only 40 - 45°C. These temperatures were within the physiological limits of these ants as determined in the laboratory (Section 8.2). Since peak transit activity occurred when surface temperatures were between 30°C and 43°C with a mean of 37°C, the ants would have experienced air temperatures of 25 - 38°C at 5 mm, with a mean of about 31°C. This corresponds with the preferred temperature of *C. detritus* workers housed at 30 % rh. (Section 8.1). Similar steep thermal gradients above the sand surface also occur in the Sahara Desert and it is significant that those species which are active at high surface temperatures i.e. *Cataglyphis* species, also have long legs (Délye 1968).

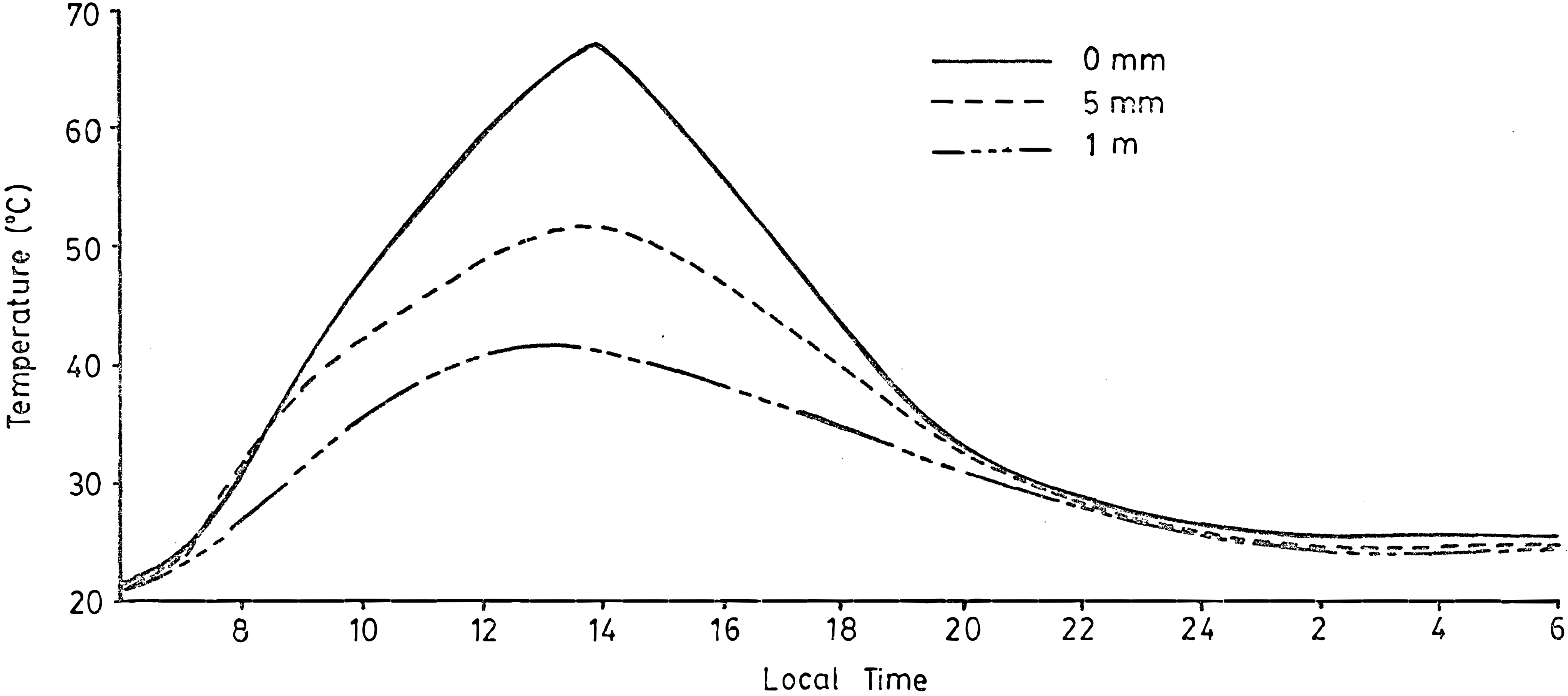


Fig. 6.4 Thermal gradient above the sand surface in the dunes of the Namib Desert in summer (Far East, 6 Feb 1982). Local time precedes sun time by one hour.

6.1.6 Numbers of Workers Entering and Leaving the Nest During Transit Activity.

In summer, the number of ants leaving or entering the nest during the day was initially low (one or two per minute), thereafter increasing rapidly to a peak with a mean number of 16,1 ± 8,0 S.E. ($N = 12$) ants min^{-1} (Fig. 6.1). The peak number of ants leaving the nest often occurred slightly earlier than that of ants returning to the nest, but during the afternoon numbers of ants entering and leaving the nest were usually similar. The number of ants active during peak transit activity varied considerably from nest to nest, however, as well as from one month to another in the same nest. Similarly the mean number of ants active throughout the day was variable, with an overall summer mean of 6,2 ± 2,9 S.E. ($N = 11$) min^{-1}. This appeared to be associated to a certain extent, although not entirely, with surface temperature. For example, on 7 October 1980 and 7 November 1980 the mean number of ants active during the day at nest MMB was 6,6 and 7,1 min^{-1} respectively, while mean surface temperatures were 37,1 and 34,0°C respectively. On 3 January 1981 mean daily transit activity was 11,1 ants min^{-1} and mean surface temperature was 42,1°C. At nest K1, however, on 3 January 1980 mean daily transit activity was 11,6 ants min^{-1} while surface temperature was 35,7°C. Yet on 22 December 1979, when mean surface temperature was 46,7°C, mean activity was only 5,31 ants min^{-1} throughout the day. These variations are probably related to the degree of hunger of the colony members and developmental stage of the brood as much as to temperature. In some nests 30 to 40 ants were active per minute during peak activity while in others peaks were as low as six to ten ants.

In winter, activity peaks were less marked than in summer, having a mean of 10,3 ± 3,6 S.E. (N = 11) min^{-1}, but the mean number of ants active throughout the day was not significantly different from that of summer, 5,1 ± 2,5 S.E. (N = 11) min^{-1}. During the intervening months mean peak activity was 17,2 ± 16,0 S.E. (N = 10) ants min^{-1} and the daily mean was 5,5 ± 5,3 S.E. (N = 9) ants min^{-1}.

The total number of ants estimated to leave a nest during a day varied from about 700 to as many as 5 000. This does not necessarily reflect the number of individuals leaving the nest since a single ant may leave and re-enter the nest many times (Harkness and Wehner 1977), but does give an idea of the number of foraging trips per nest per day.

6.1.7 Effect of Rain on Transit Activity

On the three occasions observed when rain fell for ten minutes or more all transit activity ceased. Initially, however, as the rain started to fall and immediately after a shower the numbers of ants leaving the nest to drink water from the damp sand rose markedly. Rain is known to stop foraging activity in ants from mesic environments (Gotwald 1968, Lévieux 1975, Lévieux and Louis 1975, Fowler and Roberts 1980). The Saharan ant *Camponotus thoracicus,* which is normally strictly nocturnal, will come out during the day after rainfall (Délye 1968). The same was observed with the nocturnal *C. mystaceus* in the Namib.

6.1.8 Effect of Wind on Transit Activity

Moderate winds, up to 8 or 11 km h^{-1} at a height of 5 mm did not appear to inhibit transit activity. Small workers were seen being blown off-course by 8 km h^{-1} winds, and yet they continued walking against the wind. At about 16 km h^{-1} and above, wind appeared to have a marked inhibiting effect upon activity. Figure 6.5 shows the effect of an East Wind on the activity of two nests in the same area. The entrance of nest C faced east, while the entrance of nest B was on the west side of a large mound and was relatively protected from the wind. As workers from nest B left the lee of the mound they were blown off-course by the wind and about 90 % of them returned to the nest after walking 1 - 3 m away from the nest. During each three minute observation period at nest C, from two to six workers came out of the nest briefly, but turned back again. The general pattern of transit activity during an East Wind appeared to follow the strength of the wind. As mentioned previously, the increased surface temperature caused transit activity to start at sunrise. Gradually, as both temperature and wind speed increased, transit activity decreased and finally ceased when the wind was gusting up to about 25 km h^{-1} and above. In the afternoon, when the wind dropped the ants resumed transit activity.

6.1.9 Seasonal Transit Activity

Camponotus detritus appeared to exhibit definite seasonal patterns in transit activity, dependent on changes in surface and air temperature, but showed no marked difference in the intensity of activity. Within a single nest the numbers of active ants varied from month to month, and certain nests became completely inactive during the winter months (Table 5.3). However, when the intensity of activity of all observed nests was considered as a whole, there were no seasonal differences in

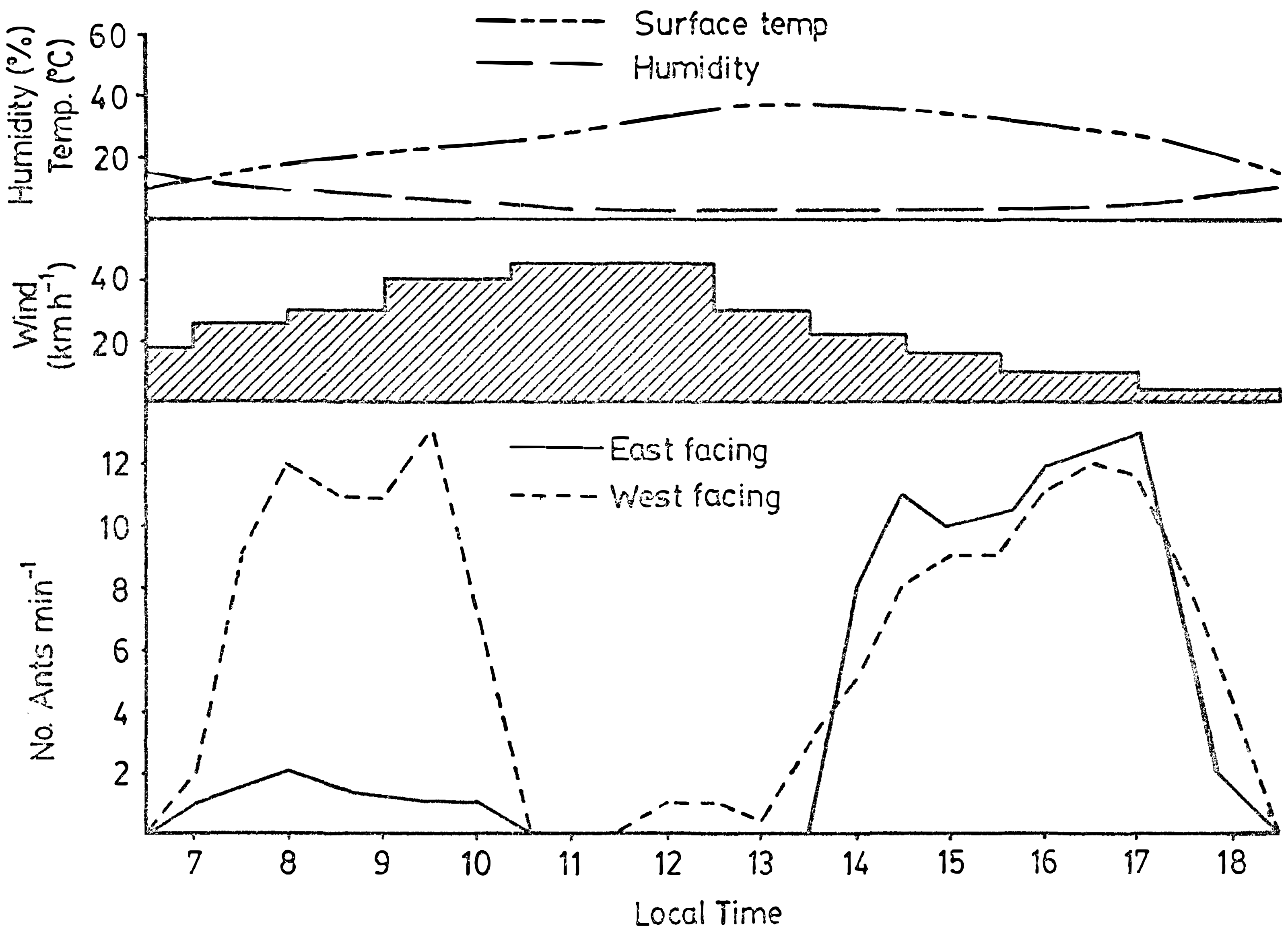


Fig. 6.5 The effect of an East Wind on the transit activity of *Camponotus detritus* observed on 14 July 1982. The lower graph shows the number of workers leaving two different nests, one with the entrance facing east, the other facing west (see text). Local time precedes sun time by one hour.

the mean number of ants leaving and entering the nest per day (Section 6.1.6) Neither were there great differences in the number of hours per day that ants were active (10 - 11 hours in summer; 9 - 10 hours in winter). Longer daylight hours and higher morning surface temperatures in summer were counteracted by the midday quiescence.

The lack of seasonality in foraging intensity, the absence of food reserves within the nest and the presence of brood throughout the year indicate that *C. detritus* has a fairly constant food supply. This food supply is maintained by the relatively uniform climatic conditions prevailing in the central Namib dune-field. Within a particular area, however, the amount of food available may vary, resulting in local activity differences.

Seasonal differences in activity occur among a wide range of ants. Like *C. detritus*, the temperate species *Formica polyctena* alternates between a bimodal and a unimodal activity pattern depending upon surface temperature (De Bruyn and Kruk-De Bruin 1972). Low winter temperatures result in a total cessation of all activity among many temperate species (Brian 1965, Sanders 1972, Mabelis 1979). Forage availability and quality greatly affect many desert species, particularly the seed harvesters, resulting in marked seasonal differences in foraging activity (Whitford *et al.* 1976, Bernstein 1979b, Briese and Macauley 1980, Whitford *et al.* 1980, Whitford *et al.* 1981). For these species in the American deserts, soil temperatures appear to act as thresholds for foraging activity, but forage availability and quality are the important regulators of forage intensity and duration (Whitford *et al.* 1980, Whitford *et al.* 1981). Colony satiation also plays an important role in regulating the activity of harvester ants. When seed stores within the nest are high no foraging activity occurs even when food is abundant on the surface (Whitford and Ettershank 1975).

Among certain carpenter ants the factors governing activity appear to vary seasonally. For example, the three species of the boreal forests, *C. herculeanus, C. noveboracensis* and *C. pennsylvanicus* show marked seasonality with no activity at all in winter (Sanders 1972). In summer, activity initiation is temperature dependent and peak activity occurs in June and July, coinciding with the period of rapid larval growth. Daily activity patterns correlate with temperature in early June, showing a midafternoon peak. However, as the season progresses the peak in activity becomes later until *C. pennsylvanicus,* in particular, becomes almost nocturnal. Fowler and Roberts (1980) found that foraging activity of *C. pennsylvanicus* is affected most strongly by temperature and saturation deficit in June, by time of day in July and by saturation deficit again in August.

6.1.10 Effect of the Environmental Gradient on Transit Activity

The same factors that controlled activity at Gobabeb, namely light and temperature, appeared to govern activity at the three other sites across the environmental gradient. Differences in activity appeared to be related to the length of time available for activity. Thus nearer the coast where temperatures are often lower, transit activity could often continue throughout the day, whereas on the same days in the Far East the midday inactivity period could last for as much as four hours.

6.2 Honeydew Collection

Camponotus detritus workers were seen on scale-infested plants 24 hours per day (Figs. 6.6 and 6.7), with significantly more ants present at night than during the day in summer ($P < 0,05$). This suggests that *C. detritus* is nocturnal as well as diurnal. However, during the day there was constant transit activity to and from the plants with a high change-over rate of foragers on the plants except during the heat of midday, while at night no movement occurred between plants or from the plants to the nest. Only 38 ± 5 % of the individually marked ants seen during the day remained out at night, and all the ants present at nightfall remained on the same plant until dawn.

In summer, the number of workers collecting honeydew was negatively correlated with ambient temperature ($P < 0,05$), with the lowest numbers of honeydew collectors occurring in the early afternoon (maximum air temperature) and maximum numbers just prior to sunset. Peak honeydew collection occurred at ambient temperatures (26 - 33°C) similar to the experimentally determined preferred temperatures of workers (Section 8.1). Of the total number of foragers present at sunset 87 ± 6 % remained on the plants throughout the night, the rest returned to the nest before darkness. During the early evening (20h00 - 24h00) about 40 - 50 % of the ants present were active while the rest remained motionless with their heads down and their legs close to their bodies. As the night progressed more and more ants became motionless. An hour or two prior to sunrise about 10 - 30 % of the foragers had distended gasters and most of these foragers left the plants shortly after sunrise to return to the nest. During the day individuals with distended gasters were

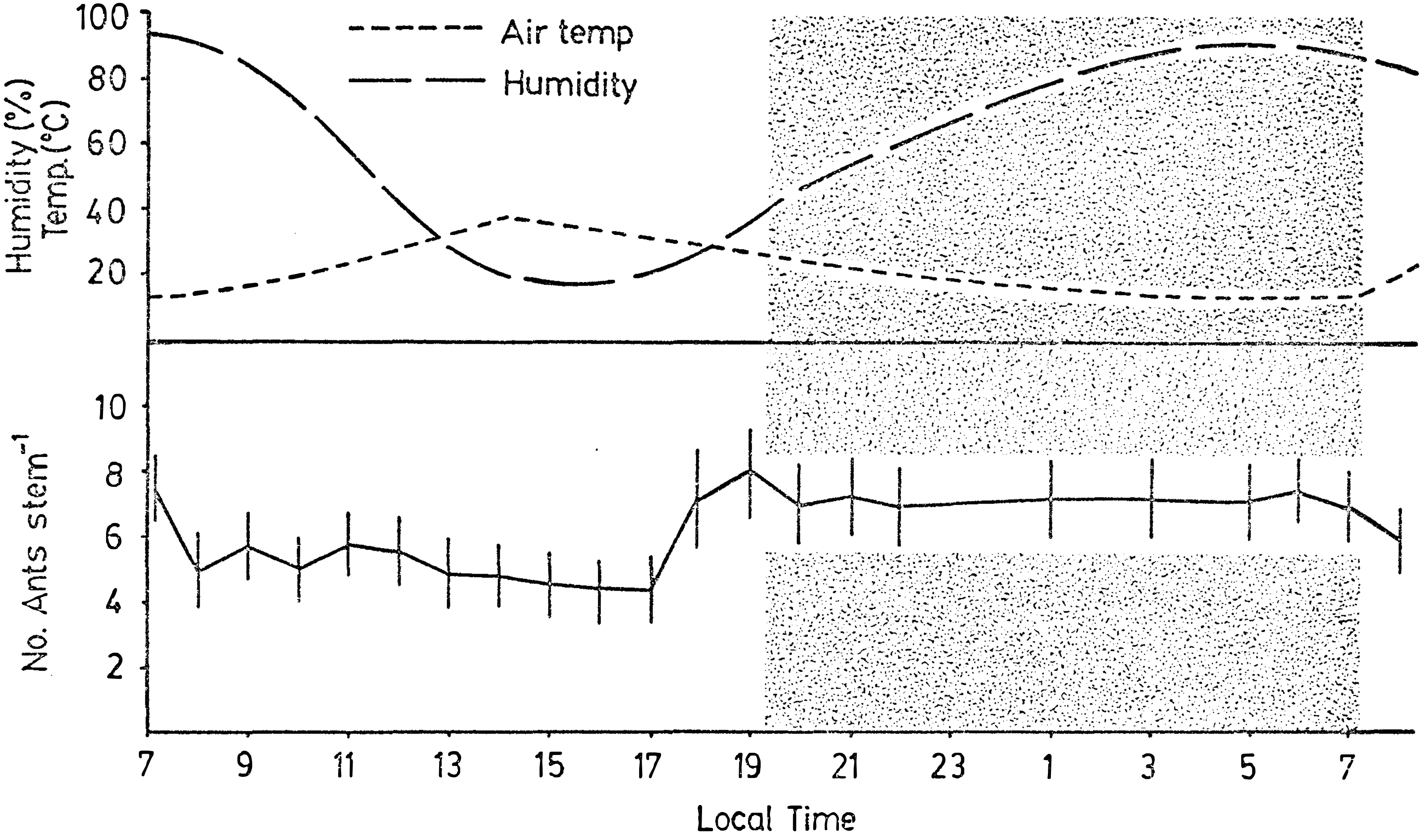


Fig. 6.6 Summer honeydew collection activity of *Camponotus detritus* workers observed on 23 Feb 1982. Each point represents a mean of activity observed on ten stems. Vertical lines indicate standard errors. Local time precedes sun time by one hour.

