The foraging ecology of two Namib Desert harvester ant species

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Forager abundance, activity, dispersion and diet of *Messor denticomis* and *Tetramorium rufescens* was studied on a monthly basis for 17 months. There were large fluctuations in forager abundance with both species exhibiting similar patterns; the first peak in abundance occurring five months after a peak in food availability and the second peak in abundance coinciding with a second, smaller pulse of food. Food supplementation experiments demonstrated that availability of food partially regulated the absolute numbers of ants foraging. Both species shared similar activity patterns with the majority of activity occurring at night. Foragers were randomly dispersed within the 16 ha study plot. Most of the food collected by both species was *Enneapogon brachystachyus* seeds. These seeds were collected during the first half of the study when seeds were apparently superabundant. With declining seed availability both species took more non-seed plant matter and arthropods. In both species, diet range fluctuated widely, reflecting opportunistic responses to food availability. Opportunism was particularly apparent when seeds were relatively scarce. Despite large interspecific differences in body size, the majority of food utilized was the same size for both species. The above patterns suggest that interspecific competition for food is not an important factor in the ecology of these ant species.

Die talrykheid, aktiwiteit, verspreiding en dieet van voersoekers van *Messor denticomis* en *Tetramorium rufescens* is maandeliks vir 17 maande bestudeer. Daar was groot fluktuasies in die talrykheid van voersoekers waarby altwee spesies gelyksoortige patrone getoon het; die eerste piek in talrykheid het vyf maande na 'n piek in voedselbeskikbaarheid voorgekom en die tweede piek in talrykheid het met 'n tweede, kleiner pols van voedsel ooreengekom. Altwee spesies het gelyksoortige aktiwiteitspatrone in gemeen en is hoofsaaklik snags aktief. Voersoekers was ewekansig versprei in die 16 ha-studieperseel. Altwee spesies het merendeels *Enneapogon brachystachyus*-sade as voedsel versamel. Hierdie sade is versamel tydens die eerste helfte van die studie toe sade blykbaar oorvloedig was. Met afnemende saadbeskikbaarheid het altwee spesies meer nie-saad-plantmateriaal en artropode benut. In altwee spesies het die omvang van die dieet wyd fluktueer wat opportunistiese gedrag ten opsigte van voedselbeskikbaarheid weerspieël. Opportunisme was veral duidelik wanneer sade betreklik skaars was. Voedselaanvullingseksperimente het gewys dat voedselbeskikbaarheid voersoekeraktiwiteit gedeeltelik reguleer. Ten spyte van groot interspesifieke verskille in liggaamsgrootte, was die meerderheid van die voedselsoorte ewe groot vir altwee spesies. Die bostaande patrone dui daarop dat interspesifieke kompetisie vir voedsel nie 'n belangrike faktor in die ekologie van die mierspesies is nie.

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Harvester ants are important components of desert ecosystems as they retrieve large quantities of seed produced after episodic rainfall and live off their stored seed reserves during dry periods when productivity is low. In the past decade there has been a surge of interest in harvester ant ecology in North American deserts and to a lesser extent in the arid and semi-arid regions of Australia (reviewed by Brown, Reichman & Davidson 1979). In contrast, harvester ants have received scant attention in the deserts of southern Africa; the only published data on foraging ecology being that of Marsh (1985). Probably the most important environmental difference between the Namib Desert and the arid regions of North America and Australia concerns productivity; on average, productivity is lower and exhibits larger fluctuations in the Namib Desert. For example, most harvester ant studies in America and Australia have occurred in regions receiving 100 – 400 mm of rain per annum, where seed production occurs at least once a year (Brown *et al.* 1979). In contrast, mean annual rainfall in the most productive region of the central Namib Desert is less than 100 mm (Lancaster, Lancaster & Seely 1984) and seed production may not occur for two consecutive years (Louw & Seely 1982). In such a system, seeds are not as reliable a resource as they are in the North American and Australian arid zones. Differences in the reliability of the seed resource may have important consequences for the foraging ecology of harvester ants.

The present study concerns two harvester ant species from a 13 species ant assemblage in the Namib Desert. *Messor denticomis* Forel is a large polymorphic species (5,5 – 11,0 mm total length) whereas *Tetramorium rufescens* Stitz is medium sized (4,0 – 5,1 mm) and monomorphic. Together these species comprise 60% of the forager density of the ant assemblage and 90% of the forager biomass (Marsh 1985). Here, patterns in diet, food abundance, forager activity and spatial occurrence of these two species are documented.

