*Insectes Sociaux, Paris*
1985, Volume 32, n° 3, pp. 313-320





# NESTS OF THE NAMIB DESERT DUNE ANT *CAMPONOTUS DETRITUS* EMERY

B.A. CURTIS (1)

*(1) Desert Ecological Research Unit, PO Box 1592, Swakopmund South West Africa, Namibia*
*Zoology Department, University of Cape Town, Rondebosch 7700, South Africa*

Reçu le 22 janvier 1985 Accepté le 5 juillet 1985

## *SUMMARY*

*Camponotus detritus* nests are simple structures excavated among the roots of perennial vegetation in the sand dunes of the Namib Desert. They comprise a series of tunnels and chambers 100 - 400 mm deep, often lined with detritus. No " royal chamber " or food stores were found. Brood was found throughout the nest, throughout the year. Nest temperatures varied considerably. Mean nest temperatures were about 32°C in summer and 20 - 23°C in winter. The number of workers per nest varied from 218 to 16,000 with a mean and standard error of 3,404 ± 570. Each colony comprised one to four nests. Only one nest per colony housed queens. Colony expansion and nest relocation occurred frequently.

## *RESUME*

**Nids de la fourmi des dunes du désert de Namibie** Camponotus detritus

Les nids de *Camponotus detritus* sont des structures simples, creusées parmi les racines de la végétation pérenne des dunes du désert de Namibie. Ils comprennent une série de tunnels et de chambres de 100 - 400 mm de profondeur, souvent tapissés avec des détritus. On ne trouve pas de « chambre royale » ou de réserves de nourriture. Le couvain se trouvait d'un bout à l'autre du nid. Les températures des nids variaient considérablement. Les températures moyennes des nids étaient d'environ 32°C en été et 20 - 23°C en hiver. Le nombre d'ouvrières par nid variait de 218 à 16 000 avec une moyenne de 3 404 ± 570. Chaque colonie comprenait un à quatre nids. Seulement un nid par colonie avait des reines. Le développement des colonies et le changement de localisation des nids avaient lieu fréquemment.

## INTRODUCTION

*Camponotus detritus* is a large (7-16 mm), polymorphic ant common in the sparsely-vegetated sand dunes of the central Namib Desert in South West Africa/Namibia (CURTIS, 1983). Nests are constructed among the roots of the perennial vegetation on the dune slopes. The major food source is honeydew, excreted by scale insects present on the perennial vegetation (CURTIS, 1985).

The purpose of this study was to examine the nests of *C. detritus* in order to answer the following questions : what is the internal structure of the nest ; what are the daily and seasonal fluctuations in nest temperature ; how many individuals are found per nest ; what is the structure of a *C. detritus* colony ?

## METHODS AND MATERIALS

### Internal structure and numbers of individuals

A total of 36 nests from different parts of the dune field were excavated 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 were removed in 50 mm layers and sifted through 2 mm mesh sieves. As the workers and alates emerged they were collected by hand (collectors wore surgical gloves) and the brood was carefully removed and later all were counted. During later excavations 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 (Polytetrafluoroethylene) at the top to prevent the ants from escaping. Ants and brood were later removed from the debris and counted. The same evening or following morning they were released as near to the old nest as possible.

### Colony structure

*Camponotus detritus* is a territorial species and workers attack conspecifics from " alien " colonies. To determine whether two nests belonged to the same colony, workers from one nest were released at the entrance to the other nest. This was repeated five times. If the nests were from the same colony, no hostility was observed. If the nests were from different colonies the " foreign " ant would immediately be attacked. These results were substantiated by observations on the activity of the ants in the dunes prior to excavation of nests.