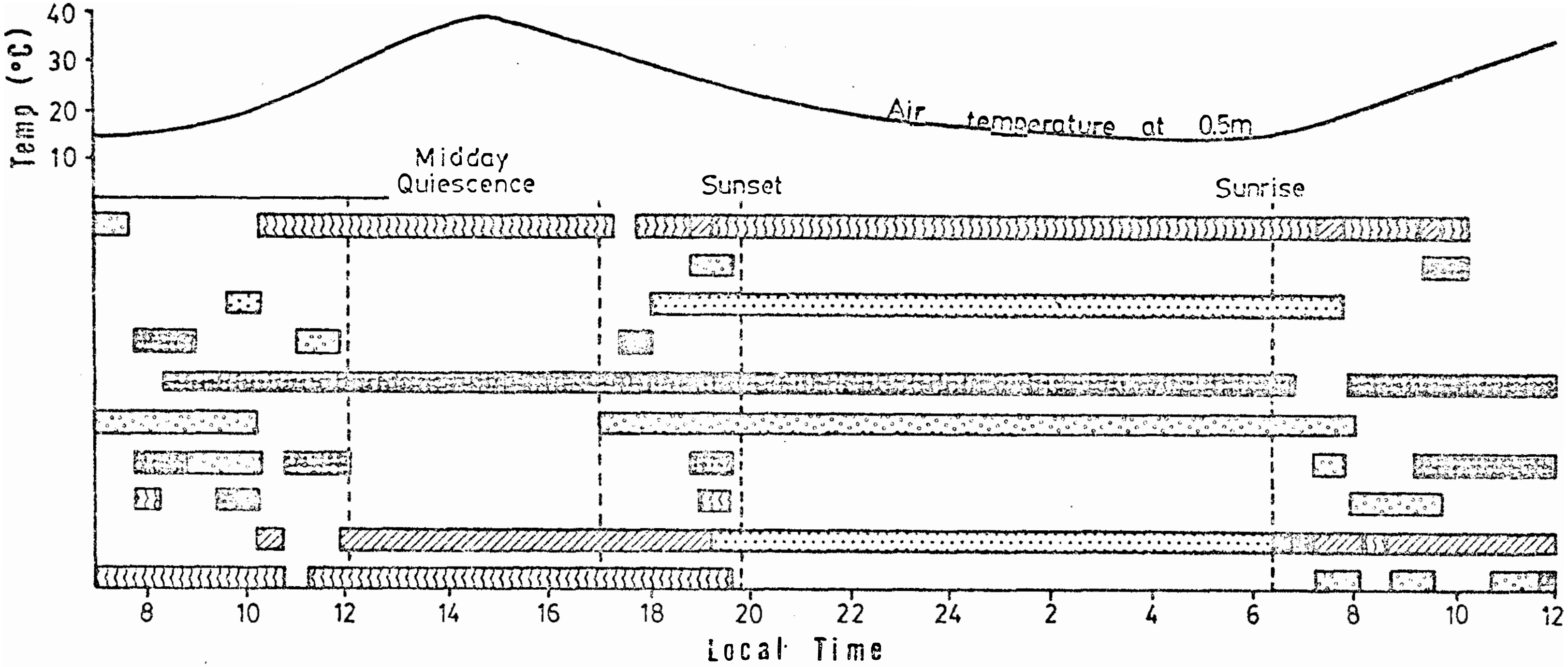


Fig. 6.7 Honeydew collection activity of ten individually marked *Camponotus detritus* workers observed on 23 and 24 Feb 1982. Each horizontal line represents the activity of one ant. Shading indicates presence on different grass stems. Open areas indicate the absence of the ant, which was presumably in the nest at that time. Local time precedes sun time by one hour.

also noticed on the plants, but in fewer numbers. There were considerable differences in the foraging time of individuals. Some of the marked ants foraged for only 30 minutes out of 48 hours whereas others remained on one plant for as much as 26 out out of 48 hours.

In winter the pattern of activity was slightly different. There was a positive correlation between the number of ants collecting honeydew and ambient temperature ($P < 0,05$), with peak numbers in the late morning and minimum numbers at night. On warm winter nights (e.g. after an East Wind) the pattern of honeydew collection was the same as it was in summer but on cold nights all ants remained totally motionless. At temperatures below 8°C ants apparently became torpid. Some fell off the plants and remained on the sand surface until the following morning. During an East Wind the number of foragers was negatively correlated with wind strength and those ants which remained on the plants sheltered on the leeward side of the thicker stems. Only where scale insects were found on the leeward side of the stems did the ants continue to collect honeydew. There was no correlation between foraging intensity and relative humidity in either winter or summer.

Only two observations were made on honeydew collection during the intervening months. On both occasions the mean numbers of honeydew collectors were the same during the day and night, but the time of maximum and minimum numbers differed on each occasion.

Although temperature appeared to be the major factor regulating honeydew collection by *C. detritus* workers, this may have been indirect, since the pattern of honeydew excretion by scale insects would influence the activity of ants, and may itself be either directly or indirectly influenced by temperature. Peak numbers of ants tending scale insects may reflect maximum daily honeydew production. Kawai and Tamaki (1969) found that maximum and minimum frequency of honeydew excretion by the scale insect, *Ceroplastes pseudoceriferus*, occurred between 18h00 - 20h00 and 06h00 - 08h00 respectively. A similar maximum peak of honeydew excretion by scale insects in the Namib during summer may be responsible for the increased numbers of ants on scale-infested plants just prior to sunset. Honeydew excretion may be higher at night than during the day as a result of the translocation of photosynthates in the plant at night, thus resulting in the presence of more ants at night. On the other hand, Myers (1957) found that the foraging rhythm of *Anoplolepis steingroeveri* was not correlated with the rate of honeydew production, but was correlated with ambient temperature. The plant/scale insect/ant interactions would provide very interesting and worthwhile possibilities for future research.

The nearctic species *C. noveboracensis* collects honeydew excreted by a membracid (Gotwald 1968). In autumn when the numbers of membracids decrease, the numbers of foraging ants also decrease. Like *C. detritus*, ants tend membracids 24 hours per day, but most activity between the nest and foraging grounds occurs during the day. At night and at low temperatures both ants and membracids remain motionless. Although honeydew collection is diurnal, these ants collected sap from a wounded plant at night.

Peaks in *C. detritus* transit activity did not correspond directly with peaks in the numbers of honeydew collectors present on the plants.

However, the numbers of workers coming to and from the scale-infested plants showed a similar pattern to that of transit activity. Not all workers which left the nest (i.e. transit activity) went to scale hosting-plants. Some went to other nests belonging to the same colony while others collected building material for the nest or scavenged for dead arthropods.

Marked *C. detritus* workers showed a fair amount of fidelity to the plants on which they collected honeydew. Although some individuals visited up to four different grass stems during the 48 hour observation, most were always found on the same grass stems and visited the same plants for up to 10 or 14 days. This fidelity is known to occur among other ant species (Ebbers and Barrows 1980). Among *Formica* and *Lasius* species each forager patrols a certain area within the colony's territory (Wilson 1971). Such behaviour can be adaptive in that, by individual workers becoming familiar with a particular part of the foraging range, the size of the colony may be increased (Carroll and Janzen 1973).

Section Seven

EFFECT OF THE ENVIRONMENTAL GRADIENT UPON DISTRIBUTION AND ABUNDANCE

7.1 Nest Density and Distribution

Figure 7.1 shows the density of *C. detritus* nests per hectare across the central Namib dune-field. There appeared to be three different densities of ant nests : low near the coast, high in the central regions and intermediate in the east. No statistically significant difference in nest density was found between Rooibank and Jumbo Valley, or between Gobabeb and Noctivaga. Differences between nest densities at Jumbo Valley and Gobabeb, Noctivaga and Mniszechi's Vlei, Jumbo Valley and Mniszechi's Vlei were all significant ($P < 0,05$), and between Mniszechi's Vlei and Far East, Gobabeb and Mniszechi's Vlei ($P < 0,1$). Along the coast there is no dune vegetation and therefore *C. detritus* is not present in the dunes, although it occurs at Sandwich Harbour, where a freshwater spring supports non-halophytic vegetation.

At each site the variance of density was greater than the mean, indicating a contagious or clumped dispersion of nests (Section 2.3.3). This would be caused primarily by the patchy distribution of vegetation, particularly marked at Rooibank and Jumbo Valley, since the ants are dependent on the vegetation both for food and nest sites. A further causal factor could be the habit of nest splitting, which may result in two or three sister nests occurring in close proximity.

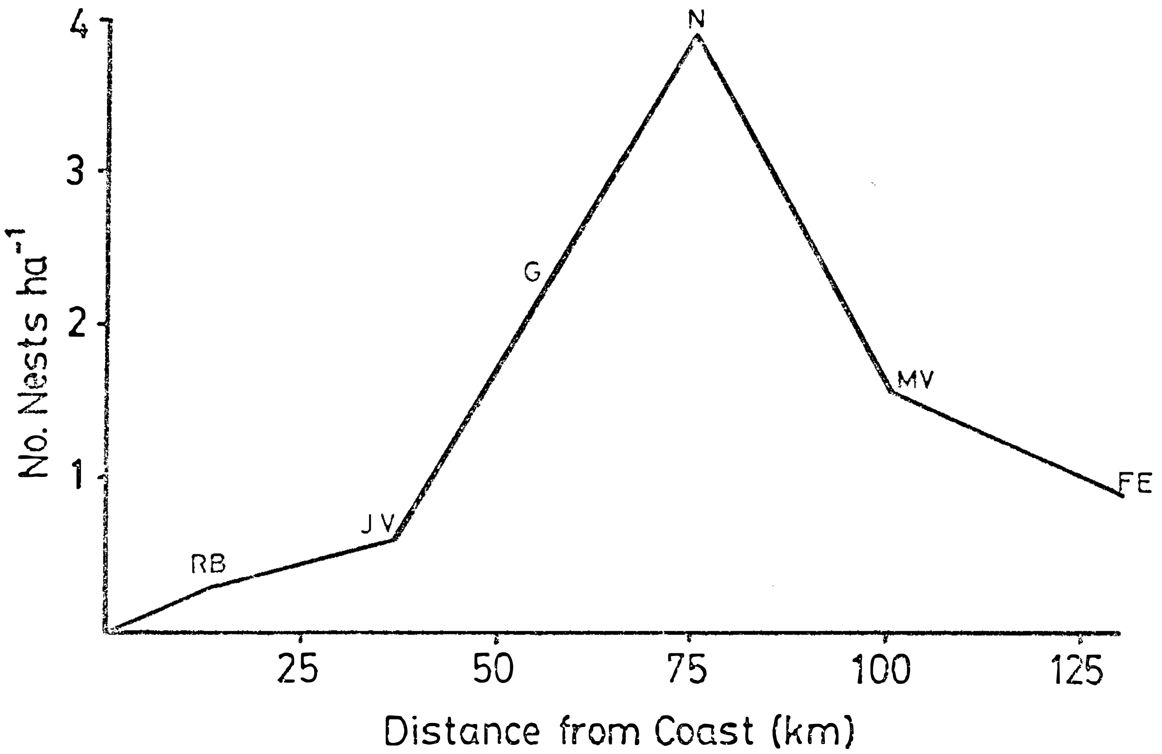


Fig. 7.1 Density of *Camponotus detritus* nests across the central Namib dune-field. Site abbreviations as in Fig. 1.1.

Figure 7.2 and Table 7.1 show the relative abundance of nests at the base of different plant species and on different parts of the dune. *Trianthema hereroensis*, which only occurs from near the coast to just east of Gobabeb, grows anywhere on the dune slope, but chiefly in hollows. *Stipagrostis sabulicola*, *S.* cf. *namaquensis* and *Eragrostis spinosa* are found mainly on the upper and mid dune slopes, while *S. lutescens* and *Asthenatherum glaucum* occur on the mid and lower slopes. At most sites the distribution of nests on the dune followed the distribution of either total vegetation cover, or else of the plant species most important for nesting. At Rooibank, Jumbo Valley and Far East, where sandy hollows occur, the majority of nests were in these areas. At most sites more nests were found on the east slope than the west and nest density increased from upper to lower slope.

There appeared to be more than one factor determining the situation of *C. detritus* nests. At Rooibank and Jumbo Valley where *T. hereroensis* is the dominant plant species all nests were found beneath this species. However at Gobabeb, although *S. sabulicola* is dominant, most nests were still found in *T. hereroensis* mounds. Although both plant species create equally large mounds of sand, apparently providing similar potential nesting sites, *C. detritus* appeared to preferentially select *T. hereroensis*, possibly because the root system is more suitable for nest construction than *S. sabulicola*, but more likely because *T. hereroensis* apparently provides a superior food supply. The degree of scale insect infestation on *T. hereroensis* appeared to be higher than that on *S. sabulicola*, but more detailed studies are required to substantiate this general observation. Apart from being a host plant for the homopterans and therefore indirectly a source of honeydew,

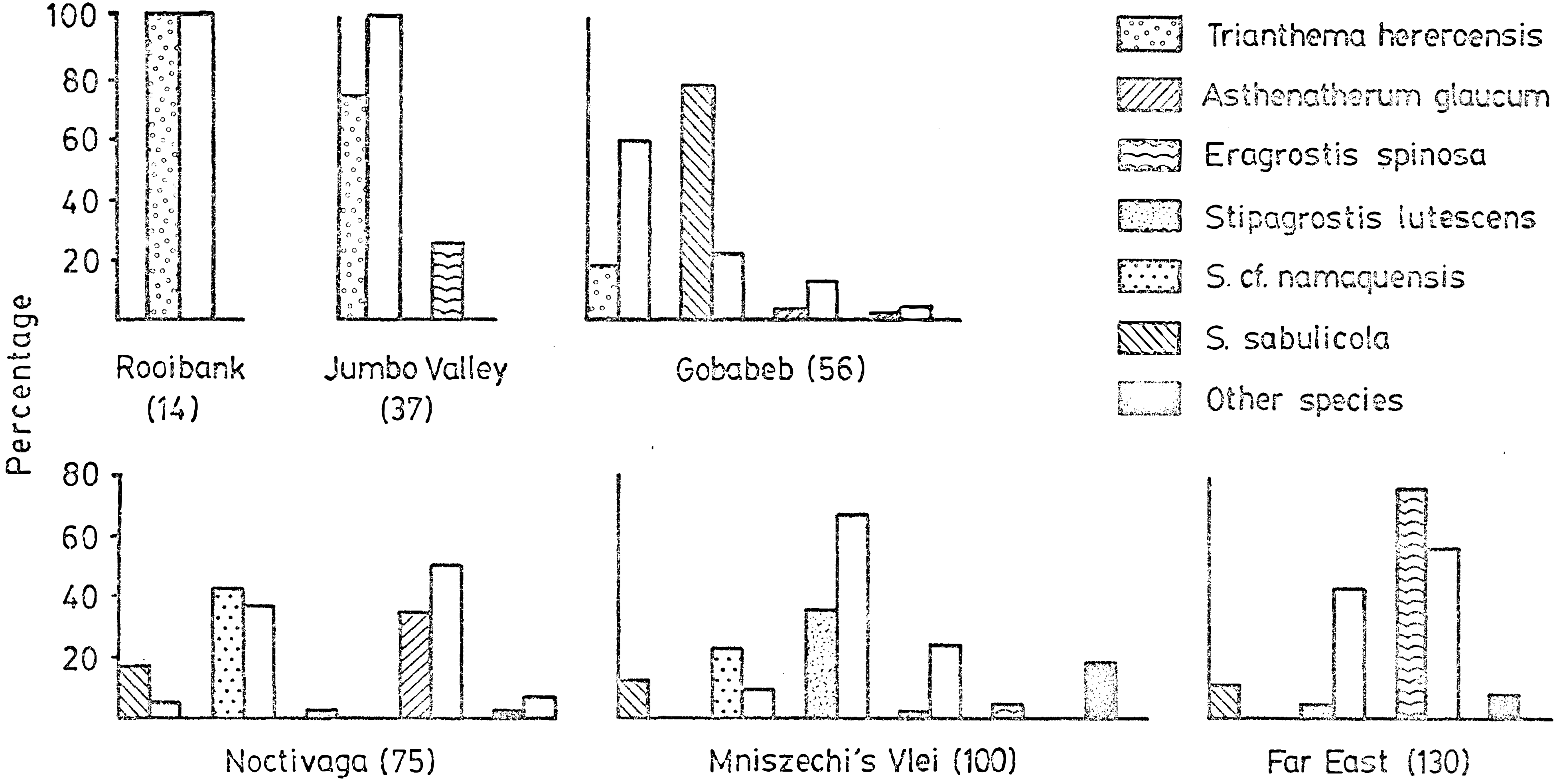


Fig. 7.2 Proportions of *Camponotus detritus* nests under different plant species, compared with the relative abundance of each plant species. Shaded bars represent plant cover. Adjacent open bars represent nest abundance. Figures in brackets indicate the distance of each site from the coast.

Table 7.1

Density and distribution of *Camponotus detritus* nests (ha^{-1}) on various parts of the dune from west to east across the dune-field, and corresponding vegetation cover (%) of those plant species preferentially used for nesting sites. Distances (km) of study sites from the coast are in brackets.