Study site

The study was conducted on flat gravel plains 3 km from Ganab (28°08'S/15°37'E). Mean annual rainfall at Ganab is 87,2 ± 91,8 mm ($\bar{X}$ ± *SD*, range = 9,9 – 375,0 mm, N = 16 years) (Lancaster *et al.* 1984). Effective precipitation, i.e. sufficient to cause germination of annual plants is 17 – 20 mm (Seely 1978) and the longest recorded period without effective rainfall at Ganab is 22 months (Lancaster *et al.* 1984). Perennial grasses, which exist as dry, rooted stubble during drought can however, grow and set seed after 12 mm of rain (pers. obs.). The period during and just prior to the present study spanned extreme fluctuations in rainfall. In 1981, 30,0 mm of rain fell over a period of six months and was insufficient to cause seed set. In 1982, 97,2 mm was recorded and this resulted in the germination of annual plants, growth of perennial plants and seed set by both groups. No effective rain fell in 1983. During the first half of 1984, 15,8 mm of rain was recorded; 12,9 mm falling in March resulting in seed set by perennial grasses.

For most of the study there was no photosynthetically

active vegetation in the habitat. In May 1982, after heavy rains stimulated plant growth, a survey using the point quadrat technique (Greig-Smith 1964) revealed the presence of 14 plant species (n = 1 033 point strikes). Eight species were grasses and in terms of proportion by number, 86,9% of the plants comprised three grass species, *Stipagrostis ciliata* (43,8%), *S. uniplumis* (22,6%) and *Enneapogon brachystachyus* (20,5%).

Methods

Forager abundance and dispersion

Surface active foragers were censused once a month for 17 months from January 1983 to May 1984 inclusive in a 16-ha plot that was subdivided into 256 cells of 25 m × 25 m. An observer moved slowly within the plot on a pedal-powered vehicle (see Marsh 1985), averaging 170 ± 30 m h^{-1} (*SD*). The observer lay face-down upon a platform situated 40 cm above the substrate. All ants encountered within a 50 cm wide transect, demarcated by two antennae projecting from the front end of the moving vehicle, were collected. An odometer recorded the length of the transect. Each census was conducted for a minimum period of 24 consecutive hours with many running for 48 h e.g. January to July 1983 inclusive and November to December 1983 inclusive. A fluorescent lamp facilitated nocturnal observations. The location and direction of the transects were determined by consulting random number tables. The observer steered a straight course until the boundary of the plot was reached at which point a new randomly selected direction was adopted. Throughout each census, the location, at a resolution of 25 m × 25 m, and time when ants were encountered were recorded.

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

$$0 = \Sigma \, p_i p_j \, / \, \sqrt{\Sigma \, p_i^2 \, \Sigma \, p_j^2},$$

where p_i and p_j are the proportions of the ath time period used by the ith and jth species respectively. Overlap values can range from zero for completely different activity patterns to unity for identical activity patterns.

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

Dietary relationships and food availability

Once a month, for 18 months, food items were removed from ants returning to the nest. An effort was made to collect a minimum of 50 food items per species from a minimum of four nests. This was not always possible as activity levels became much lower after six months and remained low for the majority of the study period. Thus for certain months no, or very little, food was collected and in others the majority of food items were collected from one to two nests only. Because of the unpredictable nature of harvester ant activity it was also not possible to sample the same nests each month. The only feasible approach was to search for active nests and sample these. Each food item was assigned to one of six taxonomic categories; four devoted to various types of seed, one to non-seed plant matter and one to arthropod matter. Dietary niche breadths were calculated using the inverse of Simpson's (1949) diversity index:

$$B = 1/\Sigma \, p_i^2,$$

where p_i is the relative proportion of the ith food category in the sample. Values of B can range from 1, for a species that exclusively utilizes one food category, to 6 for a species that utilizes all six categories equally. Each food item was dried for three days at 70°C and weighed to the nearest 0,01 mg. Interspecific comparisons of food mass were performed on a monthly basis using the Mann-Whitney U test.

The availability of food in the environment was quantified at the same time that food items were collected from ants. Each month ten 900 cm^2 square quadrats were distributed at random within the 16 ha census plot and all matter lying on and approximately 1 – 3 mm below the soil surface was collected. Each sample was passed through a series of graded sieves and all items known to be taken by ants were noted.