### Nest temperatures

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

## RESULTS

### Nest structure

*Camponotus detritus* nests are simple structures constructed among the roots of the perennial vegetation, either living or dead. In some cases the aerial parts of the plant had disappeared leaving a hardened mound around the roots in which the nest was situated. The basal area of these mounds varied from 0.1 m to 0.4 m with a height of between 0.1 and 0.3 m. Unlike certain ant and termite species, they are unable to build nests in loose sand and rely on the roots to provide a framework. One nest was found in an old termitarium and others were excavated in silt or clay deposits of dry river beds.

Most nests had one entrance hole ; 9 % had two on different sides. The majority opened to the east (including those with two holes), with the fewest opening southwards *(fig. 1)*. There was no statistically significant correlation with wind direction even though the highest frequency of wind during the year is from the south west and the lowest from the east (SEELY and STUART 1976). More than half had an accumulation of detritus either above the entire nest or just above the entrance, but there was no correlation between the degree of exposure of the nest to the sun and the presence of a detritus pile *(table I)*. Some of the completely exposed nests (9 %), situated at the base of the dunes near the interdune valley, were covered in fine quartz gravel.

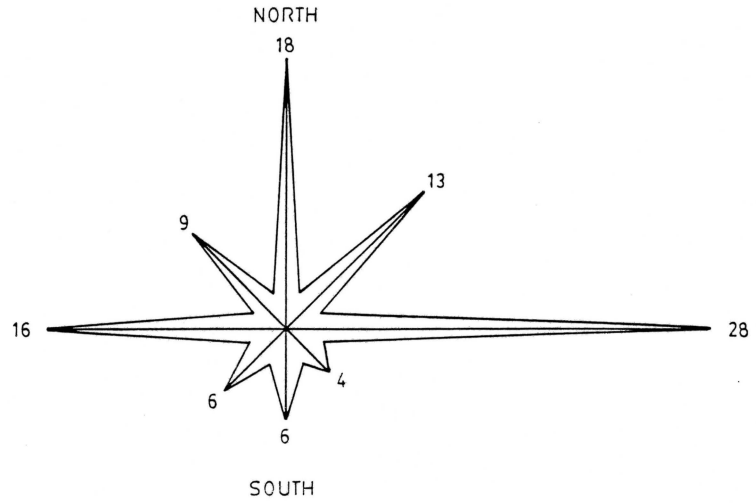


Fig. 1. — Orientation of *Camponotus detritus* nest entrances. Each value is a percentage of the total number (110) of nests observed throughout a two year period.

Fig. 1. — Orientation des entrées des nids de *Camponotus detritus*. Chaque valeur représente un pourcentage par rapport au total des nids (110) observés pendant une période de deux ans.

Internally, nests consisted of many interconnecting passages of variable length ranging from 9-22 mm in diameter, with occasional wide chambers of 30-88 mm in diameter. Most were simply tunnels in the sand, but in some (about 10 %) the walls of the passages and chambers were lined with a pliable viscous substance which hardened to form rigid tunnels. Many of the chambers were 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. No specific " royal chamber " was found, and brood of all stages of development was together throughout all nests. No food stores were found.

Table I. — Number of *Camponotus detritus* nests covered either by an accumulation of detritus or gravel.

Tableau I. — Nombre de nids de *Camponotus detritus* recouverts soit par unè accumulation de déchets soit par du gravier.

| | Nests exposed to sun | Nests shaded by plants | Total |
|---|---|---|---|
| Detritus or gravel present | 30 | 37 | 67 |
| Nothing present | 23 | 21 | 44 |
| Total | 53 | 58 | 111 |

G. adj. = 0.590 $P < 0.5$ (Sokal and Rohlf, 1981)

**Nest temperatures**

The internal temperatures of *C. detritus* nests were similar to temperatures measured simultaneously in the sand outside the nest. As expected, daily fluctuations in nest temperatures were greatest near the surface, decreasing with depth (*fig. 2*). The thermal gradient within the nest, however, was never very great at any particular time of day. Mean sommer nest temperature was 32° C *(table II)* which is the temperature chosen by the workers for the brood in the laboratory (CURTIS, *in prep*).