	Rooibank (14)	Jumbo Valley (37)	Gobabeb (56)	Noctivaga (75)	Mniszechi's Vlei (100)	Far East (130)
Nests:						
West Slope	0,1	0	2,3	4,9	0,5	0,4
East Slope	0,3	0,5	2,3	2,9	2,7	1,1
Upper Slope	0,1	0	2	2,4	0,5	1,0
Mid Slope	0,3	0,5	2	4,7	1,5	0,6
Lower Slope	-	-	3	4,7	3,1	0,6
Interdune	0,5	0	-	-	-	-
Hollows	-	*8	-	-	-	**1,3
Vegetation:						
West Slope	0,4	0,3	0,9	2,2	3,3	5,3
East Slope	0,6	0,6	0,8	0,9	5,1	10,3
Upper Slope	0,4	0,7	0,9	0,1	0,3	10,3
Mid Slope	0,6	0,3	0,7	1,9	6,4	2,7
Lower Slope	-	-	1,1	2,7	6,0	2,7
Interdune	1,2	0,2	-	-	-	-
Hollows	-	1,7	-	-	-	8,6

* The density of nests in the hollows to the north of transverse dunes is high because this is where most of the *Trianthema hereroensis* is found. However, this only constituted 9 % of the total area.

** Depressions in the dunes almost equivalent to lower dune.

T. hereroensis flowers were also found to provide nectar for the ants. A further possible advantage provided by *T. hereroensis* is the moister environment beneath the plant than is the case with *S. sabulicola* (Seely *et al.* 1977). The patchy distribution of *T. hereroensis*, in turn, would account for the patchy distribution of the ants.

Although *Asthenatherum glaucum* provided only 1 % of the vegetation cover, 14 % of the nests were constructed beneath this species commonly found near the base of the dunes where the sand is somewhat moister and more consolidated.

At the three eastern study sites a large proportion of nests were found in the most abundant plant species occurring in that area, but the distribution of nests did not correspond with the relative abundance of each plant species (Fig. 7.2). At Noctivaga and Mniszechi's Vlei the ants appeared to select *A. glaucum* while at Far East they selected *S. lutescens*, possibly due to the absence of *A. glaucum*. Proximity to food sources did not appear to have a dominant influence on the location of nest sites east of Gobabeb since *A. glaucum* does not host scale insects and the degree of infestation of *S. lutescens* and *E. spinosa* is very low compared with that of *S. sabulicola* and *S.* cf. *namaquensis*. East of Noctivaga *S. sabulicola* is not surrounded by the large mounds of sand found at Gobabeb and the roots may be too diffuse to provide sufficient cohesion of the sand for nest construction. The same may be true of *S.* cf. *namaquensis*, thus the ants are possibly unable to make nests below these plant species which occur on the upper and middle slopes. *Asthenatherum glaucum* does not create mounds either, but the roots form a closely packed network beneath the plant in which the ants can construct their galleries.

Grain size of the sandy substrate may influence the choice of nest site. Lower down the dune slope grain size increases, and this may cause the ants to nest under those species which occur lower on the dune, namely *S. lutescens* and *A. glaucum*. Soil moisture, however, also increases with the increase in grain size lower down the dune slope, and may have an equally important effect in nest site selection. In the eastern half of the dune-field *C. detritus* territories are likely to be long and narrow since the ants were found to nest on the lower and mid slopes and to collect honeydew from species occurring on the mid and upper slopes.

Three factors therefore appeared to determine the choice of nest sites of *C. detritus* : suitability of substratum, proximity to food sources and abundance of plant species. On the western side of the dune-field the latter two factors were most important since virtually all the vegetation present creates a suitable substratum. In the east, nearness to food source appeared to be counterbalanced by substratum suitability.

7.2 Number of Workers Per Nest

Tables 7.2 and 7.3 show the mean number of workers per nest at each study site, and the mean number of workers per nest constructed beneath each plant species. The large standard error indicates the variability in nest size. There was a significant difference in nest size between Rooibank and Jumbo Valley ($P< 0,05$), but not between any of the other sites. Nor was there a significant difference in nest size among the different plant species, but this does not necessarily imply that nests

Table 7.2

The mean number of *Camponotus detritus* workers per nest across the Namib dune-field. Distances (km) of study sites from the coast in brackets. N = number of nests excavated.

Study Site		Number of Workers per Nest $\overline{x}$	S.E.	N
Rooibank	(14)	728,4	305,7	5
Jumbo Valley	(37)	3344,0	1100,3	4
Gobabeb	(56)	5076,6	2700,5	5
Noctivaga	(75)	4231,3	1217,6	6
Elephant Valley	(87)	1822,8	265,3	4
Mniszechi's Vlei	(100)	3986,3	861,0	6
Far East	(130)	3926,3	1002,3	6

Table 7.3

The mean number of *Camponotus detritus* workers per nest constructed under different plant species. N = number of nests excavated.

Plant	Number of Workers per Nest $\overline{x}$	S.E.	N
Trianthema hereroensis *	1922,0	537,1	11
Trianthema hereroensis **	2916,7	763,8	6
Asthenatherum glaucum	2364,6	287,4	9
Stipagrostis lutescens	3940,0	1212,3	6
Stipagrostis sabulicola	6707,3	3125,1	4
Eragrostis spinosa	4862,3	699,2	3
Other Species	5025,7	2360,4	3

* Including Rooibank

** Excluding Rooibank

can reach any size under any plant species. Since size of ant nests is a function of age (Brian 1965, Wilson 1971), a young nest constructed at the base of *S. sabulicola* may be smaller than a mature one constructed at the base of *A. glaucum*. However, the maximum attainable size of a nest is likely to be limited by the size of the mound and area covered by the plant roots. *Asthenatherum glaucum* seldom creates large mounds and root systems are fairly shallow, whereas *T. hereroensis* and *S. sabulicola*, at Gobabeb, can form mounds up to 1 m high with a basal area of about 25 - 30 m^2. Thus a nest constructed in a *T. hereroensis* or *S. sabulicola* mound could theoretically reach a far greater size than one at the base of *A. glaucum*. The above is supported by the fact that the largest nest excavated from an *A. glaucum* plant contained only 3 542 workers, whereas the largest nest excavated from an *S. sabulicola* plant contained 15 670 workers.

Possibly the higher nest density at Noctivaga when compared with Gobabeb, resulted from the predominant choice of *A. glaucum* as a nesting site at Noctivaga. If nests constructed among *A. glaucum* roots can only attain a limited size nest splitting would be likely to occur at a higher rate than at Gobabeb. One colony found at Noctivaga had four nests, all constructed in *A. glaucum* within 2 - 3 m of each other. At Gobabeb it is not uncommon for a colony to comprise a single nest constructed in a large *T. hereroensis* or *S. sabulicola* mound.

7.3 Correlations of Ant Density With Environmental Variables

Density (number of workers ha^{-1}) and therefore biomass of *C. detritus* increased steeply from the coast inland, reaching a maximum in the central regions and thereafter decreasing slightly again (Fig. 7.3 and Table 7.4). Figures 1.3a and b show the climatic gradient across the dune-field. The only climatic variable with which *C. detritus* density was significantly correlated was mean annual temperature ($P < 0,05$). Although mean daily amplitude in temperature follows the same trend, it was not significantly correlated with *C. detritus* density. In Section Six it was concluded that temperature was the most important abiotic factor affecting the daily activity of these ants , and that the pattern of activity varied somewhat across the dune-field, depending on the daily temperature range. Thus the maximum amount of time available for transit activity may differ along the temperature gradient. However, this is unlikely to influence foraging, since at all sites excluding Rooibank, ants tended scale insects 24 hours per day. Temperature and other environmental variables affect the rate of honeydew production by homopterans (Auclair 1963, Way 1963) and may therefore indirectly affect the abundance of *C. detritus* by governing their food supply. At Rooibank no nocturnal foraging was observed, which may result in an overall decrease in the amount of food available to colonies there, thereby limiting colony size. Also, because temperature is known to affect the rate of brood development of other ant species (Wheeler 1910, Wilson 1971), it is possible that the lower mean temperatures occurring at Rooibank result in a slower rate of brood production and therefore further contribute to the low densities of *C. detritus* found there.

Since *C. detritus* was found to be dependent on vegetation for food and shelter, it was predicted that the pattern of ant density across the dune-field would correspond to that of vegetation cover. However, this association was not found with respect to total vegetation cover, since

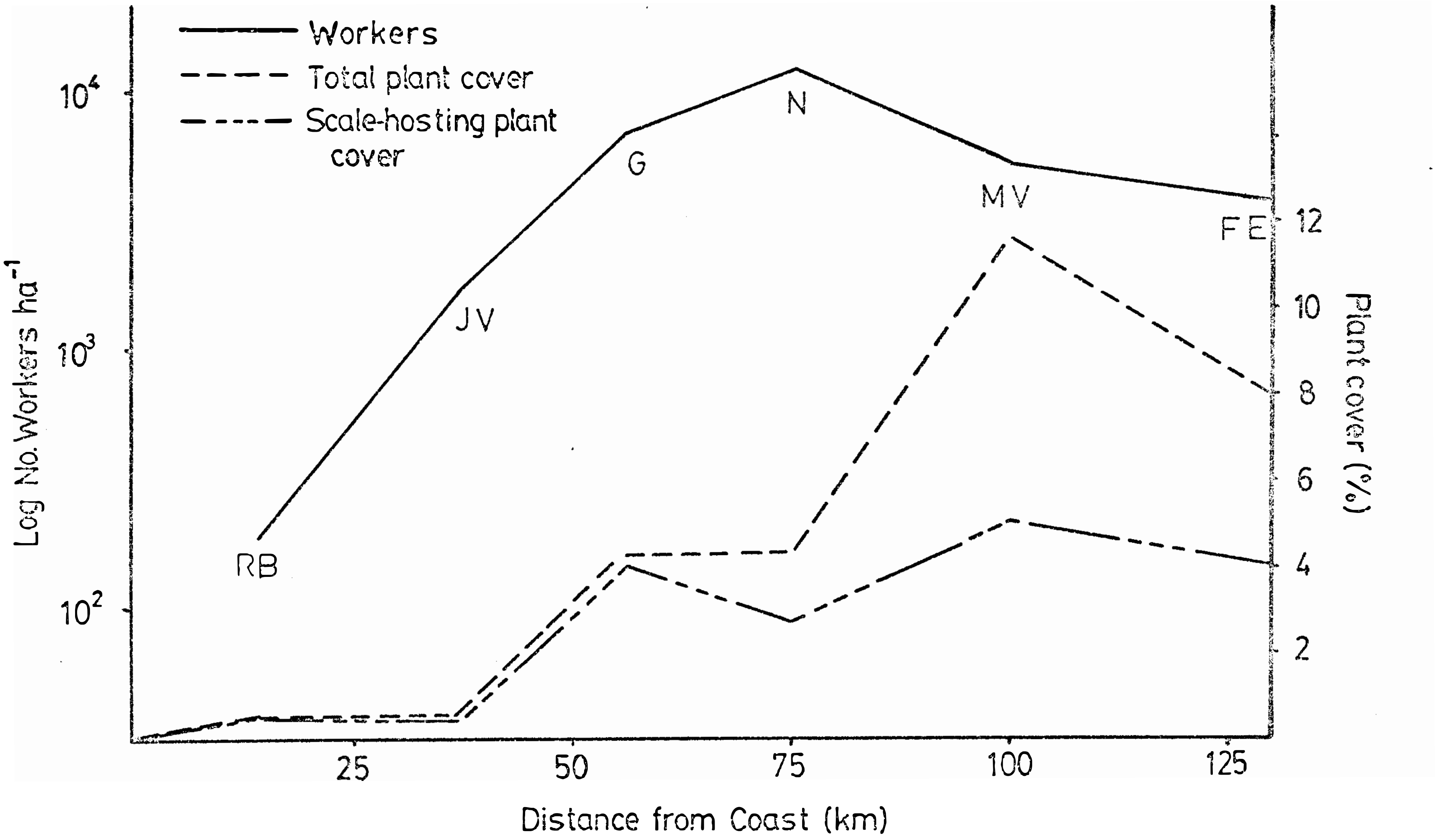


Fig. 7.3 Density of *Camponotus detritus* workers across the environmental gradient of the Namib dunefield (upper line). Lower lines represent percentage vegetation cover of all plant species present, as well as those species hosting scale insects. Site abbreviations as in Fig. 1.1.

Table 7.4

Biomass of *Camponotus detritus* workers across the Namib dune-field. Distances (km) of study sites from the coast in brackets.

		Wet Weight ($g\ ha^{-1}$)	Dry Weight ($g\ ha^{-1}$)
Rooibank	(14)	7,77	2,78
Jumbo Valley	(37)	65,37	23,47
Gobabeb	(56)	267,84	96,26
Noctivaga	(75)	477,78	171,70
Mniszechi's Vlei	(100)	210,24	75,56
Far East	(130)	142,42	51,18

not all plant species are equally susceptible to scale insect-infestation. When the density of those species most commonly hosting homopterans (Section 2.5.3), was compared with *C. detritus* density, there was a far better correlation (Fig. 7.3).

Nevertheless, plant cover still did not appear to account entirely for the pattern of ant density. The factor most likely to influence *C. detritus* is the abundance of scale insects, and the quality and quantity of honeydew they produce. No detailed study has been made on the abundance of homopterans but Table 7.5 shows preliminary estimates of the degree of infestation of *S. sabulicola* and *S.* cf. *namaquensis* by one of the more common scale insects at Gobabeb and eastwards, *Aclerda namibensis*. It should be noted that the estimated density of these scale insects was highest at Noctivaga decreasing toward the east, a pattern similar to that of *C. detritus* density from Gobabeb eastward.

At Rooibank and Jumbo valley, where *C. detritus* density was lowest, *A. namibensis* was absent and the degree of scale insect infestation of *T. hereroensis* was minimal. Nectar appeared to form a major part of the ants' diet at these sites. Different species of scale insect infest *T. hereroensis* at Rooibank and Gobabeb (Table 4.1). At Rooibank, only 4 % of the plants were visibly infested with a scale insect of the family Margarodidae. These scale insects are not sessile and were never found in large aggregations. At Gobabeb, *T. hereroensis* is infested with *Eriococcus* sp., a sessile species which forms thick clusters around the stems, and was found to infest about 20 % of *T. hereroensis* plants at Gobabeb. This greater infestation, combined with nectar from the

Table 7.5

Preliminary estimates of the degree of infestation of *Stipagrostis sabulicola* and *S.* cf. *namaquensis* by the scale insect, *Aclerda namibensis*.

	Gobabeb	Noctivaga	Mniszechi's Vlei	Far East
S. sabulicola				
Plants Infested (%)	8,9	34	44	97
Mean No. Stems Plant^{-1} (N = 10)	91,6 ± 80,7	54,8 ± 35,0	62,4 ± 31,4	76,8 ± 52,4
Mean No. Nodes Stem^{-1} (N = 30)	3,1 ± 1,9	3,9 ± 1,1	6,0 ± 2,0	4,9 ± 1,4
Mean No. Scales node^{-1} (N = 30)	5,25	4	3,1	3,9
Estimated No. Scale Insects ha^{-1}	7 379	2 154	5 854	13 469
S. cf. *namaquensis*	Does Not Occur			Does Not Occur
Plants Infested (%)	-	95	47	-
Mean No. Stems Plant^{-1} (N = 10)	-	39,5 ± 13,6	66,7 ± 4,4	-
Mean No. Nodes Stem^{-1} (N = 30)	-	5,3 ± 2,0	6,0 ± 2,3	-
Mean No. Scales Node^{-1} (N = 30)	-	2,45	2,45	-
Estimated No. Scale Insects ha^{-1}	-	22 610	12 699	-
Total Scale Insects ha^{-1}	7 379	24 764	18 553	13 469

flowers and the presence of *A. namibensis* on the grass probably accounts for the higher density of *C. detritus* at Gobabeb than in the west.

Other factors which may reduce the density of *C. detritus* east of Gobabeb are potential competitors and predators. From Noctivaga eastwards a second species of honeydew collecting ant, *Crematogaster* sp. (Section 3.16.1) has been found. This species only appears to collect honeydew from the scale insects associated with galls on *S.* cf. *namaquensis* (*Membranaria* sp. and two species of *Trionymus*). *Camponotus detritus* also tends these species, but was not found when *Crematogaster* was present. However, since *C. detritus* was observed primarily tending *A. namibensis* which *Crematogaster* was not seen tending and, since the preliminary estimates of *A. namibensis* abundance reflect the pattern of *C. detritus* density, it was thought to be unlikely that *Crematogaster* is limiting *C. detritus* through interspecific competition. *Camponotus detritus* appeared to have few predators at Gobabeb and westwards, but from Noctivaga eastwards the ant-mimicing spider, *Cosmophasis* sp., (Section 3.16.3) was seen preying on foraging *C. detritus* workers. This may have an effect on the numbers of *C. detritus*. Also the density of potential reptilian predators appeared to increase east of Gobabeb.

7.4 Comparisons With Other Studies on Environmental Gradients

Many studies have been made on plant and animal species diversity along environment gradients (e.g. Janzen and Schoener 1968, Whittacker and Niering 1975, Menge and Sutherland 1976, Rutherford 1978). In the Namib Desert sandsea changes in the abundance and species diversity of numerous arthropod species, in particular tenebrionid beetles, appear to be associated with the climatic gradient from the coast inland (Seely, pers. comm.). It is thought that peak abundances at different places across the sand-sea depend on the requirements of each species. Changes in mean temperature and relative humidity affect the distribution of beetles which produce a waxy layer to retard water loss, as well as those which do not. Like *C. detritus*, the availability of food appears to influence the distribution and abundance of many species, for instance tenebrionids and thysanurans, whose principle food source, wind blown detritus, appears to be most abundant mid dune-field. The number of ant species in the Namib dune-field increases from the coast inland. Similarly, species diversity of ants on the gravel plains increases from west to east and species which are fairly widespread appear to have peak abundances at different places along the gradient (Marsh, pers. comm.).

To the best of my knowledge, however, no comparable studies have been made of the relative change in abundance of a single ant species across an arid environmental gradient. In the Sahara Desert the majority of ant species live on the gravel plains (Bernard 1964b, Délye 1968). The number of workers per nest, as well as the relative abundance of each species in the community varies depending on the habitat.

Bernstein (1974) studied the changes in abundance of three harvester ant species along an altitudinal environmental gradient in the Mojave Desert and found that each species had peak abundances at unique points along the gradient. Time of daily foraging activity differed between species, with each exhibiting species-specific foraging temperatures. These allowed maximum foraging time per day at times of the year which coincided with maximum seed production by annuals at the altitude at which each species was most abundant. Thus both temperature and food availability (seed production) control the density of these species.

