Observations on the natural history and behaviour of the dune ant, *Camponotus detritus* Emery, in the central Namib Desert.

by

B.A. Curtis

Desert Ecological Research Unit
P.O. Box 1592
Swakopmund
9000
S.W.A./Namibia

and

Zoology Department

University of Cape Town
Rondebosch
7700
South Africa

Received: 24 October 1984
Accepted: 18 March 1985

ABSTRACT

Camponotus detritus is a formicine ant species common in the sand-dunes of the central Namib Desert. Workers showed a continuous polymorphism and a certain amount of polyethism. Queens were similar to workers in appearance but had larger, distended gasters. From 0 to 7 dealate females were found in a nest. Alate reproductives occurred in some nests throughout most of the year, but the majority were found in summer. A nuptial flight was witnessed in April. Both males and females were occasionally observed foraging outside the nest. Colony foundation appeared to be claustral. Brood was present throughout the year, with great variability in the ratio of brood to workers, and number of callows. Brood and adult transport was observed between related nests. Workers were aggressive and territorial. They appeared to use the sun's rays and possibly visual cues for orientation. Recruitment to new nest sites or new food sources was observed.

CONTENTS

1 INTRODUCTION

The large formicine ant, *Camponotus detritus,* is a common and conspicuous arthropod restricted to the dunes of the central Namib Desert where it replaces the closely related *C. fulvopilosus* De Geer which occurs throughout the rest of arid southern Africa (Skaife, 1961). Towards the west of the dune sea it is the only ant species present. In the east, where other ant species also occur, *C. detritus* still appears to be the most abundant species.

Although it is so common in the Namib dune sea, very little is known about its biology and ecology. Holm and Scholtz (1980) described it as detritivore and Seely (1978) mentioned 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 brief observations on natural history, no detailed or comprehensive study exists on this species.

Since ants are ecologically one of the dominant groups of terrestrial animals and are particularly important in desert ecosystems (Bernard, 1964; DÉlye, 1968; Wilson, 1971; Whitford, 1978; Bernstein, 1979), a two-year study was initiated to determine the role played by *C. detritus* in the Namib dune ecosystem. The present paper describes some observations on the natural history and behaviour of this species made during this study which was submitted as an M.Sc. thesis (Curtis, 1983).

The Namib Desert, situated along the west coast of southern Africa, does not experience marked seasonal climatic changes (Robinson and Seely, 1980). The fog caused by the old Benguela Current provides a fairly regular source of moisture either directly or indirectly for the plants and animals of the desert. *Camponotus detritus* is predominantly a honeydew-feeder (Curtis, in prep.), obtaining its moisture indirectly via scale insects from the perennial vegetation, among the roots of which the ants construct their nests (Curtis, in prep.).

2 MATERIALS AND METHODS

For a two-year period (August 1980 — August 1982) regular observations were made on the behaviour of *C. detritus* in its natural habitat. Data on life cycle patterns were obtained from 36 nest excavations (Curtis, in prep.) and pupae were taken to the laboratory where eclosion and behaviour of the young workers (callows) were observed.

Following the only nuptial flight observed during this period, six newly inseminated queens were taken 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 cotton wool. Sugar water was similarly given every two days and dead arthropods once per week.

3 RESULTS AND DISCUSSION

3.1 Workers

Workers are brick-red with a black gaster covered in off-white setae. On the dorsal surface of each gaster segment is a smooth area, giving the gaster a partially striped appearance. Workers show a continuous size range from 7—16 mm body length, divided into 3 arbitrary size categories for the purpose of this paper (Table 1).

Although workers of each size class performed most tasks, there was a tendency toward size-related polyethism as found among various *Camponotus* species (Wilson, 1971). There was no distinct soldier caste.

3.2 Queens

Queens are slightly longer than major workers, having smaller heads and larger gasters and thoraxes but the same coloration (Fig. 1). The gaster of a gravid queen is markedly distended and upon dissection reveals a mass of eggs with very little fat reserves (Plate 1). Only 10 out of 36 excavated nests housed queens: two contained two queens each; one (the largest nest excavated housing almost 20 000 individuals) contained eight dealate females; the remaining seven had only one queen each. Skaife (1961) similarly found queens in only two out of fifty nests of the ubiquitous southern African species, *C. maculatus*, and four out of twelve nests of *C. werhti*. Like *C. detritus*, queenless nests of the above species contained brood.

