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Effect of an environmental gradient upon the distribution and abundance of the dune ant, *Camponotus detritus*, in the central Namib Desert

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The central Namib Desert dunes, although only 130 km wide, exhibit a marked environmental gradient from the coast inland. Across this gradient mean nest density of the dune ant, *Camponotus detritus*, ranged from 0·3 to 3·9 nests per hectare while the mean number of workers per nest ranged from 728 to 5,077. Ants were least abundant in the dunes near the coast, most abundant in the central dunes and of intermediate abundance inland. The distribution of scale insects, from which their major food source, honeydew, is obtained, showed a similar pattern to that of *C. detritus*.

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Introduction

Camponotus detritus Emery is a common and conspicuous ant species apparently endemic to the central Namib dune sea (Curtis, 1985*a*). Towards the western part of the dunes it is the only ant species present whereas in the east, where other ant species also occur, *C. detritus* appears to be the most abundant species (pers. obs.). Its major food is the honeydew secretions of scale insects (Homoptera: Coccoidea) which live on the perennial dune vegetation (Curtis, 1985*b*). Workers tend scale insects at any time but most activity occurs during the day (Curtis, 1985*c*). Each colony, comprising one to four nests, maintains a discrete foraging territory. Nests are constructed in the sand beneath perennial vegetation (Curtis, 1985*d*).

The central Namib dune sea (Fig. 1) stretches from the coast to the foothills of the western escarpment and is approximately 130 km across at its widest point. The dune sea may be divided from west to east, into three sections each with differing dune types and substrate properties (Barnard, 1973). Despite its narrowness, a distinct climatic gradient exists from the coast inland (Besler, 1972). The cold Benguela Current which flows northwards along the western coast of southern Africa, and the south Atlantic anticyclone are responsible for the regular occurrence of advective fog and for the cool southwesterly winds which prevail during summer (Louw, 1972). Along the coast temperatures are lower than inland and daily fluctuation in temperature is reduced. Inland, where the moderating effect of the ocean is decreased, fluctuations in temperature and relative humidity are far greater and evaporation is higher. Rainfall is sparse and intermittent throughout the desert but is highest in the east. In general, however, the Namib does not experience marked annual climatic changes (Robinson & Seely, 1980).

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Across the dune sea, plant species diversity and abundance increase from the sparsely vegetated coastal dunes to relatively complex communities in the east (Robinson, 1976). The abundance and distribution of various arthropod species, particularly tenebrionid beetles, varies similarly across the Namib dune sea (pers. obs.).

Changes in the distribution and abundance of ant species along environmental gradients have been documented in a variety of non-desert habitats (Sanders, 1970; Brian, 1979; Boomsma & De Vries, 1980) and along an altitudinal gradient in the Mojave Desert (Bernstein, 1974) and on the gravel plains of the central Namib Desert (Marsh, 1986). In all of these studies changes in the density of the various ant species were correlated with climatic and/or physical differences.

In view of the steepness of the environmental gradient, particularly the climate, across the dune sea of the central Namib, an influence of this gradient upon the dune biota is predicted. Here we examine the possible effects of the abiotic and biotic components of this gradient on the distribution and abundance of *C. detritus*.

Materials and methods

Nest density, size and distribution were determined at six sites across the central Namib dunes (Fig. 1). The ant nests were found to be irregularly distributed because of the patchy distribution of the perennial dune plants. Consequently, at each site the numbers of nests were counted in 10 elongated 1 ha quadrats (2 km by 5 m) running parallel with the dunes on the lower, mid and upper slope. The position of each nest on the dune and the species of plant below which the nest occurred were noted. The number of plants in each quadrat