During October 1983, when forager activity levels had been depressed for several months, a food supplementation experiment was performed to test the hypothesis that the low levels of activity were partly attributable to reduced food availability. Twenty nests of each species were marked and randomly placed into two groups of 10 nests per species. The level of forager activity of each nest was estimated by counting the number of ants in a 1-m^2 quadrat which included the nest entrance. Activity counts were made between 20h00 and 21h00 for *M. denticornis* and between 07h00 and 08h00 for *T. rufescens*, periods in the diel cycle when levels of activity were high. Three activity counts, each count separated by 15 – 20 min, were made at each nest and the largest value was taken as the activity count for that nest. Maize granules were then broadcast, at a density of 100 granules m^{-2}, within a 10-m radius of 10 nests of *T. rufescens* and *M. denticornis* and activity levels of the 20 treated and 20 untreated nests were estimated 24 h later. The results were subjected to a two-way analysis of variance (Sokal & Rohlf 1981).

Results

Forager abundance and dispersion

Tetramorium rufescens was more abundant than *M. denticornis* for the majority of censuses (Figure 1). There were large fluctuations in forager density; both species exhibiting similar patterns of change. Density peaked in April in both years and thereafter decreased markedly. Forager density was relatively high during five months in the first year and for one to two months in the second year. Ant abundance was greater during the summer of 1982/83 than during the following summer.

M. denticornis and *T. rufescens* had similar diel activity patterns (Figure 2). *T. rufescens* was more diurnal than *M. denticornis* although the majority of foraging by both species occurred at night. Activity appeared to fluctuate from hour
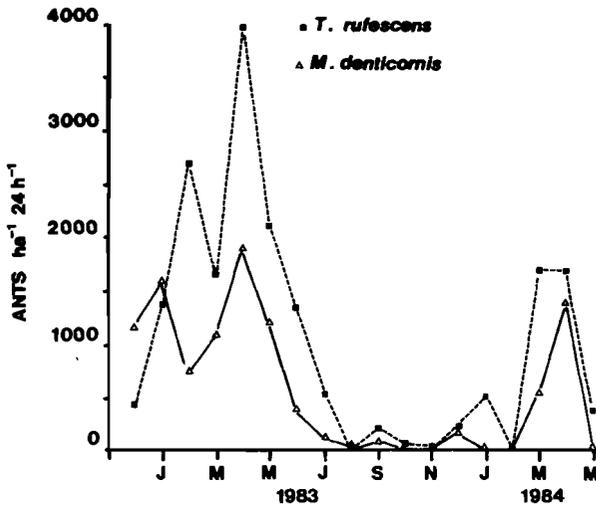
Figure 1 Temporal changes in forager density, expressed as the number of foragers encountered per hectare per day.
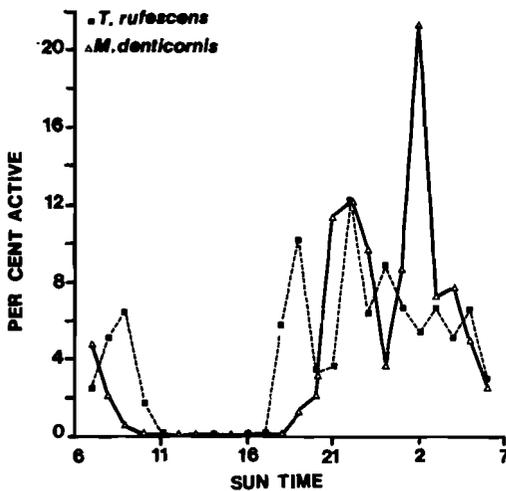

Figure 2 Diel activity patterns of *M. denticornis* and *T. rufescens*. Data are expressed as a proportion of total activity occurring over a 24-h cycle. There is considerable interspecific overlap in activity; overlap value = 0,71.

to hour but this may reflect a sampling artefact in that each sample is pooled across several days thus introducing variation from microclimatic and dispersion differences.

Of the 256 cells measuring 25 m × 25 m, 241 were sampled during periods when both species were active on the study plot. Of these 241 cells, 207 contained at least one species. No significant spatial association between the two species was apparent at this resolution ($p > 0,05$). At a resolution of 50 m × 50 m *M. denticornis* foragers occurred in 53 of 64 cells and *T. rufescens* foragers occurred in 56 of 64 cells. Thus *M. denticornis* occurred in 13,25 ha of 16 ha and *T. rufescens* occurred in 14 of 16 ha. The two species were sympatric in 45 cells, equivalent to 11,25 ha. Variance/mean ratios for both species were close to unity (*M. denticornis* = 0,94; *T. rufescens* = 0,83) and the distribution of foraging ants did not deviate significantly from random ($p > 0,05$).