There are two possible explanations for the apparent absence of queens yet presence of brood in some nests. The first is that workers are able to lay male and female eggs parthenogenically. The laying of haploid male eggs by workers is fairly common, but thelytoky (the laying of diploid female eggs) is unusual among

TABLE 1: Mean lengths (head to tip of gaster), wet and dry mass of *Camponotus detritus* adults and brood. N.D. = No data

	Length (mm)			Wet mass (mg)			Dry mass (mg)		
	x̄	S.E.	N	x̄	S.E.	N	x̄	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
Larvae	Range (mm)								
	1 — 4			4,49	0,55	38	1,22	0,09	35
	5 — 8			27,19	2,52	50	5,01	0,29	92
	9 — 13			127,17	3,85	50	16,15	0,52	50
Pupae	7 — 10			48,36	3,02	40	8,96	0,57	50
	11 — 14			145,81	5,62	26	12,72	0,48	40
Pharate adults	7 — 10			40,06	4,21	60	4,60	0,28	100
	11 — 14			121,84	3,89	24	10,43	0,54	24

ants (Wilson, 1971). There appear to be no records of thelytoky among *Camponotus*, but *Cataglyphis cursor*, a fairly closely related formicine species from the drier areas of France, has workers which are capable of producing females by thelytoky (Cagniant, 1971, 1980). Queenless laboratory colonies 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). Thelytoky is unlikely to occur in *C. detritus* since no queenless laboratory colonies produced any eggs.

The second possibility is that daughter nests are queenless and workers must transport brood from the mother nest. This is the most likely explanation because nest splitting (where the old nest becomes too small or conditions inside become unsuitable and a new nest is formed) has been observed and workers were frequently seen transporting brood from one established nest to another.

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, *C. (Myrmobrachys) senex textor* which may have as many as 23 queens in one nest (Schremmer, 1979). Large nests 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 was particularly large. Thus the number of females does not appear to be related to nest size. It is possible that only one queen was functionally laying and that the others were dealates which had not left the nest on a nuptial flight. On three occasions dealates were observed collecting honeydew with the workers up to 15 m from the nest.

3.3 Alate reproductives

Like most ant species, males are morphologically very different from females being much smaller and totally black (Fig. 1 and Plate 2; Table 1). Alates were found throughout most of the year, with a maximum in December (Table 3). Both males and females are occasionally seen just outside the nest with their heads in *Trianthema hereroensis* flowers, apparently collecting pollen or nectar. No alates were found in September or October, but nests excavated in early October contained very large larvae 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