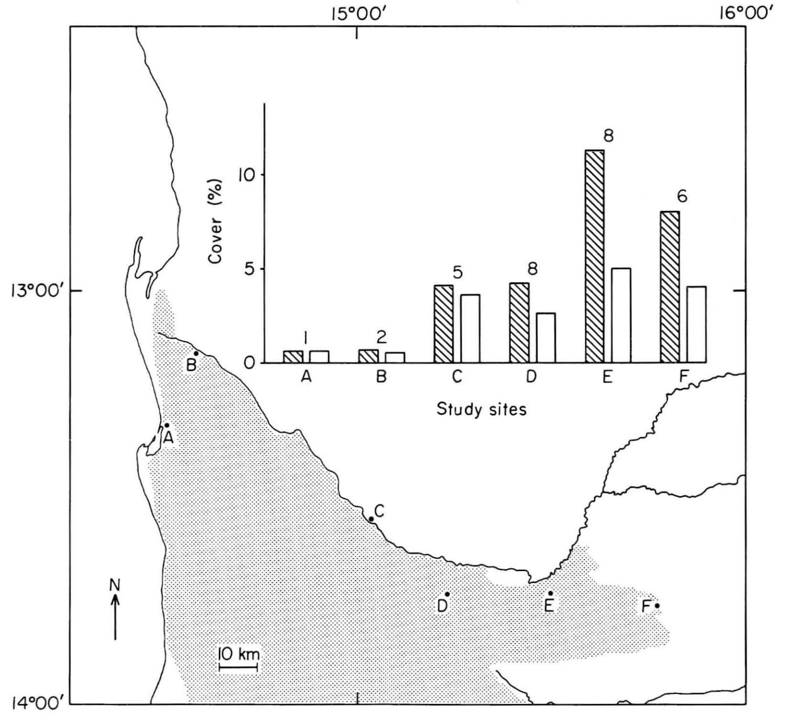

Figure 1. Map of the central Namib dunes (stippled area) with six study sites indicated. Histograms indicate the percent plant cover at each site (left bar, total plant cover; right bar, cover of plants supporting scale insects). The value above the bars indicates the number of plant species at each site.

which had *C. detritus* or any other ant species tending scale insects, was also recorded. The Kruskal–Wallis statistic (H) for several independent samples was calculated to test for differences between the numbers of nests at the various sites, followed by a multiple comparisons procedure to determine which pairs of samples differed (Conover, 1980). Nest dispersion was determined using the variance/mean ratio (Southwood, 1978) of the number of nests in the 10 quadrats at each site.

Four to six nests were excavated at each site to determine the number of ants per nest. Excavation took place in the early morning when most workers were in the nest and relatively inactive. Ants and nest material were shovelled rapidly into sieves (2-mm mesh), the sand was shaken out and the ants, brood and debris were placed in plastic buckets. Ants were later extricated from the debris and counted. Differences between numbers of ants per nest at the various sites, as well as between the numbers of ants per nest under the various plant species, were examined using Kruskal–Wallis tests.

The correspondence of the density of *C. detritus* nests with climatic variables across the environmental gradient was examined using pairwise correlation between nest density and individual climatic factors (Sokal & Rohlf, 1981). The following variables were examined: mean annual temperature, mean annual humidity, amplitude in temperature and humidity, fog and rainfall. Climatic data were obtained from Lancaster, Lancaster *et al.* (1984).

Vegetative cover was determined in each area from line intercept transects varying in total length between 2,000 and 6,000 m. Only plants with green shoots were included. The total cover of plants hosting scale insects was estimated for each site by adding the total cover of the three commonly infested species (*Trianthema hereroensis*, *Stipagrostis sabulicola* and *S.* cf. *namaquensis*) to a proportion (50% of *Cladoraphis spinosa* and 20% of *S. lutescens*) of the cover of the less commonly infested species. The relationship between the proportion of nests under different plant species and the relative abundance of the plant species at four of the six sites, was examined using Spearman rank correlation.

Estimates of the numbers of the scale insect, *Aclerda namibensis*, per plant at sites C–F were 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.

Results and discussion

C. detritus nest densities differed significantly between sites ($H = 27{\cdot}5$, d.f. $= 5$, $p < 0{\cdot}05$), being lowest in the west, highest in the central region and intermediate in the east. The multiple comparisons procedure showed that differences between nine of the sample pairs were significant at $p < 0{\cdot}05$ (Fig. 2*a*).

Great variability was found in the number of workers per nest at each site (Table 1) and in the number of workers per nest below each plant species (Table 2). No significant differences in the number of workers per nest were apparent, however, either between sites ($H = 10{\cdot}074$, d.f. $= 5$, $p > 0{\cdot}05$) or between plant species ($H = 13{\cdot}237$, d.f. $= 7$, $p > 0{\cdot}05$).

Several possible explanations for the variation in the density of nests across the Namib dune sea were considered. These included climatic factors, characteristics of plant distributions or abundance related either to potential nest sites or food availability, the distribution or abundance of scale insects, and the variation of potential biotic interactions between sites.