Sanders (1970), studying the distribution and density of *C. herculeanus* and *C. noveboracensis* colonies in three successional stages of a spruce-fir forest in northwestern Ontario, found that both the total number of ants and number of colonies were greater in immature stands. He attributed this to a greater abundance of nesting sites, since micro-environment and food sources appeared to be fairly constant throughout his study area. This is in contrast to the present study in which an excess of suitable nesting sites was found .

Only three ant species occur in a pioneer community of the "Strandvlakte" in the Netherlands of which *Lasius flavus* was the most abundant in the lower parts of the sand dunes (Boomsma and De Vries 1980). This species was found to be limited to a certain extent by the soil particle size. As with *C. detritus*, vegetation cover indirectly affected all three species occurring in that area since each was dependant on it for honeydew-producing aphids as well as nest sites. Brian (1979) found that the relative densities of two ant species occurring across a habitat gradient in a dry heath area were complementary, with one being most abundant in wetter, less exposed soils, the other in drier, more exposed soils.

It is clear that a number of factors may influence the size and density of ant colonies across an environmental gradient. For *C. detritus*, temperature was found to play an important role in regulating activity of the ants and may affect density by affecting the rate of brood development. Nevertheless, the factor which appeared to have the greatest influence was availability of food in the form of honeydew, which correlated to a certain extent with vegetation cover across the dune-field. This conclusion, however, remains speculative until further research is undertaken.

Section Eight

ECOPHYSIOLOGY

8.1 Preferred Temperature

The temperatures chosen by the workers for the brood were the same as those they chose for themselves (Fig. 8.1), with workers of different size classes showing the same temperature preferences. Temperature preference at 100 % rh was significantly higher than that at 30 % rh for both the workers (34,7 ± 1,9°C and 31,3 ± 2,4°C respectively) and the brood (34,8 ± 0,9°C and 32,7 ± 1,4°C respectively) ($P < 0,001$). Since water loss was found to be minimal at 100 % rh (Section 8.4), both workers and brood were able to tolerate higher temperatures at higher humidities. At lower humidities the increase in desiccation rate may have resulted in a lower temperature preference. Kay (1978) found a similar decrease in temperature preference with a decrease in humidity for the desert honey ant, *Myrmecocystus romainei*, which she also attributed to a response to desiccation.

Since temperature and humidity are never high simultaneously in the Namib Desert, the lower temperature preference of 31°C was a more realistic value. This temperature also corresponded with activity data (Section 6) and with the mean nest temperatures experienced in summer (Section 5.3). *Camponotus detritus* workers exhibited a far narrower range of temperature choice in the laboratory than they experience in the field or in the nest. In contrast, Kay (1978) found that the ranges

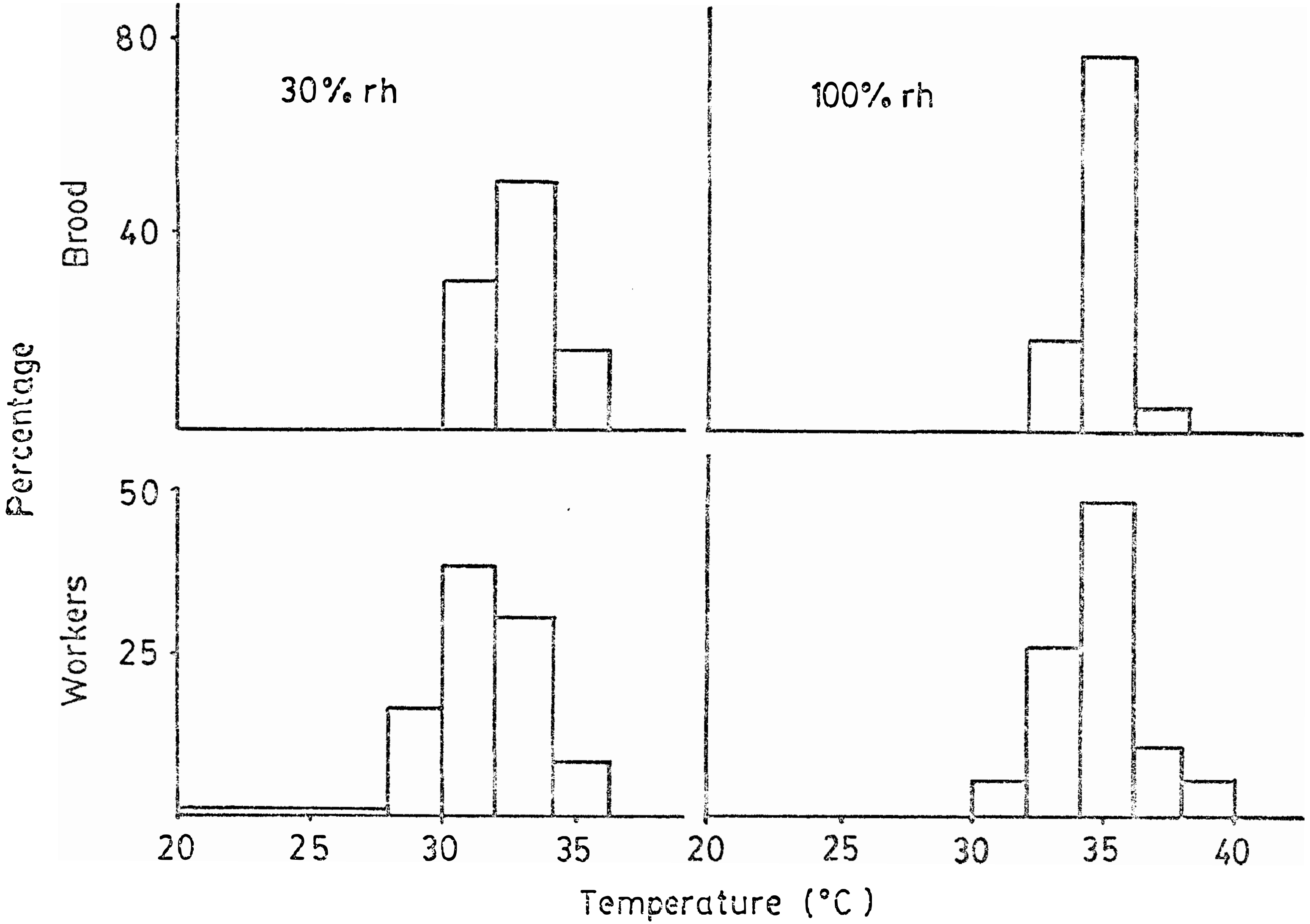


Fig. 8.1 Preferred temperatures of *Camponotus detritus* workers and brood at two different humidities (N = 120 workers and 40 brood).

of temperature choice of the desert honey ants, *Myrmecocystus* species, in the laboratory were similar to the ranges over which they were active in nature. As was the case among *C. detritus* workers of different sizes, Kay (1978) found no difference in temperature preference between species of different sizes.

Kay and others (see Kay 1978) found that many ant species, whether from arid or mesic regions, preferred temperatures between 20°C and 30°C (Table 8.1). The *Myrmecocystus* species which she studied from North American deserts, however, are all honeydew feeders which forage among vegetation and are unlikely to experience the high temperatures which occur on the dune surface. Délye (1968), on the other hand, found that *Cataglyphis* and *Acantholepis* species from the Sahara had temperature preferences between 30°C and 40°C (Table 8.1). These predominantly diurnal species live and forage on the bare sand or gravel and probably experience higher temperatures than *C. detritus* (mean annual absolute maximum air temperature at Béni Abbès , Sahara is 47,5°C (Délye 1968) and at Gobabeb it is 42,5°C (Seely and Stuart 1976)). The Saharan ant *Camponotus thoracicus* had a lower temperature preference (26 - 28°C) than *C. detritus*, but this species is nocturnal and presumably never experiences very high temperatures. Délye (1968) found that, in general, Saharan species had higher temperature preferences than their mesic congeners.

Temperature acclimatization often influences both temperature preferenda and thermal tolerances (Cloudsley-Thompson 1970) and seasonal changes in temperature preference have been shown to occur in ants (Délye 1968, Kay 1978). The present results reflect only early summer temperature preferences of *C. detritus* workers. It is possible that their

Table 8.1

Preferred temperatures of various ant species.

Species	Locality	Pref. Temp. (°C)	
Xeric			
Myrmecocystus mexicanus	New Mexico	19	1
Myrmecocystus romainei	New Mexico	23,7	1
Myrmecocystus depilis	New Mexico	23,8	1
Monomorium subopacum	Sahara	25 - 28	2
Monomorium salomonis	Sahara	25 - 29	2
Camponotus thoracicus	Sahara	26 - 28	2
Myrmecocystus mimicus	New Mexico	27	1
Messor arenarius	Sahara	30	2
Camponotus detritus	Namib	31	3
Acantholepis frauenfeldi	Sahara	36 - 38	2
Cataglyphis bicolor	Sahara	38 - 39	2
Cataglyphis albicans	Sahara	39 - 40	2
Cataglyphis emmae	Sahara	39 - 40	2
Cataglyphis lucasi	Sahara	40	2
Cataglyphis bombycina	Sahara	40 - 41	2
Mesic			
Myrmica rubra	Britain	22	4
Camponotus sylvaticus	France	25 - 27	2
Cataglyphis cursor	France	38	2

1 : Kay 1978   2 : Délye 1968   3 : Present study   4 : Brian 1973

preferences would be slightly higher later in the summer when both surface and air temperatures are higher (see Seely and Stuart 1976) and lower in winter.

Temperature preferences of other desert insects, although not directly comparable with *C. detritus* since different methods were employed, appear to be somewhat higher than those of *C. detritus*. For example, the beetles *Pimelia grandis* and *Adesmia antiqua* prefer 28 - 34°C and 34 - 38°C respectively (El Rayah 1970). Two species of desert locusts both prefer 45°C (Hafez and Ibrahim 1964 in Cloudsley-Thompson 1975). However, the behaviour of the species must also be taken into account. The diurnal Namib Desert tenebrionid beetles, for instance, forage on the bare sand where temperatures become high extremely rapidly. These beetles actually maintain elevated body temperatures (37 - 40°C) for extended periods by means of behavioural thermoregulation (Hamilton 1975, Henwood 1975). *Camponotus detritus* workers on the other hand, forage among the vegetation where temperatures are lower, and only walk across the sand intermittently.

8.2 Critical Temperatures (CT_{max} and CT_{min})

The term "critical temperature" may lead to some confusion and should be clearly defined. Some define the term "critical temperature" as that temperature at which the lipid molecules in the cuticle apparently lose their orientation, resulting in a rapid and marked increase in cuticular water loss (Hadley 1974). The ecological significance of this value is doubtful since these temperatures are often higher than upper lethal temperatures (Hadley 1974), some being as high as 99 - 101°C (Louw and

Seely 1982). Others use the term to refer to the temperature at which the animal's locomotor ability is so reduced that it loses the ability to escape from thermal conditions which would lead to its death (Bartholomew 1977). This is an ecologically more meaningful value than the former. It is also more meaningful than "lethal temperature" which is defined as the physiological temperature tolerance limits of an animal when exposed to extreme temperatures for a fixed period of time (Cloudsley-Thompson 1970). Numerous researchers have used "lethal temperature", but comparisons between different sets of data are difficult since lethal temperatures are dependent upon the length and conditions of exposure and preconditioning of the animals. Highly mobile insects such as ants are unlikely to be confined to extreme conditions for long periods, but may be exposed briefly to temperatures above the conventional "upper lethal". For this reason I have used the second definition of critical temperature, which has also been used by Whitford and his colleagues (Schumacher and Whitford 1974, Whitford and Ettershank 1975, Kay and Whitford 1978) in their work on North American desert ants.

The CT_{max} of *C. detritus* was found to be 52,8 ± 0,9°C at 100 % rh and and 53,8 ± 0,9°C at 55 % rh, yet there was no statistically significant difference between the results obtained at the two humidities. The CT_{min}, determined only at 100 % rh, was 4,6 ± 0,5°C. There was no difference in the critical temperatures between workers of different sizes. The behavioural response of *C. detritus* workers to different temperatures in the laboratory was similar to that in the field.
Below 10°C their movements were very slow, but as temperatures increased, so did the speed of movement until at surface temperatures of about 45°C

and above, the ants ran very rapidly over the sand, elevating their bodies as far off the ground as possible and lifting their legs higher than usual before replacing them. The same behavioural response to increased temperatures has been recorded for *Myrmecocystus* species (Kay and Whitford 1978). Often, at surface temperatures above 50°C, *C. detritus* workers ran to the nearest vegetation which they climbed before running to the next, behaviour also noted among *Ocymyrmex* species, in the Namib (Marsh, pers. comm.).

The results of the present study are directly comparable with those of North American species (Table 8.2), since the same methods of determining CT_{max} and CT_{min} were used in each case. The CT_{max} of *C. detritus* was similar to those of the soil surface foragers, *Pogonomyrmex* and *Novomessor* species in North America, but higher than those of the other species, which forage predominantly on plants (Whitford and Ettershank 1975, Kay and Whitford 1978). Although *C. detritus* workers were seen foraging primarily in plants, they walk long distances across the sand (up to 200 m) and would thus be exposed to high surface temperatures. The CT_{min} of *C. detritus* was also similar to that of *Pogonomyrmex* and *Novomessor* species. No direct comparisons can be made with the Saharan species since different methods were used for determining critical temperatures (Délye 1968). Nevertheless the maximum temperatures tolerated by most Saharan species appear to be a few degrees lower than *C. detritus*. An exception is *Cataglyphis* species which are able to tolerate temperatures similar to the CT_{max} of *C. detritus*.

Similarly, it is difficult to compare temperature tolerances with other

Table 8.2

Critical maximum and minimum temperatures of various desert ant species.

Species	CT_{max}	CT_{min}	
Trachymyrmex smithi neomexicanus	36,7	9,7	1
Myrmecocystus navajo	43,7	-	2
Myrmecocystus mexicanus	44,2	0,4	2
Formica perpilosa	45,2	5,2	1
Myrmecocystus romainei	46,1	12,0	2
Myrmecocystus depilis	47,4	11,6	2
Myrmecocystus mimicus	47,7	11,2	2
Novomessor cockerelli	51,7	3,6	3
Pogonomyrmex barbatus	51,7	-	4
Pogonomyrmex californicus	52,9	4,7	3
Pogonomyrmex desertorum	53,2	-	3
Pogonomyrmex rugosus	53,8	4,8	3
Camponotus detritus	53,8	4,6	5

1 : Schumacher and Whitford 1974 2 : Kay and Whitford 1978

3 : Whitford and Ettershank 1975 4 : Whitford *et al.* 1975

5 : Present study

desert arthropods since different techniques have been used in such determinations. The maximum voluntarily tolerated body temperature of Namib desert tenebrionids ranges from 42,5°C to 43,8°C (Hamilton 1975). This would presumably be somewhat lower than their CT_{max}. Hafez and Makky (1959) performed an experiment in which desert beetles, *Adesmia bicarinata*, were gradually heated (1°C every 10 minutes) until the onset of "heat stupor" at 53°C, which is comparable with the 53°C CT_{max} of *C. detritus*.

8.3 Long-Term Tolerance to Extreme Temperatures

The ability of *C. detritus* workers to tolerate 45°C for up to 24 hours was not affected by humidity (Table 8.3). Since the ants were capable of withstanding 24 hours at 45°C and 45 % rh, but died within minutes at the CT_{max} of 53°C, the lethal temperature for this species is probably between 46 - 51°C. The upper lethal temperature for *Myrmecocystus* species was between 40 and 45°C (Kay and Whitford 1978). *Myrmecocystus depilis* was able to survive for 12 hours at 45 % rh and 40°C, but died within two hours at 45°C, while *M. mexicanus* only survived two hours at 40°C and 45 % rh (Kay and Whitford 1978). Délye (1968) gives values for lethal temperatures of Saharan species as the length of time which individuals could withstand various temperatures at 0 % rh. Most species were able to survive 50°C for 10 - 20 minutes and up to an hour at 45°C (his experiments were all one hour long). *Cataglyphis* species were able to withstand temperatures of 55°C for 10 - 20 minutes. Congeneric species from France, however, were unable to withstand temperatures above 45°C, and only 10 minutes at 45°C.

Upper lethal temperatures for other desert invertebrates seem to vary between 40 and 50°C. For example, the beetle *Pimelia grandis* withstood 43°C and 10 % rh for 24 hours whereas the solifuge *Galeodes granti* survived 50°C and 10 % rh for 24 hours (Cloudsley-Thompson 1962a).

Most animals avoid excessively high temperatures, but not all avoid cold, and invertebrates are sometimes trapped and immobilized by low temperatures (Cloudsley-Thompson 1970). The CT_{min} of an insect determines the lower limits of its activity, but does not necessarily reflect the lower lethal temperature. For example, *C. detritus* became completely immobile at about 5°C but survived up to 24 hours at -1°C with no apparent ill effects (Table 8.3).

Thus *C. detritus* showed a wide range of physiological temperature tolerance, but a narrow range of preferred temperature. Both CT_{max} and the preferred temperature were fairly high for an ant, although not as high as those of other desert arthropods. The CT_{max} was higher than that likely to be experienced by a worker in the dunes under normal conditions. Temperatures in the Namib may often drop below CT_{min} but seldom below freezing (Seely and Stuart 1976). Therefore although ants may be temporarily immobilized by cold, they are unlikely to be killed by low temperatures.

8.4 Water Loss

Water loss can be expressed either as a percentage of the initial body weight or as the amount of water lost per unit area of cuticle. The latter is interesting physiologically as it gives a comparable

Table 8.3

The effect of long-term exposure to extreme temperatures on the survival of *Camponotus detritus* workers.

Temperature (°C)	rh (%)	Length of Exposure (h)	Mortality (%)	N
45 ± 2	45 ± 5	12	0	20
		24	25	20
45 ± 2	95 ± 5	12	0	20
		24	20	20
-0,5 ± 1	95 ± 5	12	0	30
		24	3	30

Table 8.4

Mean water loss per individual (% initial body weight) of *Camponotus detritus* workers held as individuals and as groups for 24 hours (N = 30).

Temp.	Humidity	Saturation Deficit	Water Loss (%)	
°C	% rh	mm Hg	Individuals	Groups
35	95	2	1,98	2,44
35	50	21	13,21	8,81
25	0	24	8,26	7,85

indication of the permeability of the cuticle. However, water loss expressed as a percentage of total body weight is ecologically more significant as it reflects the length of time an insect can be exposed to desiccating conditions before dehydration causes death. Since relative surface area decreases with increasing volume, it is to be expected that large insects would lose water relatively less rapidly than small ones such as ants and would therefore be able to tolerate extreme temperatures and humidities for longer periods. For this reason all results from the present study are expressed as percentages of original body weight (Figs. 8.2 - 8.7 and Tables 8.4 and 8.6). In order to compare the results of the present study with those of Whitford, Kay and Schumacher (1975), one experiment was performed using their method of passing moving air over the ants. No significant difference was found between the rate of moisture loss in still and moving air, however.