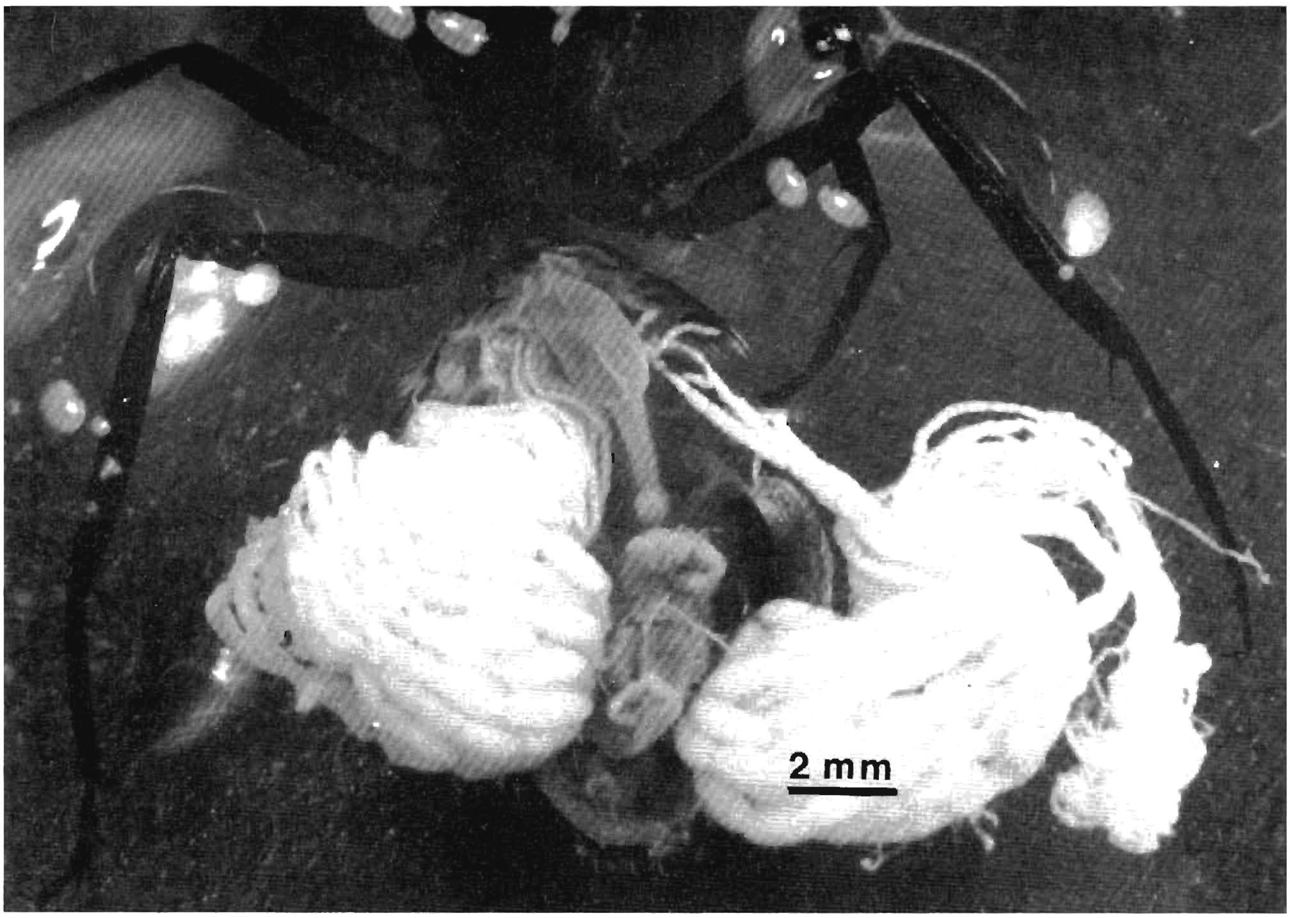


PLATE 1: *Camponotus detritus* queen dissected to show ovaries (two large white structures) containing eggs (Photo: L. Praetorius).