Abiotic factors

None of the individual climatic factors (Fig. 2) was found to be correlated significantly with nest density ($p > 0{\cdot}05$). Inspection of the values suggests, however, that nest density

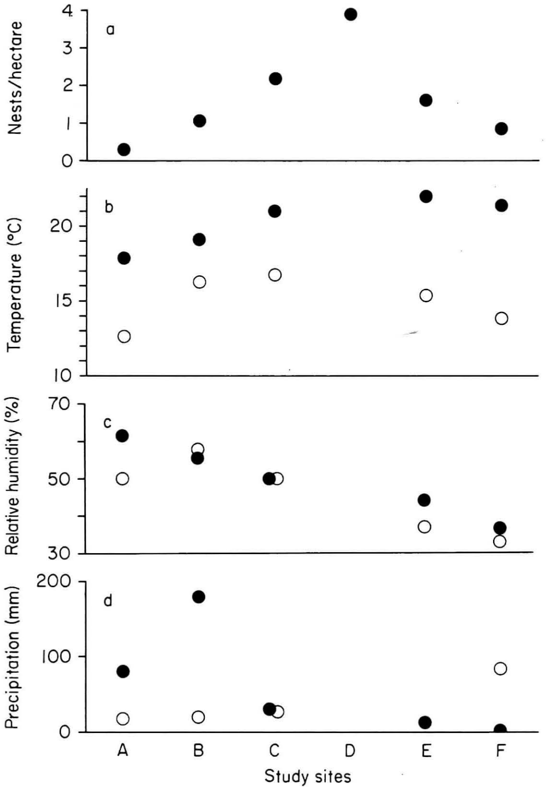

Figure 2. (*a*) Nest densities of *Camponotus detritus* across the central Namib ($n = 10$ for each site). Significant differences ($p < 0{\cdot}05$, multiple comparison test): A:C, A:D, A:E, B:C, B:D, B:E, C:F, D:E, D:F. (*b*) Mean temperature (●) and amplitude (○) across the central Namib. (*c*) Mean humidity (●) and amplitude (○). (*d*) Mean fog water precipitation (●) and rain (○).

does vary in a manner somewhat similar to that of mean annual temperature and mean temperature amplitude (Fig. 2*b*). These parameters apparently do not govern ant distributions and densities but they may well have a limited influence, since they affect three aspects of the ants' life history. Activity of *C. detritus* is controlled primarily by temperature (Curtis, 1985*b*). Near the coast (site A), where ant density is lowest, the workers forage only during the day whereas further inland, they tend scale insects over 24 hours, thus bringing more food back to the nest. Temperature is known to affect the rate of brood development of ant species (Wheeler, 1910; Wilson, 1971). Therefore, it is possible that the lower mean temperatures at site A might lead to a lower rate of brood production and contribute to the low densities of *C. detritus* found there. Various environmental variables, including temperature, 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 site A, where lower mean temperatures occurred, low production of honeydew may have led to the lack of nocturnal foraging. In the Mojave desert, Bernstein (1974) found a species-specific response to soil surface temperatures in the foraging of three harvester ant species along an altitudinal environmental gradient.

Neither humidity (Fig. 2*c*) nor rain and fog (Fig. 2*d*) values varied in a manner similar to those of nest density. The increase in rainfall from west to east results in an increase in the number of plant species and in vegetation cover in the eastern part of the central Namib dunes (Fig. 1).

Table 1. *Mean number of* Camponotus detritus *workers per nest (nest size) across the central Namib dune sea* (n, *number of nests excavated)*

Site	Mean	Standard error	*n*
A	728	305	5
B	3,344	1,100	4
C	5,076	2,700	5
D	4,231	1,217	6
E	3,986	861	6
F	3,926	1,002	6

Table 2. *Mean number of* Camponotus detritus *workers per nest constructed under various plant species* (n, *number of nests excavated)*

Plant species	Mean	Standard error	*n*
Trianthema hereroensis	1,922	537	11
Centropodia glauca	2,364	287	9
Stipagrostis lutescens	3,940	1,212	6
Stipagrostis sabulicola	6,707	3,125	4
Cladoraphis spinosa	4,862	699	3
Other species	5,025	2,360	3

Biotic factors

In this study *C. detritus* nests were found under eight species of perennial dune plants. The distribution of these eight species varied across the dune sea, with only one species, *S. sabulicola*, occurring at all six sites although it was not encountered on transects at all sites. At site A, in the west, only one plant species, *T. hereroensis*, was encountered, under which all ant nests were found. At site B 71% of the plants encountered were *T. hereroensis* and all of the nests were found beneath this species. At the other four sites, the number of ant nests found beneath a species of plant was also not directly proportional to that plant's relative abundance in the community ($p > 0{\cdot}05$) (Fig. 3). Thus, more than simply plant