Dietary relationships and food availability

For both species approximately 50 or more food items were collected for 14 months, 12 of them consecutive months (Tables 1 & 2). Activity levels and foraging success were

Table 1 Proportion of different seed categories in the diet of *Tetramorium rufescens*. The data are expressed as a percentage of *N*, the number of food items collected each month

| Year | Month | *N* | Enneapogon[a] | | *Stipagrostis* | Dicot. |
			Aerial	Basal		
1982	Jan	97	0	4,1	15,5	12,4
1982	Jun	57	86,0	0	1,8	0
1982	Aug	128	73,4	0	3,2	10,9
1982	Sep	49	73,5	0	8,2	4,0
1982	Oct	50	60,0	2,0	4,0	4,0
1982	Nov	50	54,0	0	6,0	6,0
1982	Dec	52	53,8	0	1,9	5,8
1983	Jan	54	68,5	0	1,9	0
1983	Feb	51	49,0	0	2,0	17,6
1983	Mar	50	18,0	0	14,0	4,0
1983	Apr	52	2,0	0	5,7	0
1983	May	50	0	0	0	0
1983	Jun	47	2,1	0	0	27,7
1983	Jul	50	0	4,0	20,0	24,0
1983	Aug	28	0	25,0	21,4	7,1
1983	Sep	53	0	0	1,9	0
1983	Oct	28	0	0	21,4	3,6
1984	Mar	51	2,0	0	2,0	2,0
1984	May	50	0	2,0	32,0	4,0

[a]See text for explanation of the terms aerial and basal *Enneapogon* seed

Table 2 Proportion of different seeds in the diet of *Messor denticornis*. The data are expressed as a percentage of *N*, the number of food items collected each month

| Year | Month | *N* | Enneapogon[a] | | *Stipagrostis* | Dicot. |
			Aerial	Basal		
1982	Jan	91	0	18,7	19,8	8,8
1982	Jun	86	40,7	0	47,7	0
1982	Aug	79	92,4	0	5,1	2,5
1982	Sep	51	92,2	2,0	3,9	0
1982	Oct	50	88,0	4,0	0	0
1982	Nov	50	90,0	6,0	0	0
1982	Dec	56	78,6	7,1	3,6	0
1983	Jan	50	86,0	12,0	2,0	0
1983	Feb	50	36,0	30,0	16,0	2,0
1983	Mar	50	48,0	24,0	12,0	0
1983	Apr	48	12,5	33,3	6,3	4,2
1983	May	51	13,7	15,7	7,8	29,4
1983	Jun	35	5,7	22,8	2,9	0
1983	Jul	51	3,9	23,5	9,8	0
1983	Aug	4	0	50,0	0	0
1983	Sep	50	0	40,0	0	0
1983	Oct	50	2,0	24,0	2,0	2,0
1984	Mar	40	7,5	2,5	2,5	7,5
1984	May	50	2,0	4,0	56,0	6,0