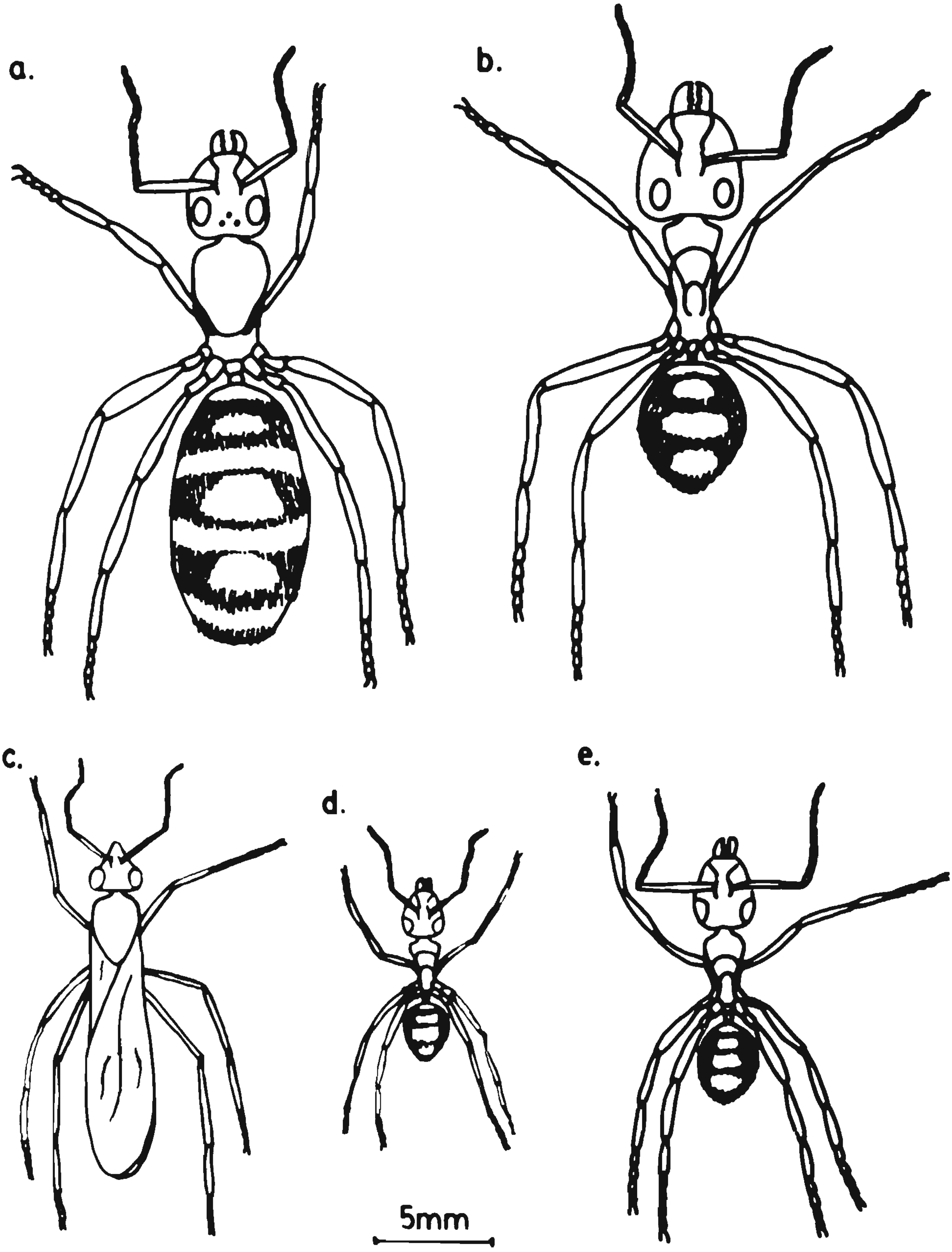


FIGURE 1: Relative size of members of a *Camponotus detritus* colony. a. Queen b. "Major worker" c. Male d. First worker produced by newly inseminated queen e. Typical "minor" worker.

flight. Failing the latter, alates possibly remain in the nest until the following winter. Like *C. detritus,* alates of two southern African species, *C. maculatus* and *C. werthi* occur in the nest in autumn and winter (Skaife, 1961).

Not all nests excavated contained alates. Presumably, as in other ant species (Wilson, 1971), a colony must reach a certain state of maturity before producing alates. Pricer (1908) estimated that colonies of *C. pennsylvanicus* and *C. ferrugineus* require from three to six years to reach maturity.

3.4 Nuptial flights

Only one nuptial flight was witnessed. This occurred in the eastern dunes on a sunny April mid-morning following about 3 mm rainfall the previous afternoon. We noticed hundreds of males at the top of the tallest grass stems above the nest, while females and workers were moving about outside the nest entrance. Half an hour later the males took to the air and within 15 minutes the majority had left the grass clump. Many did not fly far, landing within 5 m of the nest. Immediately the females began climbing up the grass stems and flying away. Some fell off the grass and had to climb up again while others took off from the ground. 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 obviously occurred at other nests 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 ant species and conspecific workers.

3.5 Colony foundation

After the nuptial flight females were seen 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 occurring in seven North American *Camponotus* species (Mintzer, 1979).

All six *C. detritus* queens collected laid eggs which hatched after 19 to 22 days and larvae pupated 15 days later. Workers took 30 days to eclose. As usual among ants (Pricer, 1908; Wilson, 1971) the first workers were smaller than subsequent ones (about 4 mm). The development time for the first brood was similar to that recorded for various other *Camponotus* species. Among the seven species which Mintzer (1979) studied in the laboratory, the egg to larva period was 20 to 33 days, larva to pupa took 12 to 14 days and first workers eclosed 17 to 28 days later.

3.6 Brood

The brood showed a drop in mass as the larvae metamorphosed into adults inside the pupal cocoons (Table 1). This is to be expected as larvae cease feeding after pupation and live on stored fat reserves until eclosion. The mean wet mass of eggs was 0,43 ± 0,10 mg and length was 1,51 ± 0,07 mm. Comparable data for other desert ant species were not found.

Unlike many temperate ant species which show marked seasonality in brood production (Wilson, 1971; Dartigues and Passera, 1979), every *C. detritus* nest excavated throughout the year contained brood at all stages of development. There was, however, great variability in the relative proportions of brood at different stages of development, as well as in the num-

TABLE 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

TABLE 3: Seasonality of alate production in *Camponotus detritus* nests (Aug 1980 — Aug 1982). Percentages are of the total number of adults per nest of all nests excavated. P = alates observed outside unexcavated nests.

Month		Males (%)		Females (%)		Number of nests	
		x̄	S.D.	x̄	S.D.	Housing alates	Excavated
January	P	0		0		0	4
April	P	present		present		1	2
May		0,9	0,9	0,2	0,3	4	7
June	P	1,3	1,9	0,1	0,1	3	4
July		0			0	0	1
August	P	—	—	—	—	—	—
September		0		0		0	4
October		0		0		0	11
December		0,4	0,9	24,2	8,6	5	5

ber of callows present per nest. The ratio of workers to pupae varied from 1:0,02 to 1:0,58 and the number of callows as a percentage of the total number of workers ranged from 0 to 18%. These variations appeared to be correlated neither with season nor location of nests in the dune sea.

Other southern African ant species also show variation in the relative proportions of brood present throughout the year, but this is generally associated with season and climate (Broekhuysen, 1948; Steyn, 1954). Peak numbers of brood of *C. 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). Workers: pupae ratios of the East African weaver ant, *Oecophylla longinoda,* varied from 1 : 0,03 to 1 : 0,87 (Way, 1954). The ratio within a single nest of the tropical *C. solon* was 1 : 0,84 (LÉvieux, 1975).