As expected, the rate of water loss was found to increase with increasing saturation deficit at 35°C (Fig. 8.2), but the increase was not linear. Similar curves, in which the rate of increase in water loss with rise in saturation deficit is initially rapid, thereafter gradually declining, have been found for other invertebrates (Edney 1977). Bursell (1974) found that water loss of the tsetse fly, *Glossina,* is controlled by spiracular activity, which depends not only upon ambient humidity, but also on the extent of fly's water reserves.

Saturation deficit alone did not appear to control the rate of water loss in *C. detritus*. At 25°C and 0 % rh, although saturation deficit was higher than at 35°C and 50 % rh (24 mm Hg and 21 mm Hg respectively), the rate of water loss was significantly lower ($P < 0,001$). Thus both

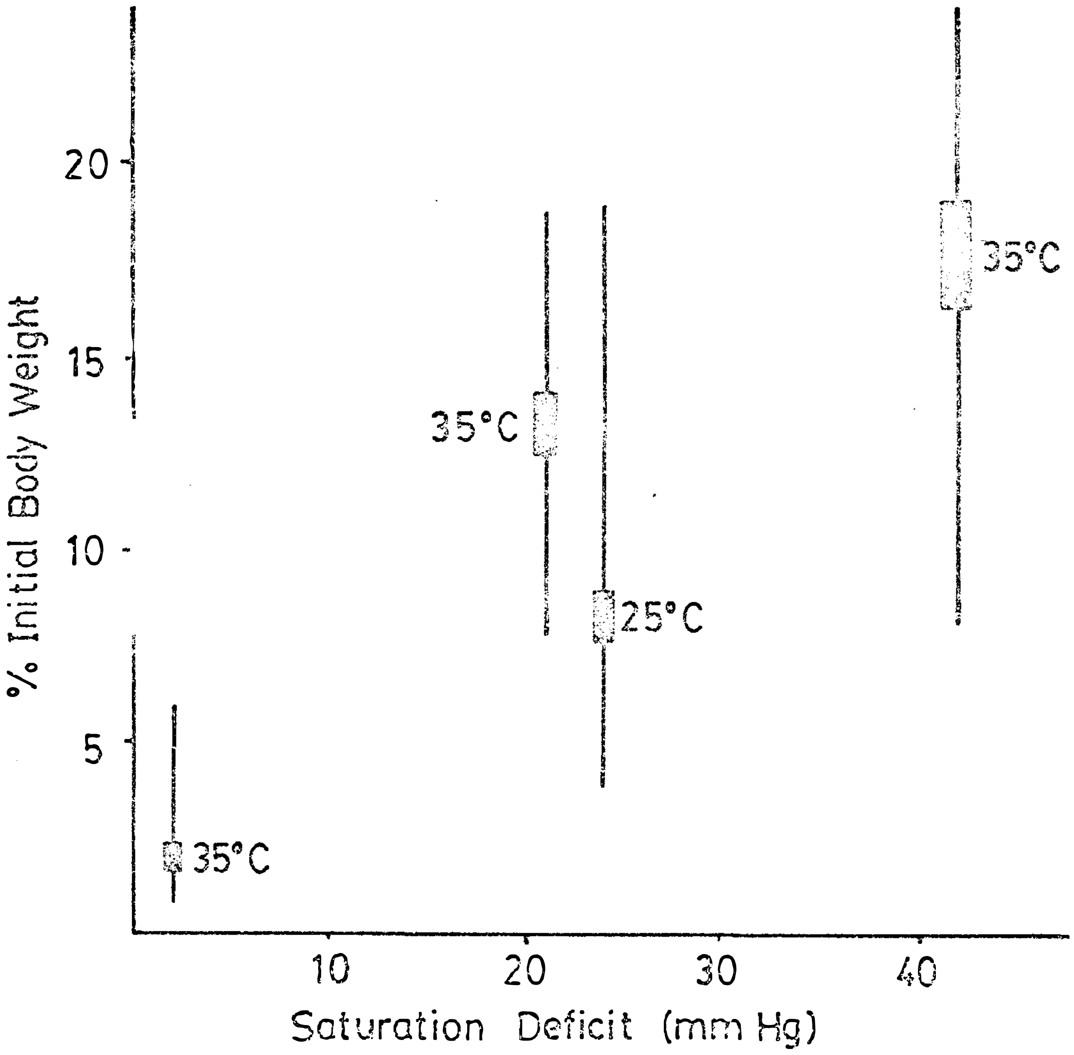


Fig. 8.2 Water loss over 24 hours of *Camponotus detritus* workers (as % of initial body weight) at various temperatures and saturation deficits. Broad vertical lines represent standard error, narrow lines represent range. (N = 30)

temperature and saturation deficit appeared to affect the rate of water loss. Nel (1965) found a similar effect of temperature on the rate of water loss in the Australian ant *Iridomyrmex detectus*. When the ants were kept at a constant saturation deficit and temperature was allowed to rise, water loss increased. Similarly, in the pugnacious ant, *Anoplolepis custodiens*, the increase in rate of water loss with rising temperature was greater than the decrease with rising humidity (Louw 1968). Louw did not appear to take saturation deficit into account, however.

Control of water loss by spiracle closure has been demonstrated for many insects (Cloudsley-Thompson 1975). Among Saharan desert ant species temperature has a noticable effect on spiracular behaviour (Délye 1965). At low temperatures spiracles remain closed for long periods while the ants are inactive but above a certain species-specific temperature spiracles remain open, thus increasing the rate of water loss. These results can be explained on the basis of increased metabolic rate and the concomitant increase in oxygen demand. For *Messor aegyptiacus* and *Camponotus compressus* this temperature is 30°C and for *Monomorium salomonis* and *Cataglyphis bombycina* it is 45°C, which appears to be unusually high. Similarly, *C. detritus* may increase spiracular opening at temperatures between 25°C and 35°C, thus accounting for the more rapid rate of water loss at higher temperatures.

Certain arthropods are able to absorb water vapour from unsaturated air (Edney 1977). For example, the Namib Desert thysanuran *Ctenolepisma terebrans* can absorb water vapour from humidities as low as 47 % (Edney 1971). Since *C. detritus* lost moisture at all humidities, including 95 % where saturation deficit was only 2 mm Hg, it would appear that these ants are incapable of absorbing water vapour through the cuticle from unsaturated air. Nel (1965) and Délye (1968) have also shown that other ant species are incapable of absorbing moisture from saturated or near-saturated air.

The rate of water loss of *C. detritus* was rapid during the first three hours exposure, thereafter decreasing (Fig. 8.3). A similar decrease in the rate of water loss after the first 24 hours was noted among those individuals desiccated for four days (Fig. 8.4). It is a common phenomenon that the rate of water loss among arthropods is initially rapid owing to loss of water bound in the cuticle (Edney 1977). Sometimes the elimination of faeces near the start of the experiment is also responsible for an initially rapid rate of weight loss (Nicholson 1980). However, no faecal material was produced by *C. detritus* in the present experiments. The rates of water loss during the first three to six hours at high temperature and low humidity are ecologically most meaningful since in nature such conditions prevail for a few hours during the middle of the day. Many workers only foraged for a few hours per day, while during the desiccating conditions of midday, most ants returned to the nest, where lower temperatures and presumable higher humidities retarded water loss. Individuals remaining out of the nest at midday were generally in the shade of plants, and could have been obtaining moisture from their diet of honeydew.

Rate of water loss was a function of the size of the workers (Figs. 8.3 and 8.5). The rate at which water loss decreased with increasing worker size was a function of the temperature and saturation deficit under

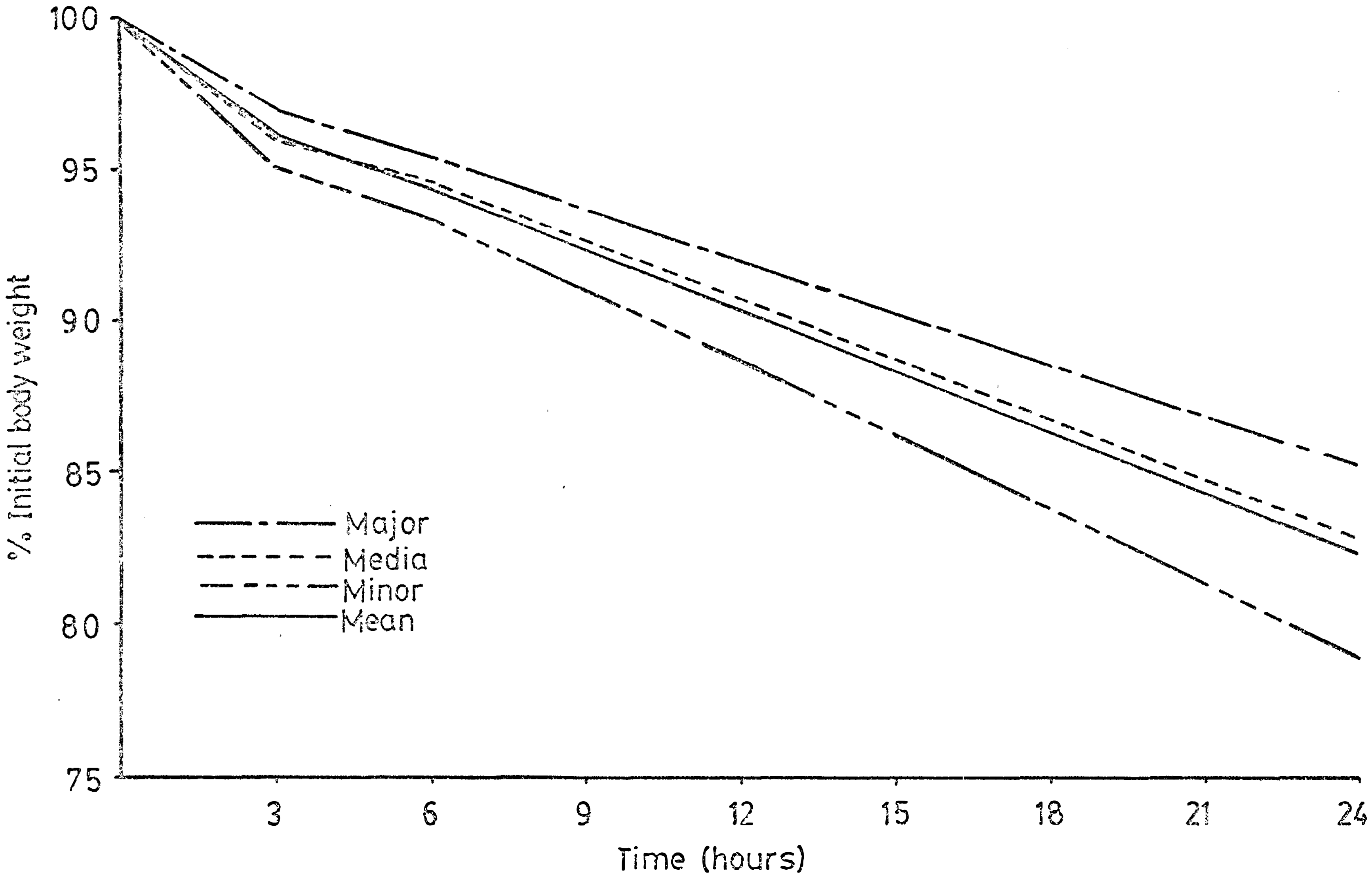


Fig. 8.3 Rate of water loss (as % of initial body weight) of different sizes of *Camponotus detritus* workers, as well as mean of all sizes, at 35°C and 0 % rh. (N = 10 workers per size class)

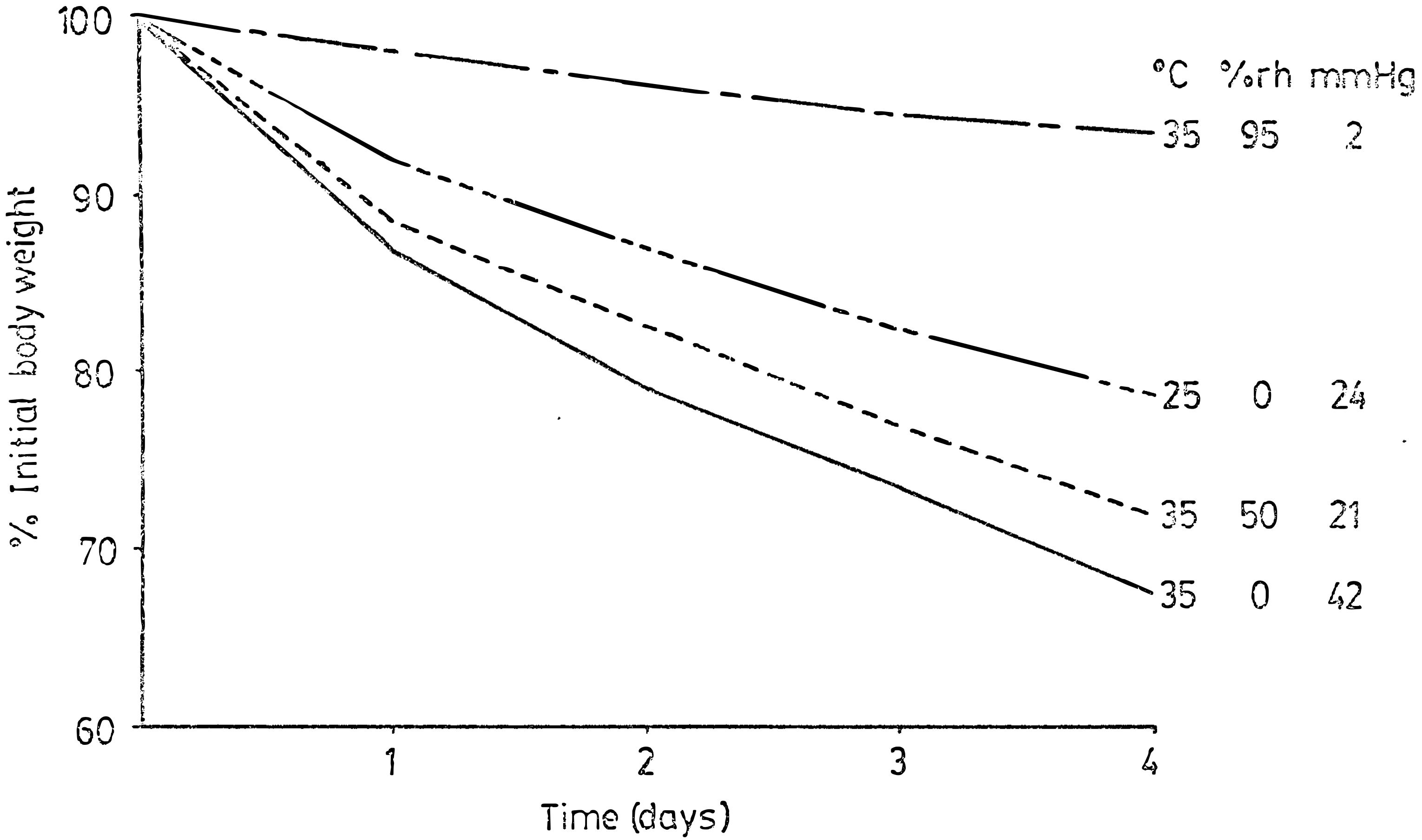


Fig. 8.4 Long-term rate of water loss (as % of initial body weight) of *Camponotus detritus* workers under different conditions of temperature, humidity and saturation deficit. (N = 26, 30, 16, 16 respectively)

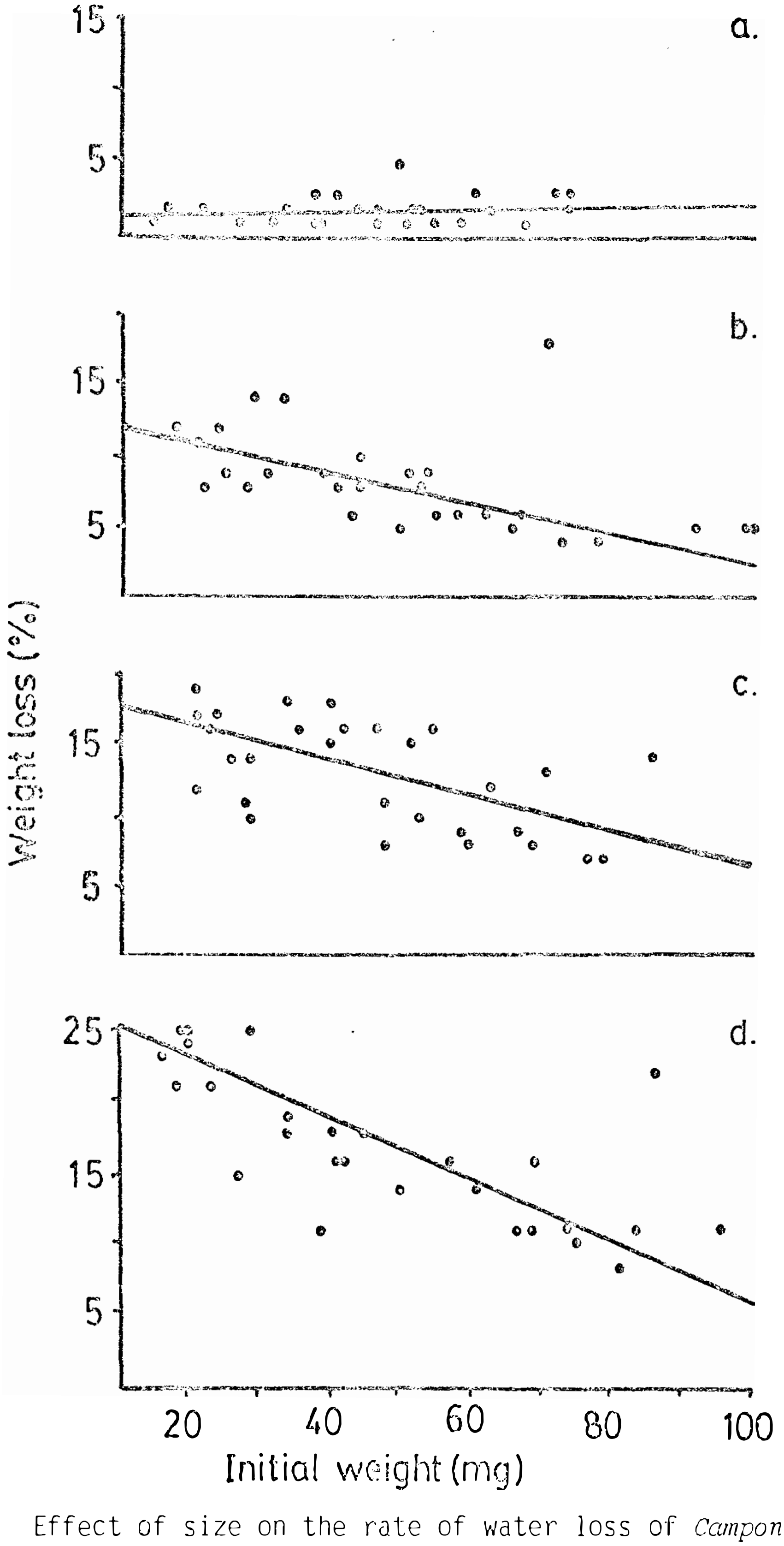


Fig. 8.5 Effect of size on the rate of water loss of *Camponotus detritus* workers exposed to experimental conditions for 24 hours. Each point represents one individual.
A = 35°C, 95 % rh and 2,11 mm Hg Saturation deficit.
B = 25°C, 0 % rh, 23,76 mm Hg
C = 35°C, 50 % rh, 21,09 mm Hg.
D = 35°C, 0 % rh, 42,18 mm Hg.

which the ants were kept (Fig. 8.5). However, at 95 % humidity there was no statistically significant difference in the rate of desiccation of different sized workers. Survival time of different sized individuals was a function of the rate of water loss (Fig. 8.6). Thus minor workers which had a greater rate of desiccation, did not survive as long as major workers. From this it seems reasonable to predict that minor workers, due to their more rapid rate of water loss and decreased survival time would remain out of the nest for shorter periods than major workers. There was however, no correlation between the size of an individually marked worker and the length of time it remained out of the nest (Section 6.2).