[a]See text for explanation of the terms aerial and basal *Enneapogon* seed

very low in August 1983 and between November 1983 and February 1984 inclusive and little or no food could be collected for these periods. *M. denticornis* consistently collected more seeds than *T. rufescens* (Figure 3). Both species, however, primarily collected seeds for the first 13 months and thereafter the amount of seeds in the diet declined considerably. Seeds only again became relatively common in the diet of both species in May 1984.
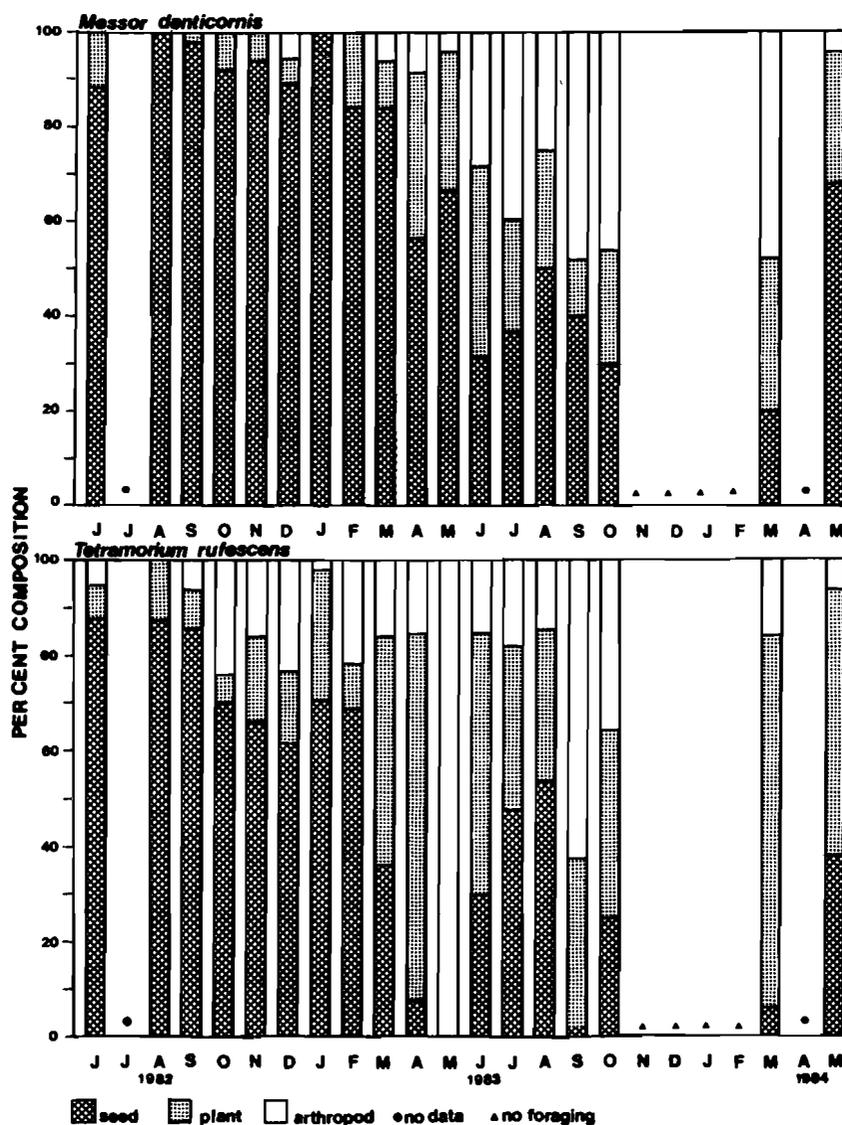
Figure 3 Composition of forage of *M. denticornis* and *T. rufescens*. Data are expressed as a per cent of the number of items taken from returning ants each month.

The majority of seeds collected by both ants were *Enneapogon brachystachyus* (Tables 1 & 2). This species of grass produces two types of seed, 'aerial seeds' which are borne at the distal portion of the plant and 'basal seeds' which are located at ground level. Each basal seed was enclosed within a hard woody capsule and was typically collected in clusters of up to ten seeds attached to a piece of grass stem. The entire food item was therefore large relative to the aerial seeds which occurred as discrete individuals surrounded by a light feathery capsule and which were collected individually by the ants. Before the relatively heavy rains of 1982, and hence before new seed had been introduced into the environment, no aerial *Enneapogon* seed occurred in the diet of either ant species but basal *Enneapogon* seed, various other grass seeds (particularly *Stipagrostis* spp.) and unidentified dicotyledon seeds were taken. For several months from June 1982 onwards, after the rains, aerial *Enneapogon* seeds were prominent in the diets of both species. From February 1983, when aerial *Enneapogon* seeds started becoming less prominent in their diets *M. denticornis* started taking progressively more basal *Enneapogon* seeds, whereas, with the exception of the August 1983 sample, *T. rufescens* took very little basal *Enneapogon* seed. The presence of other seed types in the diets of both species fluctuated greatly from month to month.

Dietary shifts in *M. denticornis* were more consistent than those in *T. rufescens*. In *M. denticornis*, the amount of arthropod matter in the diet increased progressively as the proportion of seeds declined. In contrast, although arthropods were consistently more abundant in the diet of *T. rufescens*, the contribution that arthropods made to its diet varied considerably from month to month (Figure 3). For example, arthropods made up 15% of the diet in April and June 1983 and 100% in May 1983.