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.*

3.7 Callows

Young workers which eclosed in the laboratory were yellow with white setae on the gaster. As the cuticle gradually darkened the gastral setae became off-white, until after about 20 days the callows were the same colour as in mature ants. In the laboratory, they were negatively phototactic. 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 to 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 all *C. detritus* workers was to face the source of alarm with jaws open and gaster raised above the level of the rest of the body. 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 (Plate 3a), although the response of workers towards intruders varied. Major workers tended to attack more readily than minors, while the smallest workers usually retreated rapidly. Alate and dealate females exhibited the aggressive posture with raised gaster, but males showed no aggression.

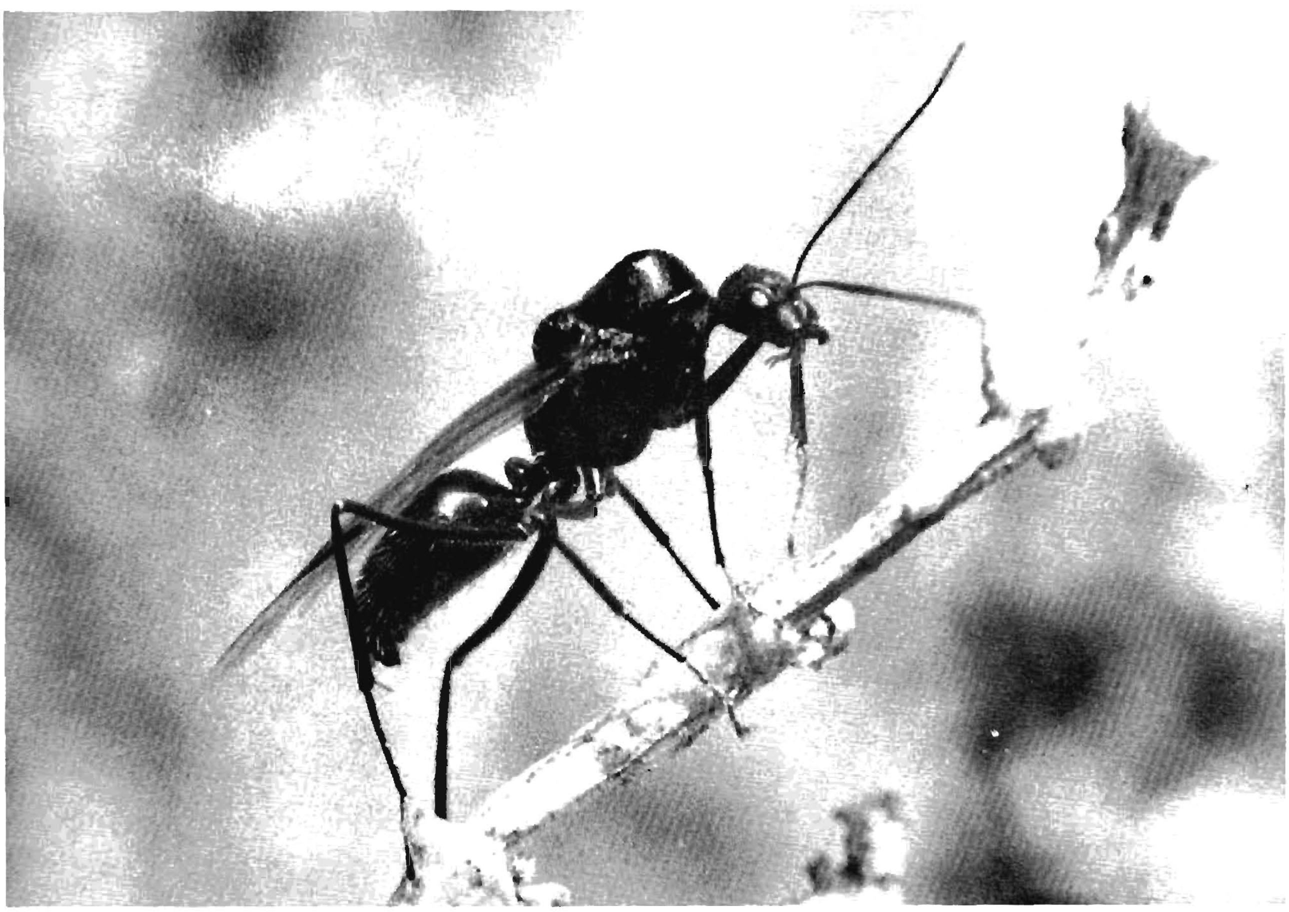


PLATE 2: Alate male *Camponotus detritus.*

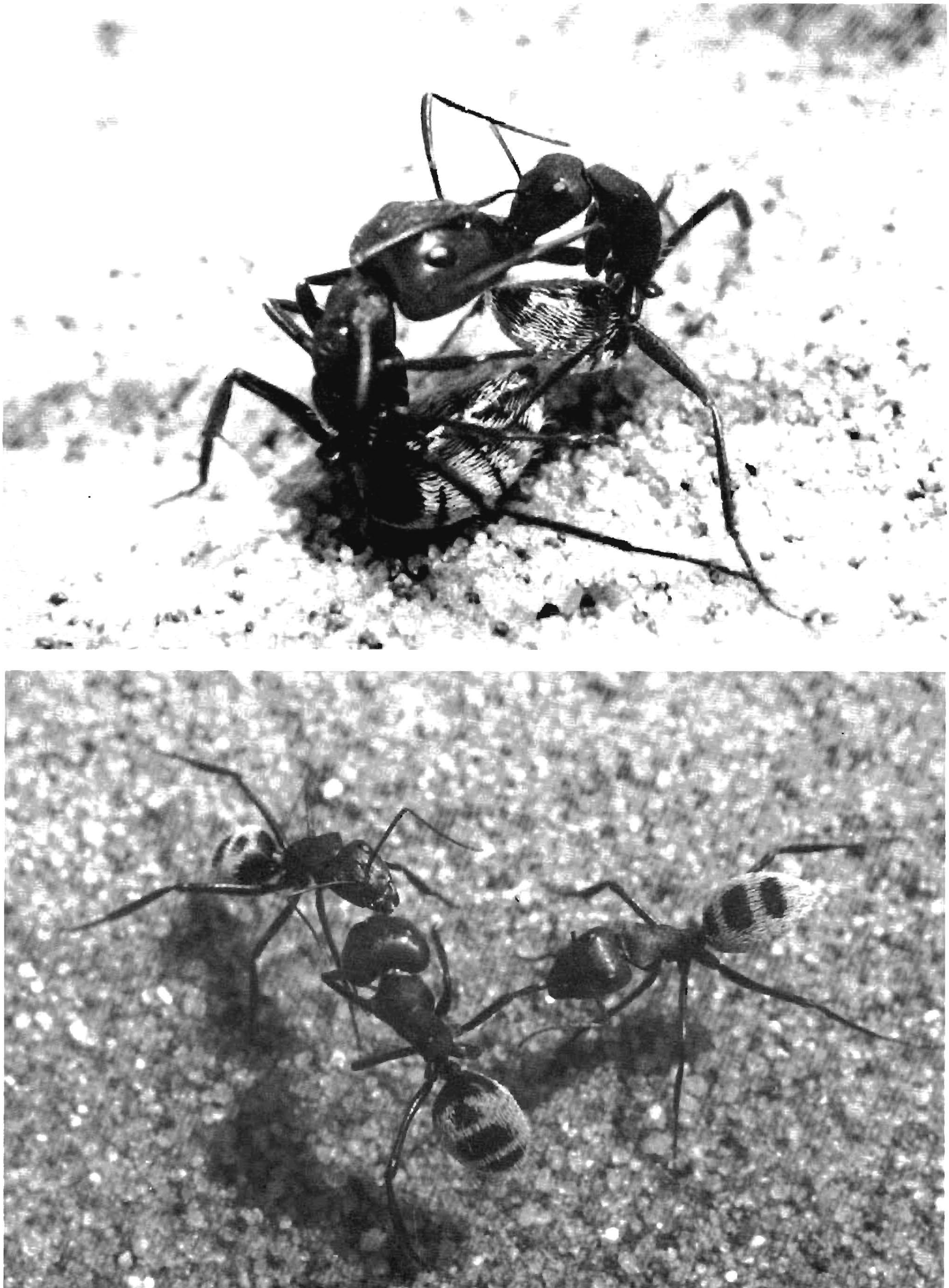
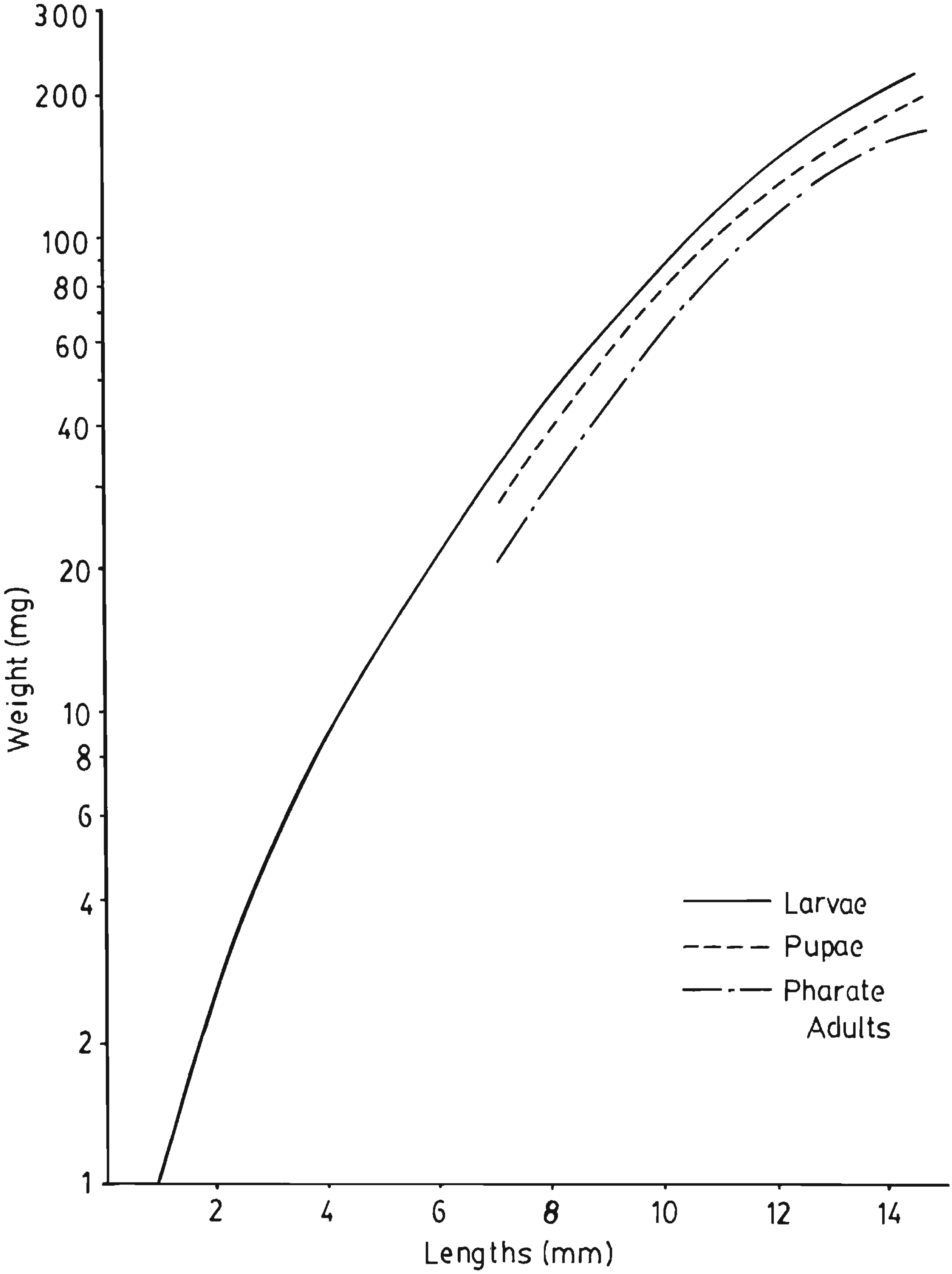