Since ants are social animals, and are in close contact with one another in the nest, the difference in water loss between groups of ants and individual ants was also examined. At 35°C and 95 % rh, and at 25°C and 0 % rh there was no significant difference in the rates of water loss between groups and individuals (Table 8.4). However, at 35°C and 50 % rh, the groups lost significantly less water than the individuals ($P < 0,01$). This could have been caused by the formation of a boundary layer of moist air surrounding the ants, thereby decreasing the water vapour gradient between the animal and the environment. Movement of air between ants grouped together would also be reduced, further minimizing water loss.

Another possibility involves a behavioural or physiological response of the ants as a result of being in a group. Wilson (1971) has modified the definition of Grassé (1946 in Wilson 1971) in which he describes a "group effect" as "any alteration in behaviour or physiology within a

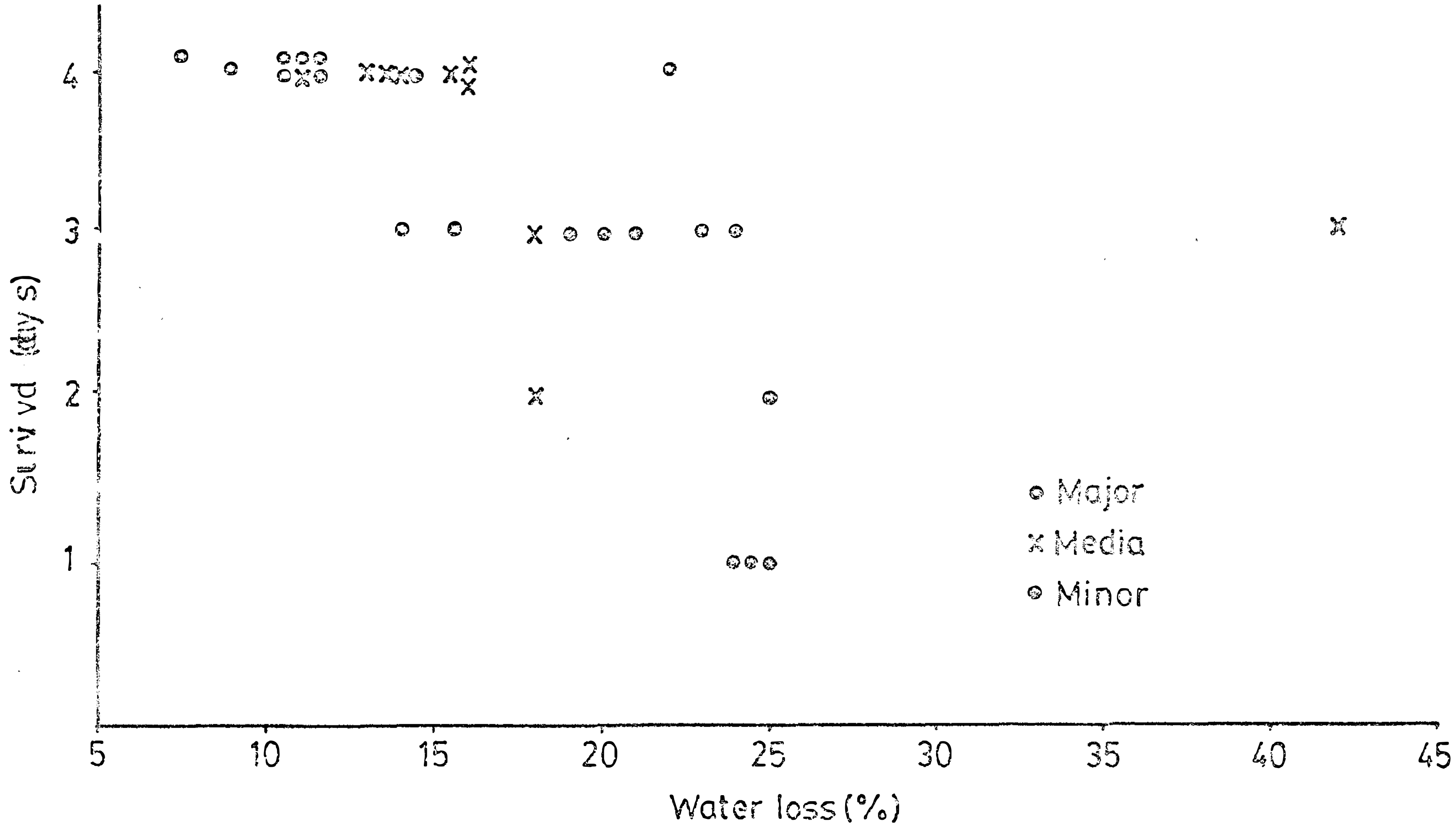


Fig. 8.6 Relationship between rate of desiccation and length of survival of different sized *Camponotus detritus* workers held at 35°C and 0 % rh. Each symbol represents an individual.

species brought about by signals that are directed in neither space nor time". For the most part "group effect" refers to behavioural response such as social facilitation, but the "group effect" has been shown to affect both fecundity and longevity of queens and workers (Wilson 1971). Gallé (1978) found a "group effect" in the oxygen consumption of three species of ants. Thus it is possible that the "group effect" could influence the rate of water loss of *C. detritus* workers. For example, the ants housed in groups may have been less active, which in turn would result in a lower respiration rate and therefore lower water loss.

Mortality rate was also reduced by grouping. No mortality occurred among those individuals housed at 25°C for 5 days. The rate of mortality of individuals at 35°C was the same at both 0 % and 50 % rh (Fig. 8.7a), while the mortality among ants housed as a group at 35°C and 50% rh was significantly lower ($P < 0,05$) (Fig. 8.7b). This could have been due partly to a decrease in the rate of water loss, but possibly also because of trophallaxis, which was observed during the experimental period. In this manner, smaller individuals dehydrating more rapidly than larger ones could obtain moisture from the latter.

In an arid environment such as the Namib, where temperatures are often high and humidities low, and water is not freely available, an animal's ability to conserve water is of utmost importance. The term "desiccation resistant" may refer to the animal's ability to tolerate large water losses and low body water content, or the restriction of water loss by various means (Edney 1977). Among desert arthropods there is little evidence for the former (Edney 1974) but considerable evidence for the latter (Cloudsley-Thompson 1975, Edney 1977, Louw and Seely 1982).

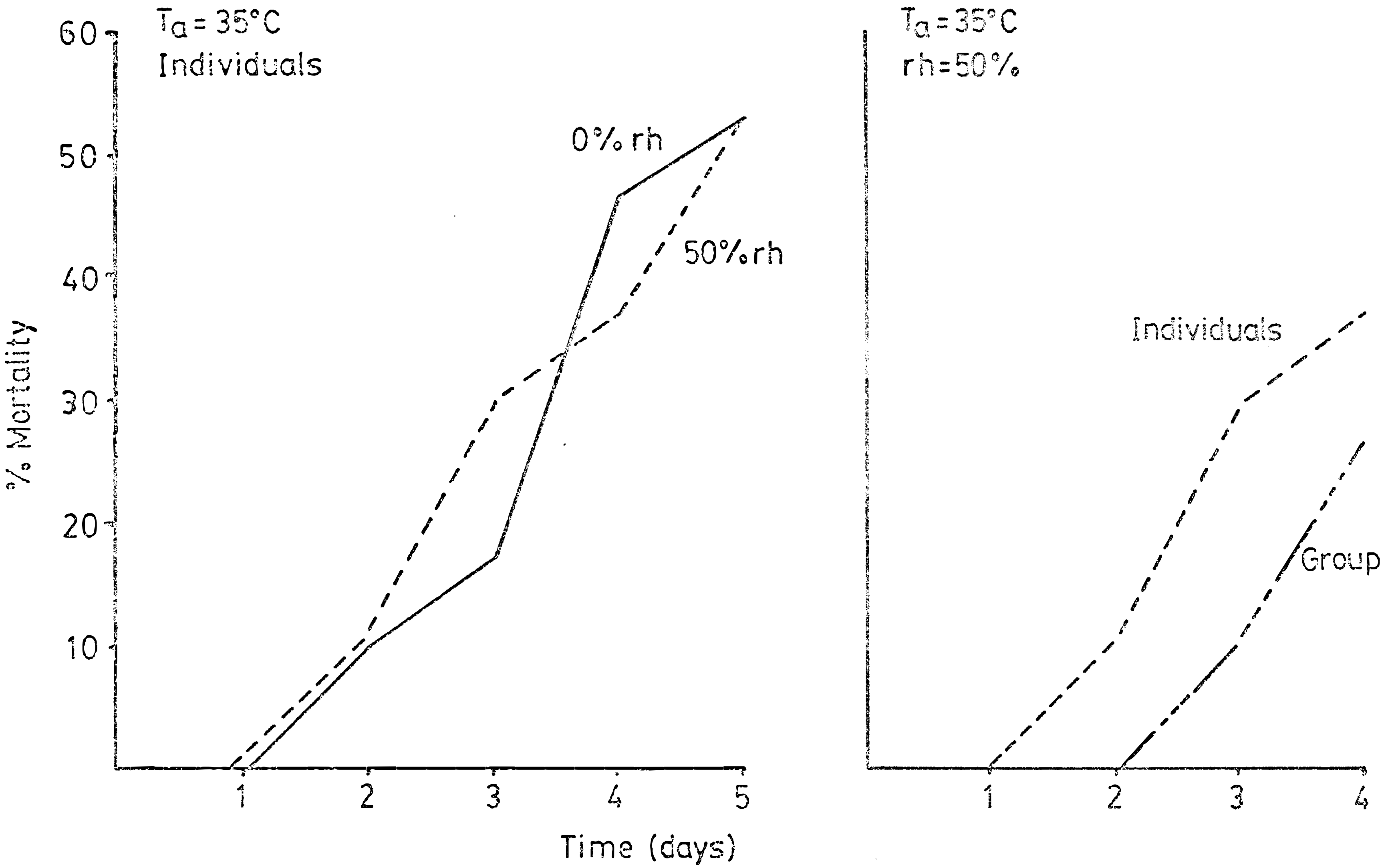


Fig. 8.7 Mortality rate of *Camponotus detritus* workers held under different conditions (N = 30).

In general, desert arthropods can withstand losses of about 30 % of body weight (Edney 1977). Sahara Desert ants died after a loss of 30 - 38 % (Délye 1968), as did the Algerian species *Camponotus barbaricus xanthomelas* and *C. cruentatus* (Cagniant 1971). However, *C. detritus* was able to tolerate a loss of 30 - 60 % of the initial body weight. Similarly, workers of three species of *Pogonomyrmex* died only after a weight loss of up to 57 % (Whitford *et al.* 1975). Thus the ability to tolerate large losses of body water appears to be an adaptation of some, although not all, desert ants.

One of the main avenues of water loss in invertebrates is from the integument. Among most arthropods, integumentary water loss is reduced to a greater or lesser extent by a well-structured cuticle (Edney 1977), particularly marked among desert scorpions (Cloudsley-Thompson 1961, Hadley 1970) and tenebrionid beetles (Edney 1971, Hadley and Louw 1980, McClain pers. comm.). Compared with other desert arthropods (Table 8.5), *C. detritus* was found to have a highly permeable cuticle. The higher surface area to volume ratio of these small arthropods would place them at a distinct thermal disadvantage which would contribute to their high rate of water loss. When the rates of water loss of minor workers (i.e. the highest rates in the present study) were compared with those of other desert ant species, however, it was clear that *C. detritus* had a very low rate of water loss for an ant (Table 8.6). All the Sahara Desert species which Délye (1968) studied had much lower rates of water loss than their mesic congeners from France.

When the behaviour of ants and sympatric tenebrionids is compared, it is

Table 8.5

Rate of water loss of various desert arthropods in dry air.

Species		Water Loss (mg cm^{-2} h^{-1})	
25°			
Zophosis testudinaria	(Beetle)	0,02	1
Hadrurus arizonensis	(Scorpion)	0,03	2
Zophosis mniszechi	(Beetle)	0,03	1
Onymacris plana	(Beetle)	0,04	1
Onymacris marginipennis	(Beetle)	0,07	1
Camponotus detritus	(Ant)	0,14	3
33 - 35°			
Leiurus quinquestriatus	(Scorpion)	0,02	4
Buthotus minax	(Scorpion)	0,04	5
Camponotus detritus	(Ant)	0,33	3

1 : McClain (in prep.)   2 : Hadley 1970   3 : Present study

4 : Cloudsley-Thompson 1961   5 : Cloudsley-Thompson 1962b

Table 8.6

Water loss per hour of various ant species in dry air expressed as percentage of initial body weight.

XERIC	25°C	30°C	35°C	40°C	
Camponotus detritus (small)	0,44		0,9		1
Camponotus thoracicus		1,3		2,5	2
Novomessor cockerelli			2,08		3
Cataglyphis bombycina		2,0		4,7	2
Pogonomyrmex (4 sp.)			2,33		3
Messor arenarius		3,0		4,1	2
Formica perpilosa			4,17		3
Cataglyphis albicans and C. emmae		4,7		7,3	2
Cataglyphis bicolor		3,3		5,6	2
MESIC					
Camponotus sylvaticus		3,0		6,4	2
Messor barbarus		6,4		11,0	2
Cataglyphis cursor		6,7		14,0	2
Pheidole pallidula		8,1		20,8	2

1 : Present study   2 : Délye 1968   3 : Whitford *et al.* 1975

apparent that cuticular impermeability is not as essential to the ants as it is to the beetles. The latter forage on the sand surface, often on the slipface where surface temperatures are highest, and subsist largely on a diet of dry detritus. In contrast, *C. detritus* workers foraged among the vegetation for a predominantly liquid diet and were only briefly exposed to the desiccating conditions on the sand surface. Thus, although ants may not be as well adapted physiologically or morphologically to retard water loss as other desert arthropods, by virtue of their behaviour they are able to escape the desiccating conditions of an arid environment.

Section Nine

GENERAL DISCUSSION

Ecologically, social insects are one of the dominant groups of terrestrial animals, the biomass and energy consumption of which exceed that of vertebrates in most terrestrial ecosystems (Wilson 1971). Numerically the most abundant of the social insects, ants are a highly successful group exhibiting a great diversity of ecological and social adaptations. The importance of ants in most desert ecosystems has already been mentioned (Bernard 1964a, Délye 1968, Whitford 1978a, Bernstein 1979a).

It has been suggested that ants are not physiologically well adapted to arid environments, but that they employ behavioural means of escaping the extreme climatic conditions (Délye 1968, Schumacher and Whitford 1974, Kay 1978). Simply by virtue of their social nature ants are able to overcome many of the problems faced by solitary arthropods. The construction of elaborate nests enables them to modify the internal micro-environment, thereby ensuring optimal conditions for brood development and providing a retreat for workers during the most severe hours of the day, as well as providing a storage place for food.

Their use of chemical communication facilitates territorial defense and foraging. Task specialization ensures that foraging, nest and territory defense, nest repair and care of the reproductive queen and brood all occur concurrently. The evolution of a sterile worker caste frees the reproductive female from all tasks besides reproduction. By means of trophallaxis all individuals can be kept at a similar state of hunger or thirst. Workers exposed to dehydrating conditions can be replenished by nest mates either inside or outside the nest (Sudd 1967, Wilson 1971, Oster and Wilson 1978).

It is obvious, simply by walking through the dunes of the Namib, that *Camponotus detritus* is a very successful species of insect. The question is, to what extent is *C. detritus* behaviourally and physiologically preadapted to life in an arid environment? With regard to behaviour and natural history, the present study revealed that *C. detritus* exhibited few peculiarities. As for most *Camponotus* species, worker polymorphism resulted in some task specialization, but retained flexibility. Thus, although the majority of foraging was performed by minor workers, major workers assisted in retrieving food items too large for the minors.

The simple nest construction among the roots of dune vegetation enabled these ants to exploit a fairly wide range of nesting sites as well as allowing them to excavate new nests with relative ease, either when old nests became too small or when environmental factors such as the encroachment of a dune or strong winds destroyed the nest. The habit of nest splitting, which also occurs among temperate species, led to multi-nest colonies which may seem maladaptive since workers appeared to waste considerable time and energy walking backwards and forwards between mother and daughter nests. Nevertheless, should one nest be destroyed suddenly, workers could rapidly transport brood to an established sister nest. It appeared that *C. detritus* colonies only had a queen in one of the nests and that brood was transported by the workers to daughter nests. This seemed a hazardous task for a desert species since it occurred during the day and brood was thus exposed to desiccating external conditions and predators. Murray (1981) observed *Meroles cuneirostrus*, a lizard, robbing *C. detritus* of its "prey", some of which may have been brood.

One factor contributing to the success of *C. detritus* appeared to be its ability to reproduce all year round, as a result of fairly high temperatures throughout the year combined with a constant food supply. Presumably the dangers associated with diurnal brood transport were outweighed by the advantages of multi-nest colonies and constant brood production.

An apparent disadvantage of the relatively simple nest construction was the lack of efficient nest thermoregulation. Although a very narrow range of temperatures was chosen for the brood by the workers under laboratory conditions, in nature, however, the brood did not appear to need specific temperatures.

In most ant colonies alates are parasitic on the colony until conditions are favourable for a nuptial flight, after which they leave the nest (Wilson 1971). *Camponotus detritus* alates, in contrast, appeared to forage near the nest. The conditions favourable for a nuptial flight were not established, but rainfall appeared to be important. This form of precipitation is unpredictable, however, and may not occur for extended periods, particularly in the west. An interesting field for future research would be to consider the possibility that alate females lose their wings and act either as a fat storage depot or as foragers when nuptial flights do not occur.