**Colony structure, expansion and nest relocation ; number of adults per nest**

Most *C. detritus* colonies comprised more than one nest ; sometimes as many as five. Sister nests were sometimes only 0.5 m apart, other times as much as 100 m or more. The number of workers per nest varied considerably across the dune-field from only 218 to as many as 15 670 with a mean nest size of 3 404 ± 510 S.E. workers. Total colony size was also variable. The large nest housing 15 670 workers had a sister nest and together the colony had 20 038 workers. A smaller colony comprising four nests had a total of under 1000 workers.

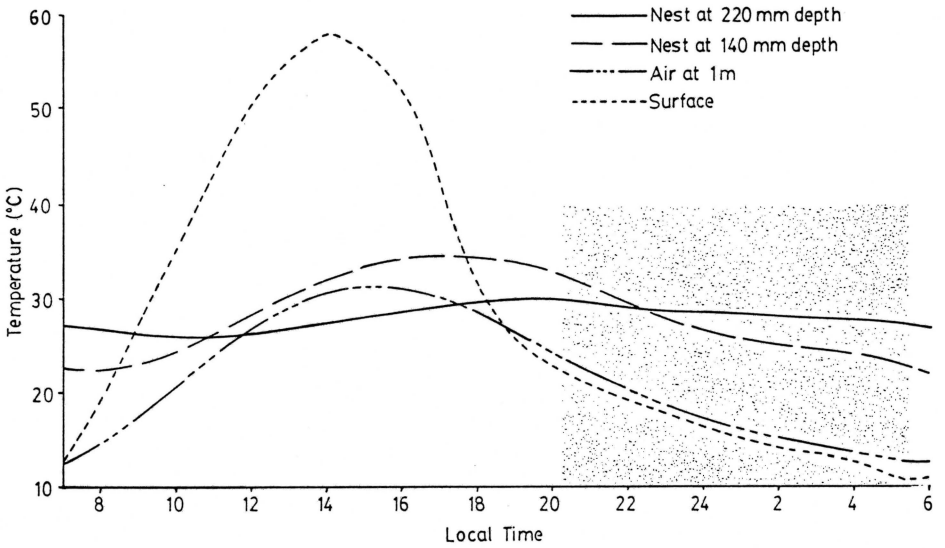


Fig. 2. — Daily temperature fluctuations in a *Camponotus detritus* nest measured on 6 Jan. 1981, together with the temperatures of the adjacent level sand surface and air at 1 m. Local time precedes sun time by one hour.

Fig. 2. — Variations quotidiennes de la température enregistrée le 6 janvier 1981 à l'intérieur d'un nid de *Camponotus detritus*, sur la surface du sable à proximité du nid et dans l'air à 1 m de hauteur. L'heure locale est en avance d'une heure sur l'heure solaire.

Table II. — *Camponotus detritus* nest temperatures in summer (November-February) and winter (May-August) at two different depths.

Tableau II. — Température des nids de *Camponotus detritus* en été (Novembre-Février) et en hiver (Mai-Août) à deux profondeurs différentes.

| Depth | Nest Temperatures (C) | | | |
|---|---|---|---|---|
| Summer | Max. | Min. | Mean | 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 |

Nest relocation was observed on four occasions, usually when a nest was covered by a sanddune. The workers then excavated a new nest nearby and transported brood and inexperienced workers across. On three occasions colony expansion was seen, presumably when conditions in the old nest became too crowded. Workers continued to use the original nest, but excavated another " sister " nest nearby to which they transported brood and inexperienced workers. Gravid females were only found in one nest per colony and workers were seen transporting brood to sister nests.