PLATE 3: Fighting between *Camponotus detritus* workers. a) Note that the gasters are tucked underneath the bodies to spray formic acid (Photo: E. McClain). b) Two workers pulling on a "foreigner".

3.9 Territoriality

Camponotus detritus was found 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. Territory size varied considerably, probably as a function of the size of the colony and the abundance of scale insects present (Table 4). As with most ant species (Hölldobler, 1971; Stradling, 1978; Skinner, 1980),



nests were seldom situated in the middle of territories and nests belonging to other colonies 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, one nest was 170 m from its furthest foraging grounds while a plant only 25 m from the nest was utilised 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 aggressiveness of the workers.

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 (Plate 3b). 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 as noted by Wilson (1971). Firstly, although defended territories appeared to be persistent 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. Thus *Camponotus detritus* workers were highly aggressive towards "foreign" conspecifics and also attacked *C. mystaceus* and *C. maculatus* workers, but showed no hostility towards ants of other genera.

TABLE 4: *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 distance 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
			x̄	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

3.10 Orientation

Camponotus detritus did not appear to use pheromone trails for orientation. The movement of sand would probably rapidly destroy such trails (see section 3.12). The majority of workers moved singly across the sand. Only those recruiting nest-mates to new food or nest sites were observed to be laying trails.

Since workers never crossed 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. Orientation to polarised light occurs among several *Camponotus* species (Wilson, 1971).

3.11 Brood and adult transport

A fairly common occurrence among ants is the transporting of brood and inexperienced workers by the most active and experienced workers during emigration from one nest to another (Wilson, 1971); behaviour which was often observed in *C. detritus.* The transporter held the transportee, usually a minor worker, by the jaws while the body of the transportee was tucked underneath that of the transporter in the pupal position with the legs and antennae held close to the body. When a male was transported he was either held by the jaws and dragged or grasped by the neck and lifted in an oblique position, remaining motionless with legs and antennae folded. Alate females were merely held by the jaws and dragged. This carrying behaviour of *C. detritus* closely resembles that of *C. sericeus* (Möglich and Hölldobler, 1974) and *C. socius* (Hölldobler, 1971).