Water is the major limiting factor in any desert ecosystem (Louw and Seely 1982). For *C. detritus*, however, the major food source, honeydew, seemed to provide a constantly available source of moisture. This is possible over most of the desert because of the efficient use of condensed fog-water by scale-infested plants (Seely *et al.* 1977, Louw and Seely 1980). Since *C. detritus* foraged among the vegetation where temperatures are lower than those on the surface, workers could collect honeydew throughout the day. Thus rainfall only indirectly influenced the food availability of this species in that it limited the germination and growth of plants.

In the dunes potential nesting sites seemed to be readily available but food was apparently limiting. Consequently each ant colony defended the scale insects in its territory, attacking and killing intruding conspecifics. Territoriality was therefore apparently an adaptive trait, limiting the number of colonies which could become established in the dune-field.

In an environment where the substrate is constantly moving and changing, chemical trails would probably not last very long. These ants appeared to rely on light in some form for navigation and orientation and used pheromones only for recruitment and other forms of short-term communication.

Trophallaxis is particularly adaptive in an arid environment where the rate of desiccation is high. One individual could obtain liquid from another without having access to the source of moisture. Grouping behaviour appeared to lower the desiccation rate under conditions in which desiccation would have been high for solitary individuals. This, combined with trophallaxis, appeared to increase the survival time of *C. detritus* workers at extreme temperatures and humidities.

Camponotus detritus was found to be physiologically better adapted to desertic conditions than many other ant species, in addition to exhibiting behaviour which, although not unique to a desert species, allowed it to exploit an extreme and unstable environment. Its thermal tolerance, which ranged from 4 to 53°C, theoretically enabled workers to be active outside the nest for 24 hours per day throughout most of the year. Even on cold winter nights when air temperatures precluded movement, workers still remained at their foraging grounds. This may be a further adaptive trait, allowing the ants to maintain a constant vigilance on food supplies.

Although high by comparison with other desert arthropods, *C. detritus* had an exceptionally low rate of water loss for an ant. In addition, it was able to tolerate high losses of tissue water. This, combined with its predominantly liquid diet allowed it to be present on the vegetation throughout the most desiccating periods of the day.

Temperature appeared to be the major factor controlling activity, both for ants on the ground and those foraging on the plants. Since *C. detritus* was the only or dominant ant species in the Namib dunes, it was able to utilize the full thermal range available to it, unlike species of the North American deserts, where interspecific competition has lead to temporal partitioning of food resources (Bernstein 1974, Schumacher and Whitford 1974, Whitford and Ettershank 1975, Chew 1977, Davidson 1977b). Nor was the activity of *C. detritus* restricted by seasonality in food production, as occurs among seed harvesting species (Briese and Macauley 1980, Whitford *et al.* 1980, Whitford *et al.* 1981). Workers behaviourally avoided excessively high temperatures by remaining either in the nest or on plants during midday and were seldom exposed to air temperatures exceeding about 45°C. Light determined whether activity took the form of transit activity or nest maintenance and honeydew collection. Like many desert ant species (Whitford 1978a), *C. detritus* was therefore neither strictly diurnal nor nocturnal. Wind speed and humidity appeared to play minor roles in the regulation of *C. detritus* activity.

In a warm environment such as a desert where the physical conditions necessary for brood development are uniformly available, communities of desert ants are more likely to be structured on the basis of competition for food than for nest sites (Davidson 1977a). Intraspecific competition, which selects for an increase in niche breadth, is opposed by interspecific competition, leading to temporal and spatial resource partitioning within particular feeding guilds (Chew 1977, Davidson 1977a). Specialists are generally more common in areas where productivity is higher (Louw and Seely 1982) and species diversity of ants has been found to increase with increasing heterogeneity of vegetation (Culver 1974, Davidson 1977a). Opportunism and flexibility, on the other hand, are characteristics of many of the larger, longer-lived species inhabiting areas where environmental conditions are variable and unpredictable and productivity is low (Louw and Seely 1982).

From the coast to about midway across the dune-field *C. detritus* was the only species of ant found on the dune plinth, thus there was no interspecific competition with other ants to restrict niche breadth. An ant colony, regarded as a whole, is large and long-lived, therefore one would expect *C. detritus* to be an opportunistic generalist occupying a wide niche breadth. To a certain extent *C. detritus* was a specialist since its main diet was found to be honeydew. However, it was opportunistic in its honeydew collection, tending any homopterans. It was also opportunistic in its scavenging behaviour, its nectar collection, its rapid exploitation of new and transient food sources, such as migrating maggots and, to some extent in its choice of nest site.

In the eastern dune-field, where productivity and habitat heterogeneity are greater, and other ant species are present, *C. detritus* appeared to exhibit the same behaviour as at Gobabeb. Its chief potential diurnal competitor, *Crematogaster* sp., appeared to avoid competition by predominantly tending the gall-forming scale insect, *Membranaria* sp., on *Stipagrostis* cf. *namaquensis* which *C. detritus* only rarely tended. The nocturnal species *C. maculatus* and *C. mystaceus* are honeydew feeders (Skaife 1961) but were never seen collecting honeydew. Thus, as the dominant species in the honeydew-feeding guild, *C. detritus* appeared to be relatively free from the effects of direct interspecific competition.

Competition for honeydew from other insect species appeared to be virtually absent, and was unlikely to have had a major effect on *C. detritus*. Flies were observed on scale insect-infested stems, but these were usually chased away by the ants. On one occasion I saw a male mutilid wasp alighting near scale insects.

Many insects were seen collecting nectar or pollen from *T. hereroensis* flowers and dead animal matter was also scavenged by tenebrionid beetles. Food sources which were likely to produce the greatest competition with other species, such as detritus and seeds, appeared not to be utilized at all by *C. detritus*.

What then, is the role of *C. detritus* in the Namib Desert dune ecosystem? Being a member of the dune base and plinth communities described by Robinson and Seely (1980), it appears to occupy a unique position as major utilizer of honeydew which places it in the role of a secondary consumer in Seely and Louw's (1980) simple food chain. It was not possible to determine the exact contribution of *C. detritus* to the total biomass of the dune fauna since no data on other animals were available during the present study period (1981). The study by Seely *et al.* (1977) of the satelite fauna of *Trianthema hereroensis* showed that these ants contribute about 11 % of the biomass while honeydew-producing coccoids represent 46 %. Seely and Louw (1980) also showed that biomass varies considerably from dry to wet periods. They found that total faunal biomass (dry weight) at Gobabeb increased from 100 to 600 g ha^{-1} while that on the dune slopes, where *C. detritus* occurs, increased from 80 to 990 g ha^{-1}. Biomass of *C. detritus* measured at Gobabeb during the present study was 96 g ha^{-1}. As 1981 may be regarded as a fairly dry period, the contribution of *C. detritus* to the total dune fauna is therefore likely to be fairly high.

The relationship between ants and scale insects appeared to be very close, since density of *C. detritus* across the environmental gradient was most closely correlated with temperature and apparent abundance of scale insects. Detailed study of ant territories at Bannoch Burn showed a general decline in the number of ant nests over a two year period, closely associated with the death of perennial vegetation and the resultant decline in numbers of scale insects. Indirectly *C. detritus* may have affected the growth of plants infested with scale insects by reducing the number of parasites and predators of the scale insects, thereby increasing the populations of the latter and hastening the death of host plants.

The marked increase in the biomass of animals found by Seely and Louw (1980) was accompanied by an increase in plant biomass. *Stipagrostis sabulicola* increased 2,4 fold and *Trianthema hereroensis* increased 19 fold. Presumably therefore, since rainfall affects vegetation, it would likewise affect the coccoid populations and indirectly *C. detritus* abundance. Thus the biomass of *C. detritus* would be likely to increase during a wet period.

The major factor limiting *C. detritus* appeared to be intraspecific competition for food. Nitrogen is a limiting factor in the Namib (Seely and Louw 1980) and may influence production in this species. If *C. detritus* was indeed utilizing bird faeces as a food source it would be filling another unique role in the recycling of nitrogen in the dune-field.

The excellent mimicry of *C. detritus* by the spider *Cosmophasis* sp.

suggests a close association between the two species. It is likely therefore, that *C. detritus* is an important prey of the spider. The role of *C. detritus* as prey to larger animals did not appear to be particularly great, presumably because of its unpalatability.

Thus *C. detritus*, although physiologically not as well adapted to an arid environment as many other desert arthropods, showed a comparatively strong resistance to high temperatures and desiccation for an ant. It behaviourally avoided harsh external conditions, utilizing its environment to the full and thereby playing an important role in the dune ecosystem as secondary consumer, exploiting an otherwise largely untapped resource, honeydew. In turn, the relatively uniform supply of honeydew is dependent on the efficient use of condensed fog-water, which may be considered a prominent feature of the ecology of the Namib dune-field, by the host plants.

REFERENCES

ANONYMOUS, 1944. *Weather on the Coasts of Southern Africa. South Africa (Union of).* Vol.2, part 1, p.38. Cape Town: South African Meteorological Service of the Royal Navy.

AUCLAIR, J.L. 1963. Aphid feeding and nutrition. *Ann. Rev. Entomol.,* 8: 439-490.

AYRE, G.L. 1963. Laboratory studies on the feeding habits of seven species of ants. *Can. Entomol.,* 95: 712-715.

BARNARD, W.S. 1973. Duinformasies in die sentrale Namib. *Tegnikon* December: 2-13.

BARTHOLOMEW, G.A. 1977. Body temperature and energy metabolism. In: *Animal Physiology: Principles and Adaptations.* 3rd edition. Ed. Gordon, M.S. pp. 364-449. Collier Macmillan, London. 699p.

BEGON, M. 1979. *Investigating Animal Abundance.* Edward Arnold, London. 97p.

BERNARD, F. 1951. Adaptations au milieu chez les fourmis Sahariennes. *Bull. Soc. Hist. Nat. Toulouse.,* 86: 88-96.

______, 1960. Notes écologiques sur diverses fourmis Sahariennes. *Trav. Inst. Rech. Sahariennes Univ. Alger,* 19: 51-63.

______, 1964a. Densité de la faune au Sahara. Premiers résultats obtenus par la méthode des carrés. *Trav. Inst. Rech. Sahariennes Univ. Alger,* 23: 45-60.

, 1964b. Recherches écologiques sur les fourmis des sables Sahariennes. *Rev. Ecol. Biol. Sol.,* 1: 615-638.

, 1968. *Les fourmis (Hymenoptera, Formicidae) d'Europe occidentale et septentrionale. Faune de l'Europe et du Bassin Méditerranéen.* No. 3. Mason & Cie, Paris. 411p.

BERNSTEIN, R.A. 1974. Seasonal food abundance and foraging activity in some desert ants. *Am. Nat.,* 108: 490-498.

, 1979a. Relations between species diversity and diet in communities of ants. *Ins. Soc.,* 26: 313-321.

, 1979b. Schedules of foraging activity in species of ants. *J. Anim. Ecol.,* 48: 921-930.

______ and GOBBEL, M. 1979. Partitioning of space in communities of ants. *J. Anim. Ecol.,* 48: 931-942.

BESLER, H. 1972. Klimaverhältnisse und klimageomorphologische Zonierung der zentralen Namib (Südwestafrika). *Stuttgarter Geographische Studien,* 83: 1-209.

BOOMSMA, J.J. and DE VRIES, A. 1980. Ant species distribution in a sandy coastal plain. *Ecol. Entomol.*, 5: 189-204.

BOSE, K.C. and RAY, S.K. 1975. Influence of ants on the predators and parasites of aphids. *Indian J. Anim. Res.*, 9: 63-67.

BRANDT, D.C. 1980. Thermal diffusivity of the organic material of a mound of *Formica polyctena* in relation to the thermoregulation of the brood (Hymenoptera, Formicidae). *Neth. J. Zool.*, 30: 326-344.

BRIAN, M.V. 1950. The stable winter population structure in species of *Myrmica*. *J. Anim. Ecol.*, 19: 119-123.

, 1955. Food collection by a Scottish ant community. *J. Anim. Ecol.*, 24: 336-351.

, 1965. *Social Insect Populations*. Academic Press Inc., London. 135p.

, 1973. Temperature choice and its relevance to brood survival and caste determination in the ant *Myrmica rubra* L. *Physiol. Zool.*, 46: 245-252.

______, 1979. Habitat differences in sexual production by two co-existent ants. *J. Anim. Ecol.*, 48: 943-954.

BRIESE, D.T. and MACAULEY, B.J. 1980. Temporal structure of an ant community in semi-arid Australia. *Aust. J. Ecol.*, 5: 121-134.

BROEKHUYSEN, G.J. 1948. The brown house ant (*Pheidole megacephala* Fabr.). *Dept. Agric. Entomol. Series (South Africa).* No. 18, Bulletin No. 206.

BROZA, M. 1979. Dew, fog and hygroscopic food as a source of water for desert arthropods. *J. Arid Environs.,* 2: 43-49.

BURNS, D.P. 1973. The foraging and tending behaviour of *Dolichoderus taschenbergi* (Hymenoptera, Formicidae). *Can. Entomol.,* 105: 97-104.

BURSELL, E. 1974. Environmental aspects: Humidity. In: *The Physiology of Insecta.* Ed. Rockstein, M. III: 44-84. Academic Press, New York 692p.

CAGNIANT, H. 1971. Résistance relative a la sécheresse et au froid de quelques fourmis d'Algérie. *Bull. Soc. Hist. Nat. Toulouse,* 107: 135-145.

_____, 1979. La parthénogenèse thélytoque et arrhénotoque chez la fourmi *Cataglyphis cursor.* Cycle biologique en élevage des colonies avec reine et des colonies sans reine. *Ins. Soc.,* 26: 51-60.

, 1980. La parthénogenèse thélytoque et arrhénotoque des ouvrieres de la fourmi *Cataglyphis cursor* Fonscolombe. Étude en élevage de la productivité des societes avec rein et des societes sans reine. *Ins. Soc.,* 27: 157-174.

CARROLL, C.R. and JANZEN, D.H. 1973. Ecology of foraging by ants.

Ann. Rev. Ecol. Syst., 4: 231-259.

CEUSTERS, R. 1977. Social homeostasis in colonies of *Formica polyctena* Foerst (Hymenoptera, Formicidae): Nestform and temperature preferences. *Proc. Eighth Int. Congr. Int. Union Stud. Soc. Insects (Wageningen)*. pp. 111-112.

CHEW, R.M. 1959. Estimates of ant colony size by the Lincoln Index method. *J. New York Entomol. Soc.*, 67: 157-161.

, 1977. Some ecological characteristics of the ants of a desert shrub community in southeastern Arizona. *Am. Nat.*, 98: 33-49.

CLARK, P.J. and EVANS, F.C. 1954. Distance to nearest neighbour as a measure of spatial relationships in populations. *Ecology*, 35: 445-453.

CLOUDSLEY-THOMPSON, J.L. 1961. Observations on the biology of the scorpion *Leiurus quinquestriatus* (H & E) in the Sudan. *Entomol. Mon. Mag.*, 97: 153-155.

, 1962a. Lethal temperatures of some desert arthropods and the mechanisms of heat death. *Entomol. Exp. Appl.*, 5: 270-280.

______, 1962b. Some aspects of the physiology of *Buthotus minax* (Scorpiones: Buthidae) with remarks on other African scorpions. *Entomol. Mon. Mag.*, 98: 243-246.

, 1970. Terrestrial invertebrates. In: *Comparative Physiology* *of Thermoregulation.* Ed. Whittow, G.C. 1: 15-77. Academic Press, New York. 333p.

______, 1975. Adaptations of arthropoda to arid environments. *Ann. Rev. Entomol.,* 20: 261-283.

COENEN-STASS, D., SCHAARSCHMIDT, B. and LAMPRECHT, I. 1980. Temperature distribution and calorimetric determination of heat production in the nest of the wood ant, *Formica polyctena* (Hymenoptera, Formicidae). *Ecology,* 61: 238-244.

CONWAY, J.R. 1980. The seasonal occurrence of sexual brood and the pre-nuptial and post-nuptial behaviour of the honey ant *Myrmecocystus mexicanus* in Colorado, U.S.A. *J. New York Entomol. Soc.,*88: 7-14.

CREIGHTON, W.S. and CRANDALL, R.H. 1954. New data on the habits of *Myrmecocystus melliger* Forel. *Biol. Rev. C.C.N.Y.,* 16: 2-6.

CULVER, D.C. 1974. Species packing in Caribbean and north temperate ant communities. *Ecology,* 55: 974-988.

DARTIGUES, D. and PASSERA, L. 1979. Larval polymorphism and the apparition of female castes in *Camponotus aethiops* (Hymenoptera, Formicidae). *Bull. Soc. Zool. Fr.,* 104: 197-208.

DAVIDSON, D.W. 1977a. Species diversity and community organization in desert seed-eating ants. *Ecology,* 58: 711-724.

______, 1977b. Foraging ecology and community organization in desert seed-eating ants. *Ecology*, 58: 725-737.

DE BRUYN, G. and KRUK-DE BRUIN, M. 1972. The diurnal rhythm in a population of *Formica polyctena* Först. *Ekol. Pol.*, 20: 117-127.

DÉLYE, G. 1965. Anatomie et fonctionnement des stigmates de quelques fourmis (Hymenoptera, Formicidae). *Ins. Soc.*, 12: 285-290.

______, 1968. Recherches sur l'écologie, la physiologie et l'éthologie des Fourmis du Sahara. Unpublished Ph.D. thesis, University of Aix-Marseille, France.

DOBRZAŃSKA, J. 1959. Studies on the division of labour in ants of the genus *Formica*. *Acta Biol. Exp., Warsaw*, 19: 57-81.

DUELLI, P. 1972. The relation of astromenotactic and anemomenotactic orientation mechanisms in desert ants, *Cataglyphis bicolor*. In: *Information Processing in the Visual Systems of Arthropods*. Ed. Wehner, R. pp. 261-286. Springer, Berlin. 334p.

EBBERS, B.C. and BARROWS, E.M. 1980. Individual ants specialize on particular aphid herds (Hymenoptera, Formicidae; Homoptera, Aphididae). *Proc. Entomol. Soc. Wash.*, 82: 405-407.

EDNEY, E.B. 1971. Some aspects of water balance in tenebrionid beetles and a thysanuran from the Namib Desert of southern Africa. *Physiol. Zool.*, 44: 61-76.

______, 1974. Desert arthropods. In: *Desert Biology*. Ed. Brown, G.W. Jr. 2: 311-383. Academic Press, New York. 601p.

______, 1977. *Water Balance in Land Arthropods*. Springer-Verlag, Berlin. 282p.

EL RAYAH, E.A. 1970. Some reactions of two desert beetles, *Adesmia antiqua* and *Pimelia grandis* (Tenebrionidae) to temperature. *Ent. Exp. Appl.*, 13: 286-292.

EMERY, C. 1898. Beiträge zur Kenntniss der paläarktischen Ameisen. *Öfversigt af Finska Vetenskapssocietetens Förhandlinger*, 20: 124-151.