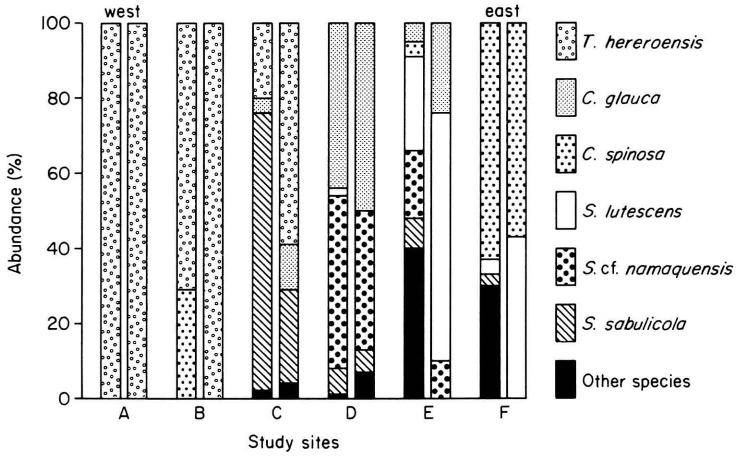

Figure 3. Relative abundance of seven plant species (left bar) and of plants with *C. detritus* nests (right bar) at the six study sites.

species distribution patterns appear to determine the location of *C. detritus* nests. The density of *C. detritus* nests also did not vary directly with the number of plant species or with the percentage vegetation cover across the Namib dunes, although the trend is in the same direction (Figs 1 and 2).

C. detritus was somewhat selective in its choice of nest plants (Fig. 3) but the availability of potential nest plants appeared not to be a limiting factor, since at each study site less than 10% of suitable nest plants were occupied. This is in contrast to *Camponotus herculeanus* and *C. noveboracensis* colonies studied by Sanders (1970), where nest sites were limiting.

At five of the six sites an index of nest clumping (the variance/mean ratio; Southwood, 1978) was greater than 1·0, suggesting a contagious dispersion of nests. However, only at site B was this ratio statistically different from 1·0 ($I_D = 37{\cdot}5$, d.f. $= 9$, $p < 0{\cdot}005$).

A large proportion of nests at the three eastern study sites was found below the most abundant plant species occurring in that area, but the distribution of nests did not correspond entirely with the relative abundance of each plant species (Fig. 3). Neither did proximity to food sources appear to have a dominant influence on the location of nests. *S.* cf. *namaquensis* and *S. sabulicola* host the majority of scale insects and yet most nests were under *Centropodia glauca*, which does not host scale insects, or *S. lutescens* and *C. spinosa*, which have minor infestations. One possible reason that *S.* cf. *namaquensis* and *S. sabulicola* are not used much for nesting east of site D, is that although they are within the foraging ranges of *C. detritus*, these species grow on the upper dune slopes and are not surrounded by the large mounds of relatively stable sand found under *S. sabulicola* at site C. *C. glauca* does not create mounds either, but its roots form a closely packed network on the lower dune slopes in which the ants can construct their galleries. As a result, *C. detritus* territories in the east were often long and narrow, since the ants were frequently found to nest under plants living on the lower and mid slopes and collect honeydew from plants occurring on the mid and upper slopes.

Sand grain size may also influence the choice of nest site, as Boomsma & De Vries (1980) found, although this parameter does not vary widely across the dune sea. Grain size increases lower down the dune slope (Robinson & Seely, 1980), and this may cause the ants to nest under those species, such as *C. glauca* and *S. lutescens*, which occur lower on the dune. Soil moisture, however, also increases with the increase in grain size lower down the dune slope (Louw & Seely, 1980), and may have an equally important effect in nest site selection. In the west a further possible advantage provided by *T. hereroensis*, the favoured nest plant, is the environment beneath this plant which is more moist than that found beneath *S. sabulicola* (Seely, de Vos *et al.*, 1977).

The abundance of food (i.e. scale insects) for *C. detritus*, was observed to be related to the distribution of plant species and their abundance. At sites B and C, for example, *T. hereroensis* plants were favoured nest sites (Fig. 3). This could be because the degree of scale insect infestation on *T. hereroensis*, although not extensive, appeared to be higher than on the other scale-supporting species present, *S. sabulicola*, possibly as a result of the higher moisture content of *T. hereroensis* (Louw & Seely, 1980). Apart from being a host plant for the scale insects and therefore, indirectly, a source of honeydew, *T. hereroensis* flowers also provide nectar for the ants (Curtis, 1985*b*). The patchy distribution of *T. hereroensis*, in turn, may account for the patchy distribution of ants at the western sites.