## DISCUSSION

The structure of *C. detritus* nests is not unlike many other desert ants particularly the Saharan species (DÉLYE 1968). The simple construction among the roots of dune vegetation has enabled *C. detritus* 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 destroy the nest. The habit of nest splitting, which occurs commonly among ants (WILSON 1971, MÖGLICH and HÖLLDOBLER 1974, MABELIS 1979), has led to multi-nest colonies which seems maladaptive since workers appeared to waste considerable time and energy walking between sister nests. Nevertheless, should one nest be destroyed suddenly, workers could rapidly transport brood to an established sister nest.

Queenless nests containing brood occur in both *C. maculatus* and *C. werthii* (SKAIFE 1961) suggesting that this is not an unusual phenomon for *Camponotus* species. The transport of brood across open sand from the queen's nest to sister nests seems a hazardous task for a desert species since it occured 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 (CURTIS *in press*). Presumably the dangers associated with diurnal brood transport were outweighed by the advantages of multi-nest colonies and constant brood production.

The variability in nest size is probably due to a number of factors, such as nest age, location, 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 may be responsible for small, yet fully reproductive nests.

Marked variation in nest size also occurs among other *Camponotus* species. (PRICER 1908, WILSON 1959, SANDERS 1970, LÉVIEUX 1975). 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 seems 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.

An apparent disadvantage of the relatively simple nest construction was the lack of nest thermoregulation. Although a very narrow range of temperatures was chosen for the brood by the workers under laboratory conditions (CURTIS, *in prep*), in nature the brood did not appear to need specific temperatures, since they were found throughout the nest at varying temperatures. The lower winter temperatures may have been responsible for a decrease in brood production in winter, but did not cause brood production to cease.

ACKNOWLEDGEMENTS. — This paper is part of an M. Sc. thesis submitted to the University of Cape Town, R.S.A. I thank: Prof. G.N. LOUW and Dr. M.K. SEELY for supervision of the project; the Desert Ecological Research Unit, Gobabeb, funded by the C.S.I.R. (R.S.A.) and the Transvaal Museum, for use of vehicles, equipment and other research facilities; the Department of Agriculture and Nature Conservation, S.W.A./Namibia for use of facilities and permission to work in the Namib-Naukluft Park; the C.S.I.R. (R.S.A.) and the University of Cape Town for financial support; D.E.R.U. assistants for help with excavations.

## References

CURTIS B.A., 1983. — Behavioural and physiological ecology of the Namib Desert dune ant, *Camponotus detritus* Emery. Unpubl. M. Sc. *thesis*, University of Cape Town, South Africa.

CURTIS B.A., 1985. — The dietary spectrum of the Namib Desert dune ant, *Camponotus detritus Emery*. *Insect. Soc.*, *32*, 78-85.

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

LÉVIEUX J., 1975. — La nutrition des fourmis tropicales. I. Cycle d'activité et régimes alimentaires de *Camponotus solon* (Forel) (Hymenoptera, Formicidae). *Insect. Soc. 22*, 381-390.

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

MÖGLICH M., 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). Unpubl. B. Sc. (Hons) thesis, University of the Witwatersrand, Johannesburg, South Africa.

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

SANDERS C.J., 1970. — The distribution of carpenter ant colonies in the spruce-fir forests of northwestern Ontario. *Ecology, 51,* 865-873.
SEELY M.K., STUART P., 1976. — Namib climate : 2. The climate of Gobabeb, ten-year summary 1962/72. *Namib Bulletin* 1.
SKAIFE S.H., 1961. — The study of Ants. Longmans, Cape Town. 178 p.
SOKAL R.R., ROHLF F.J., 1981. — Biometry. Second Edition. Freeman and Co, San Fransisco.
WHEELER W.M., 1910. — *Ants : Their structure, Development and Behaviour.* Columbia University Press, New York, 663 p.
WILSON E.O., 1959. — Some ecological characteristics of ants in New Guinea rainforests. *Ecology, 40,* 437-447.
WILSON E.O., 1971. — *The Insect Societies.* Belknap Press of Harvard University Press, Cambridge, Massachusetts, 548 p.