3.12 Recruitment

Group recruitment to new nest sites and new food sources was observed. A worker would leave the nest dragging its gaster along the ground, followed by one to twenty other workers in a highly excited state. Every so often the leader would stop and remain 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 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. On one occasion five alate females were seen following a major worker from one nest to a sister nest of the same colony — rather unusual behaviour.

The pheromone secreted by the leader apparently keeps the followers in a state of excitement but 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 range of chemical recruitment techniques among the Formicidae from very simple, involving only two ants, up to a highly sophisticated form involving communicatory dances and many ants. Examples of each form can be found within the genus *Camponotus*, but most species, including *C. detritus*, seem to be at an intermediate stage.

4 CONCLUSION

In most aspects of its natural history and behaviour *C. detritus* is typical of the fairly advanced formicine ants. It does, however, exhibit a few rather unusual characteristics. Foraging by alates is virtually unheard of among ants. The presence of dealate nonreproductive females in the nest is not a common phenomenon, nor is the leading of alate females from one nest to another by a worker, except perhaps, when conditions in one nest make it essential for all the inhabitants to move to another. *Camponotus detritus* is a successful species which has managed to establish itself in the relatively harsh environment of the Namib dune field.

5 ACKNOWLEDGEMENTS

This paper forms part of an M.Sc. thesis submitted to the University of Cape Town. I should like to thank Prof. G.N. Louw and Dr M.K. Seely for supervision of the project; the Desert Ecological Research Unit, Gobabeb, 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. (South Africa) for a post-B.Sc. (Hons) bursary and D.E.R.U. technicians for help with field-work.

6 REFERENCES

BERNARD, F.
1964: Densité de la faune au Sahara. Premiers resultats obtenus par la méthode des carrés. *Trav. Inst. Rech. Sahariennes Univ. Alger* **23**: 45—60.

BERNSTEIN, R.A.
1979: Relations between species diversity and diet in communities of ants. *Ins. Soc.* **26**: 313—321.

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

BROEKHUYSEN, G.J.
1948: The brown house ant (*Pheidole megacephala* Fabr.). *Dept. Agric. Entomol. Series* No. 18, Bull. 266. 40pp.

CAGNIANT, H.
1979: La parthénogenèse thélytoque et arrhénotoque chez la fourmi *Cataglyphis cursor.* Cycle biologique en elevage 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.* Étude en élevage de la productivité des societes avec reine et des societes sans reine. *Ins. Soc.* **27**: 157—174.

CURTIS, B.A.
1983: Behavioural and physiological ecology of the Namib Desert dune ant, *Camponotus detritus* Emery. M.Sc. thesis, University of Cape Town, R.S.A.

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

DÉLYE, G.
1968: Recherches sur l'écologie, la physiologie et l'éthologie des fourmis du Sahara. Ph.D. thesis, University of Aix-Marseille, France.

HÖLLDOBLER, B.
1962: Zur Frage der Oligogynie bei *Camponotus ligniperda* Latr. und *C. herculeanus* L. (Hymen; Form). *Z. Ang. Entomol.* **49**: 337—352.

1971: Recruitment behaviour in *Camponotus socius* (Hymen; Form). *Z. Vergl. Physiol.* **75**: 123—142.

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

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

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.

MINTZER, A.
1979: Colony foundation and pleometrosis in *Camponotus* (Hymen; Form). *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.

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

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

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

SCHREMMER, F.
1979: Die nahezu unbekannte neotropische Weberameise *Camponotus (Myrmobrachys) senex* (Hymen; Form). *Entomol. Gen.* **5**: 363—378.

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

SKAIFE, S.H.
Harvard University Press, Cambridge, Massachusetts. 548 pp.
1961: *The study of ants.* Longmans, Cape Town. 178 pp.

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

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

STRADLING, D.J.
1978: Food and feeding habits of ants. *Production Ecology of ants and termites.* IBP 13. ed. M.V. Brian. Cambridge University Press. pp 81—106.

WAY, M.J.
1954: Studies of the life history and ecology of the ant *Oecophylla longinoda* Latr. *Bull. ent. Res.* **45**: 93—112.

WHEELER, W.M.
1910: *Ants: their structure, development and behaviour.* Columbia University Press, New York. 663 pp.

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

WILSON, E.O.
1971: *The Insect Societies.* Belknap Press of Harvard University Press, Cambridge, Massachusetts, 548 pp.