At the three eastern study sites, *S. sabulicola* and *S.* cf. *namaquensis* host the majority of scale insects whereas *S. lutescens* and *C. spinosa* support very minor infestations. *S.* cf. *namaquensis* is absent from the easternmost site and the percentage cover of other plant species hosting scale insects also decreases at site F, implying that food may be limiting *C. detritus* at the easternmost sites.

The factor thought to have the most important direct influence on *C. detritus* is the abundance of scale insects and the quality and quantity of honeydew produced, irrespective of the host plant species. No detailed study has been made of the abundance of the scale insects but Table 3 shows preliminary estimates of the degree of infestation of *S.*

Table 3. *Estimates of the degree of infestation of* Stipagrostis sabulicola *and* S. *cf.* namaquensis *by the scale insect,* Aclerda namibensis

	Site			
	C	D	E	F
S. sabulicola				
Plants infested (%)	9	34	44	97
Mean number of stems/plant ($n = 10$)	91·6 ± 80·7	54·8 ± 35·0	62·4 ± 31·4	76·8 ± 52·4
Mean number of nodes/stem ($n = 30$)	3·1 ± 1.9	3·9 ± 1·1	6·0 ± 2·0	4·9 ± 1·4
Mean number of scales/node ($n = 30$)	5·25 ± 2·3	4·0 ± 1·2	3·1 ± 1·3	3·9 ± 1·8
Estimated number of scale insects/hectare	7,400	2,200	5,900	13,500
S. cf. *namaquensis*				
Plants infested (%)	—	95	47	—
Mean number of stems/plant ($n = 10$)		39·5 ± 13·6	66·7 ± 4·4	—
Mean number of nodes/stem ($n = 30$)	—	5·3 ± 2·0	6·0 ± 2·3	—
Mean number of scales/node ($n = 30$)	—	2·45 ± 0·8	2·45 ± 1·1	—
Estimated number of scale insects/hectare		22,600	12,700	—
Total scale insects/hectare	7,400	24,800	18,500	13,500

Values expressed as mean ± standard error.

Aclerda

sabulicola and *S.* cf. *namaquensis* by *A. namibensis*. The estimated density of these scale insects was highest at site D, decreasing towards the west and east, a pattern similar to that of *C. detritus* density.

At sites A and B, where *C. detritus* density was lowest, *A. namibensis* was absent and the degree of infestation by other scale insect species of *T. hereroensis* was minimal. At site A, only 4% of the plants were visibly infested with a scale insect of the family Margarodidae. These scale insects were never found in large aggregations. At site C, about 20% of the *T. hereroensis* plants were infested with *Eriococcus* sp., a sessile species which forms thick clusters around the stems. This comparatively extensive infestation, combined with the presence of *A. namibensis* on *S. sabulicola*, probably accounts for the higher density of *C. detritus* at site C than in the west.

Competition and predation may also be partly responsible for the reduction in abundance of *C. detritus* east of site C. From site D eastwards a second species of honeydew-collecting ant, *Crematogaster* sp., was found. This species appeared to collect honeydew only from the scale insects *Membranaria* sp., associated with galls on *S.* cf. *namaquensis*, and from two species of *Trionymus*. *C. detritus* also tended these species but was not found when *Crematogaster* was present. *C. detritus* was observed primarily tending *A. namibensis*, which *Crematogaster* did not use, and, since the estimates of *A. namibensis* abundance reflect the pattern of *C. detritus* density, it was thought to be unlikely that *Crematogaster* limits *C. detritus* through interference competition.

C. detritus appeared to have few predators from site C westwards but from site D eastwards the ant-mimicking spider, *Cosmophasis* sp., was seen preying on foraging *C. detritus* workers (Curtis, 1983). The density of potential reptilian and avian predators also increases east of site D (pers. obs.).

Thus, a number of factors may influence the distribution and abundance of *C. detritus* nests across the environmental gradient of the central Namib dunes, although the present study does not allow statistical confirmation of these possible relationships. Lower temperatures in the west may affect nest density directly through their effect on ant behaviour and growth, and indirectly through their effect on the scale insects. Neither the distribution nor the abundance of dune plants appears directly to limit ant abundance, although the distribution and abundance of scale insects living on the plants may have an effect. The clumped distribution of ant nests appears to be related primarily to edaphic factors prevailing at each site. Community interactions may also influence the abundance of *C. detritus* in the eastern part of its range.

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