FOWLER, H.G. and ROBERTS, R.B. 1980. Foraging behaviour of the carpenter ant, *Camponotus pennsylvanicus* (Hymenoptera, Formicidae) in New Jersey. *J. Kans. Entomol. Soc.*, 53: 295-304.

GALLÉ, L. Jr. 1978. Respiration as one of the manifestations of the group effect in ants. *Acta Biol. Szeged*, 24: 111-114.

GEIGER, R. 1973. *The Climate near the Ground*. Havard University Press, Cambridge, Massachusetts. 611p.

GOETSCH, W. 1953. *Vergleichende Biologie der Insektenstaaten*. Geest & Portig K.-G., Leipzig. 482p.

GÖSSWALD, K. 1958. Neue Erfahrungen über Einwirkung der Roten Waldameise auf den Massenwechsel von Schadinsekten sowie einige methodische

Verbesserungen bei ihrem praktischen Einsatz. *Proc. Intern. Congr. Entomol. 10th Montreal, 1956*, 4: 567-571.

GOTWALD, W.H. Jr. 1968. Food gathering behaviour of the ant *Camponotus noveboracensis* (Fitch). *J. New York Entomol. Soc.*, 76: 278-296.

GRASSÉ, P.-P. 1946. Sociêtés animales et effet de groupe. *Experientia*, 2: 77-82.

GRAY, R.A. 1952. The composition of honeydew excreted by pineapple mealybugs. *Science*, 115: 129-133.

HADLEY, N.F. 1970. Water relations of the desert scorpion *Hadrurus arizonensis*. *J. Exp. Biol.*, 53: 547-558.

, 1974. Adaptational biology of desert scorpions. *J. Arachnol.*, 2: 11-23.

______, and LOUW, G.N. 1980. Cuticular hydrocarbons and evaporative water loss in two tenebrionid beetles from the Namib Desert. *S. Afr. J. Sci.*, 76: 298-301.

HAFEZ, M. and IBRAHIM, M.M. 1964. The possible receptors of humidity and temperature in two Egyptian grasshoppers *Aiolopus thalassinus* F. and *Sphingonotus carinatus* Sauss. *Bull. Soc. Entomol. Egypt*, 48: 245-257.

______, and MAKKY, A.M.M. 1959. Studies on desert insects in Egypt.

III. On the bionomics of *Adesmia bicarinata* Klug. *Bull. Soc. Entomol. Egypt*, 43: 89-113.

HAGAN, K.S. 1958. Honeydew as an adult fruit fly diet affecting reproduction. *Proc. Intern. Congr. Entomol. 10th, Montreal*, 3: 25-30.

HAMILTON, W.J. III. 1975. Coloration and its thermal consequences for diurnal desert insects. In: *Environmental Physiology of Desert Organisms*. Ed. Hadley, N.F. pp. 67-89. Dowden, Hutchinson & Ross, Stroudsburg, Pa. 283p.

______, and SEELY, M.K. 1976. Fog basking by the Namib Desert beetle *Onymacris ungricularis*. *Nature*, 262: 284-285.

HARKNESS, R. and WEHNER, R. 1977. *Cataglyphis*. *Endeavour, New Series*, 1: 115-121.

HENWOOD, K. 1975. A field-tested thermoregulation model for two diurnal Namib Desert tenebrionid beetles. *Ecology*, 56: 1329-1342.

HINGSTON, R.W.G. 1929. *Instinct and Intelligence*. Macmillan Co., New York. 296p.

HÖLLDOBLER, B. 1962. Zur frage der Oligogynie bei *Camponotus ligniperda* Latr. und *C. herculeanus* L. (Hymenoptera, Formicidae). *Z. Ang. Entomol.*, 49: 337-352.

_, 1964. Untersuchungen zum Verhalten der Ameisenmännchen während der imaginalen Lebenszeit. *Experientia,* 20: 329.

______, 1971. Recruitment behaviour in *Camponotus socius* (Hymenoptera, Formicidae). *Z. vergl. Physiol.,* 75: 123-142.

, 1976. Tournaments and slavery in a desert ant. *Science,* 192: 912-914.

_ and LUMSDEN, C.J. 1980. Territorial strategies in ants. *Science,* 210: 732-739.

______, MÖGLICH, M. and MASCHWITZ, U. 1974. Communication by tandem running in the ant *Camponotus sericeus. J. comp. Physiol.,* 90: 105-127.

______ and WILSON, E.O. 1977. The number of queens: an important trait in ant evolution. *Naturwissenschaften,* 64: 8-15.

HOLM, E. and SCHOLTZ, C.H. 1980. Structure and pattern of the Namib Desert dune ecosystem at Gobabeb. *Madoqua (Windhoek),* 12: 3-39.

HOLT, S.J. 1955. On the foraging activity of the wood ant. *J. Anim. Ecol.,* 24: 1-34.

JANZEN, D.H. and SCHOENER, T.W. 1968. Differences in insect abundance and diversity between wetter and drier sites during a tropical dry season. *Ecology,* 49: 96-109.

KAWAI, S. and TAMAKI, Y. 1969. Honeydew excretion of *Ceroplastes pseudoceriferus* Green (Homoptera, Coccidae) and its application to evaluate insecticides. *Jap. J. appl. Entomol. Zool.*, 13: 150-158.

KAY, C.A.R. 1978. Preferred temperatures of desert honey ants (Hymenoptera, Formicidae). *J. Therm. Biol.*, 3: 213-218.

______ and WHITFORD, W.G. 1978. Critical thermal limits of desert honey ants: Possible ecological implications. *Physiol. Zool.*, 51: 206-213.

KOCH, C. 1962. The Tenebrionidae of southern Africa XXXI. Comprehensive notes on the tenebrionid founa of the Namib Desert. *Ann. Tvl. Mus.*, 24: 61-106.

LAMB, K.P. 1959. Composition of the honeydew of the aphid *Brevicoryne brassicae*(L.) feeding on swedes (*Brassica napobrassica* D.C.). *J. Insect Physiol.*, 3: 1-13.

LAMON, B. and TOPOFF, H. 1981. Avoiding predation by army ants: defensive behaviours of three ant species of the genus *Camponotus*. *Anim. Behav.*, 29: 1070-1081.

LEDOUX, A. 1949. Le cycle évolutif de la fourmi fileuse (*Oecophylla longinoda* Latr.). *Compte Rendu de l'Académie des Sciences, Paris*. 229: 246-248.

, 1950. Recherche sur la biologie de la fourmi fileuse (*Oecophylla longinoda* Latr.). *Ann. Sci. Nat.*, 12: 313-461.

LÉVIEUX, J. 1975. La nutrition des fourmis tropicales. I. Cycle d'activité et régime alimentaire de *Camponotus solon* (Forel) (Hymenoptera, Formicidae). *Ins. Soc.*, 22: 381-390.

_____, 1977. La nutrition des fourmis tropicales. V. Eléments de synthèse. Les modes d'exploitation de la biocoenose. *Ins. Soc.*, 24: 235-260.

_____ and LOUIS, D. 1975. La nutrition des fourmis tropicales. II. Comportement alimentaire et régime de *Camponotus vividus* (Smith) (Hymenoptera, Formicidae). Comparaison intragénérique. *Ins. Soc.*, 22: 391-404.

LOUW, G.N. 1972. The role of advective fog in the water economy of certain Namib Desert animals. *Symp. Zool. Soc. Lond.*, 31: 297-314.

and HOLM, E. 1972. Physiological, morphological and behavioural adaptations of the ultrapsammophilous Namib Desert lizard *Aporosaura anchietae* (Bocage). *Madoqua (Windhoek) II*, 1: 67-85.

_____ and SEELY, M.K. 1980. Exploitation of fog water by a perennial Namib dune grass, *Stipagrostis sabulicola*. *S. Afr. J. Sci.*, 76: 38-39.

_____ and SEELY, M.K. 1982. *Ecology of Desert Organisms*. Longman, London. 194p.

LOUW, J.F. 1968. Die invloed van temperatuur en relatiewe humiditeit op die gewigverlies van die malmier, *Anoplolepis custodiens* (Smith). *S. Afr. Tydskr. Landbouwet.*, 11: 575-582.

MABELIS, A.A. 1979. Wood ant wars. The relationship between aggression and predation in the red wood ant (*Formica polyctena* Först). *Neth. J. Zool.*, 29: 451-620.

MAHDIHASSAN, S. 1977. The black ant *Camponotus compressus* feeding on urea. *J. Bombay Nat. Hist. Soc.*, 74: 197-199.

MALTAIS, J.B. and AUCLAIR, J.L. 1952. Occurrence of amino acids in the honeydew of the crescent-marked lily aphid, *Myzus circumflexus* (Buck.). *Can. J. Zool.*, 30: 191-193.

MENGE, B.A. and SUTHERLAND, J.P. 1976. Species diversity gradients: synthesis of the roles of predation, competition and temporal heterogeneity. *Am. Nat.*, 110: 351-369.

MINTZER, A. 1979. Colony foundation and pleometrosis in *Camponotus* (Hymenoptera, Formicidae). *Pan-Pac. Entomol.*, 55: 81-89.

MÖGLICH, M. and HÖLLDOBLER, B. 1974. Social carrying behaviour and division of labour during nest moving in ants. *Psyche*, 81: 219-236.

MURRAY, G.W. 1981. The food of the Namib wedge-snouted sand lizard, *Meroles cuneirostris* (Strauch)(Lacertidae) and comparison with that of the Namib sand-diving lizard *Aporosaura anchietae* (Bocage) (Lacertidae). Unpublished B.Sc.(Hons) thesis, University of the Witwatersrand, Johannesburg, South Africa.

MYERS, N.J. 1957. Studies on the biology of ants associated with citrus trees. Unpublished Ph.D. thesis, Rhodes University, Grahamstown, South Africa.

NAGEL, J.F. 1962. Fog precipitation measurements on Africa's Southwest Coast. *Notos*, 1: 51-60.

NEL, J.J.C. 1965. Influence of temperature and relative humidity on water loss in the workers of the meat ant, *Iridomyrmex detectus* (Smith)(Dolichoderinae: Hymenoptera). *Aust. J. Zool.*, 13: 301-315.

NICOLSON, S.W. 1980. Water balance and osmoregulation in *Onymacris plana*, a tenebrionid beetle from the Namib Desert. *J. Insect Physiol.*, 26: 315-320.

NIXON, G.E.J. 1951. *The association of ants with aphids and coccids.* Commonwealth Inst. Entomol., London. 36p.

OSTER, G.F. and WILSON, E.O. 1978. *Caste and Ecology in the Social Insects.* Monographs in Population Biology 12. Princeton University Press, Princeton, New Jersey. 352p.

PRICER, J.L. 1908. The life history of the carpenter ant. *Biol. Bull.*, 14: 177-218.

ROBINSON, E.R. 1976. Phytosociology of the Namib Desert Park. Unpublished M.Sc. thesis, University of Natal, Pietermaritzburg, South Africa.

ROBINSON, M.D. and CUNNINGHAM, A.B. 1978. Comparative diet of two Namib Desert sand lizards (Lacertidae). *Madoqua (Windhoek)*, 11: 41-53.

______ and SEELY, M.K. 1980. Physical and biotic environments of the southern Namib dune ecosystem. *J. Arid Environs.*, 3: 183-203.

RUTHERFORD, M.C. 1978. Karoo-fynbos biomass along an elevational gradient in the western Cape. *Bothalia*, 12: 555-560.

SALAMA, H.S. and RIZK, A.M. 1969. Composition of the honeydew in the mealybug, *Saccharicoccus sacchari*. *J. Insect Physiol.*, 15: 1873-1875.

SANDERS, C.J. 1964. Biology of carpenters ants in New Brunswick. *Can. Entomol.*, 96: 894-908.

, 1970. The distribution of carpenter ant colonies in the spruce-fir forests of northwestern Ontario. *Ecology*, 51: 865-873.

______, 1972. Seasonal and daily activity patterns of carpenter ants (*Camponotus* spp.) in northwestern Ontario (Hymenoptera, Formicidae). *Can. Entomol.*, 104: 1681-1687.

SCHMIDT-NIELSEN, K. 1975. *Animal Physiology: Adaptations and Environment*. Cambridge University Press, Cambridge. 699p.

SCHREMMER, F. 1979. Die nahezu unbekannte neotropische Weberameise *Camponotus (Myrmobrachys) senex* (Hymenoptera, Formicidae). *Entomol. Gen.*, 5: 363-378.

SCHUMACHER, A. and WHITFORD, W.G. 1974. The foraging ecology of two species of Chihuahuan Desert ants: *Formica perpilosa* and *Trachyrmyrmex smithi neomexicanus* (Hymenoptera; Formicidae). *Ins. Soc.*, 21: 317-330.

SEELEY, T. and HEINRICH, B. 1981. Regulation of temperature in the nests of social insects. In: *Insect Thermoregulation.* Ed. Heinrich, B. pp. 160-234. John Wiley & Sons, New York. 328p.

SEELY, M.K. 1978a. Fog consumers of the Namib Desert. *S.W.A. Annal*, 34: 48.

, 1978b. The Namib Dune Desert: an unusual ecosystem. *J. Arid Environs.*, 1: 117-128.

, 1979. Ecology of a living desert: twenty years of research in the Namib. *S. Afr. J. Sci.*, 75: 298-303.

______, DE VOS, M.P. and LOUW, G.N. 1977. Fog imbibition, satellite fauna and unusual leaf structure in a Namib Desert dune plant, *Trianthema hereroensis*. *S. Afr. J. Sci.*, 73: 169-172.

______ and STUART, P. 1976. Namib climate: 2. The climate of Gobabeb; ten-year summary 1962/72. *Namib Bulletin*, 1: 7-9.

SEVASTOPULO, D.G. 1978. The black ant *Camponotus* sp. feeding on urea. *J. Bombay Nat. Hist. Soc.*, 75: 511-512.

SKAIFE, S.H. 1961. *The Study of Ants*. Longmans, Cape Town. 178p.

SKINNER, G.J. 1980a. Territory, trail structure and activity patterns in the wood ant, *Formica rufa* in limestone woodland in northwestern England. *J. Anim. Ecol.*, 49: 381-394.

, 1980b. The feeding habits of the wood ant, *Formica rufa* (Hymenoptera, Formicidae) in limestone woodland in northwestern England. *J. Anim. Ecol.*, 49: 417-434.

SOUTHWOOD, T.R.E. 1978. *Ecological Methods.* 2nd edition. Chapman & Hall, London. 524p.

STEYN, J.J. 1954. The pugnacious ant (*Anoplolepis custodiens* Smith) and its relation to the control of citrus scales at Letaba. *Mem. Entomol. Soc. S. Afr.*, 3: 1-96.

STRADLING, D.J. 1978. Food and feeding habits of ants. In: *Production Ecology of Ants and Termites.* I.B.P. 13. Ed. Brian, M.V. pp. 81-106. Cambridge University Press, Cambridge. 409p.

SUDD, J.H. 1967. *An Introduction to the Behaviour of Ants.* Arnold, London. 200p.

TEVIS, L. 1958. Seeds. *Ecology*, 39: 695-704.

TRANIELLO, J.F.A. 1977. Recruitment behaviour, orientation and the organization of foraging in the carpenter ant, *Camponotus pennsylvanicus. Behav. Ecol. Sociobiol.*, 2: 61-79.

ULE, E. 1905. Ueber Blumengärten der Ameisen am Amazonenstrom. *Verh.*

Gesell. Deutsch. Nat. Aerzte, 76: 245-249.

WALLWORK, J.A. 1970. *Ecology of Soil Animals*. McGraw-Hill, London. 283p.

WALOFF, N. and BLACKITH, R.E. 1962. The growth and distribution of the mounds of *Lasius flavus* (Fabricius)(Hymenoptera, Formicidae) in Silwood Park, Berkshire. *J. Anim. Ecol.*, 31: 421-437.

WAY, M.J. 1963. Mutualism between ants and honeydew-producing homoptera. *Ann. Rev. Entomol.*, 8: 307-344.

WEHNER, R. and FLATT, I. 1972. The visual orientation of desert ants, *Cataglyphis bicolor*, by means of terrestrial cues. In: *Information Processing in the Visual Systems of Arhtropods*. Ed. Wehner, R. pp. 295-302. Springer, Berlin. 334p.

_____ and RÄBER, F. 1979. Visual and spatial memory in desert ants, *Cataglyphis bicolor* (Hymenoptera, Formicidae). *Experientia*, 35: 1569-1571.

WHEELER, W.M. 1908. Honey ants with a revision of the American Myrmecocysti. *Bull. Amer. Nat. Hist.*, 24: 345-397.

, 1910. *Ants: Their Structure, Development and Behaviour*. Columbia University Press, New York. 663p.

, 1921. A new case of parabiosis and the "ant gardens" of British Guiana. *Ecology*, 2: 89-103.

WHITFORD, W.G. 1978a. Structure and seasonal activity of Chihuahua Desert ant communities. *Ins. Soc.*, 25: 79-88.

, 1978b. Foraging in seed-harvesting ants *Pogonomyrmex* spp. *Ecology*, 59: 185-189.

______, DEPREE, D.J., HAMILTON, P. and ETTERSHANK, G. 1981. Foraging ecology of seed-harvesting ants, *Pheidole* spp., in a Chihuahuan Desert ecosystem. *Am. Mid. Nat.*, 105: 159-167.

______, DEPREE, D.J. and JOHNSON, P. 1980. Foraging ecology of two Chihuahuan Desert ant species: *Novomessor cockerelli* and *Novomessor albisetosus*. *Ins. Soc.*, 27: 148-156.

______ and ETTERSHANK, G. 1975. Factors affecting foraging activity in Chihuahuan Desert harvester ants. *Environ. Entomol.*, 4: 689-696.

______, JOHNSON, P. and RAMIREZ, J. 1976. Comparative ecology of the harvester ants *Pogonomyrmex barbatus* (F. Smith) and *Pogonomyrmex rugosus* (Emery). *Ins. Soc.*, 23: 117-132.

______, KAY, C.A. and SCHUMACHER, A.M. 1975. Water loss in Chihuahuan Desert ants. *Physiol. Zool.*, 48: 390-397.

WHITTACKER, R.H. and NIERING, W.A. 1975. Vegetation of the Santa

Catalina Mountains, Arizona. V. Biomass, production and diversity along the elevation gradient. *Ecology*. 56: 771-790.

WILLOUGHBY, E.J. 1971. Biology of larks (Aves: Alaudidae) in the central Namib Desert. *Zool. Afr.*, 6: 133-176.

WILSON, E.O. 1959. Some ecological characteristics of ants in New Guinea rainforests. *Ecology*, 40: 437-447.

, 1965. Trial sharing in ants. *Psyche*, 72: 2-7.

, 1971. *The Insect Societies*. Belknap Press of Harvard University Press, Cambridge, Massachusetts. 548p.