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

The majority of arthropods collected were termites. These were occasionally taken alive but most were dead on arrival at the nest and were frequently very dry and dismembered indicating that they had been scavenged. Large *Hodotermes* sp. (dry mass per individual 2,0 – 5,0 mg) were primarily taken by *M. denticornis* and comprised the majority of the arthropod fraction of the diet in September and October 1983 and March 1984. Smaller *Trinervitermes* sp. (dry mass per indivi-

dual 0,7 − 1,5 mg) were frequently taken by *T. rufescens* and made up the entire diet sample in May 1983. *T. rufescens* also collected *Hodotermes* sp. on occasion and the arthropod component of the diet in September 1983 was made up almost exclusively by this species of termite.

The diet range of *T. rufescens* fluctuated markedly from month to month with no apparent order to the pattern, whereas, although the diet range of *M. denticornis* varied widely, the pattern of change was less random (Figure 4). For example, diet range in *M. denticornis* remained consistently low for six consecutive months, August 1982 to January 1983.
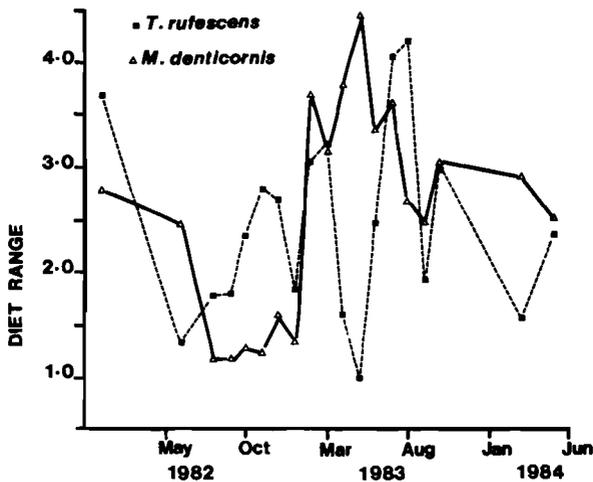

Figure 4 Temporal changes in the diet range of *M. denticornis* and *T. rufescens*.

Thereafter the diet range increased and remained relatively high for the remainder of the study period. Diet range in both species fluctuated more when seeds did not form a major dietary component. *M. denticornis* collected significantly larger food items than *T. rufescens* for the majority of sample months (Table 3) and a combined probability test (Sokal & Rohlf 1981) revealed that over the entire study period this relationship was significant ($p < 0,001$). During the period June 1982 to January 1983, however, when aerial *Enneapogon* seeds were common dietary components for both species, food particle size did not differ between the species except for August 1982 when *M. denticornis* took significantly smaller items than *T. rufescens*.

Adding food to the environment resulted in an increase of forager activity in both species (Table 4). There were significantly increased levels of activity in all nests that received additional food relative to activity levels in the same nests 24 h previously (ANOVA, df 1 36; $F = 10,087$; $p < 0,005$) and relative to unmanipulated control nests assessed on the same day (ANOVA, df 1 36; $F = 25,675$; $p < 0,001$). Pre-treatment control and experimental nests supported the same levels of activity dependent on species (ANOVA, df 1 36; $F = 0,388$; $p > 0,5$) whereas control groups showed a significant decrease in activity level from Day 1 to Day 2 (ANOVA, df 1 36; $F = 4,608$; $p < 0,05$). Thus the response to food supplementation was probably even more pronounced than that indicated in Table 4. *M. denticornis* nests supported higher levels of activity than *T. rufescens* nests in all treatment groups (ANOVA, df 1 36; $F = 24,848$; $p < 0,001$).

Food availability varied considerably during the study

Table 3 Monthly dry masses of food particles for *M. denticornis* and *T. rufescens* (levels of significance determined by Mann-Whitney *U* test)

Year	Month	\bar{X}	± SE	N	\bar{X}	± SE	N	P
			M. denticornis			*T. rufescens*		
1982	Jun	0,40	0,03	86	0,33	0,03	57	NS
1982	Aug	0,32	0,02	81	0,36	0,03	129	0,001
1982	Sep	0,36	0,05	52	0,31	0,31	48	NS
1982	Oct	0,52	0,14	50	0,50	0,07	50	NS
1982	Nov	1,24	0,48	50	0,35	0,05	48	NS
1982	Dec	1,28	0,55	54	0,41	0,06	49	NS
1983	Jan	1,04	0,32	50	0,42	0,06	54	NS
1983	Feb	1,73	0,38	50	0,42	0,12	50	0,001
1983	Mar	2,64	0,67	50	0,53	0,07	50	0,02
1983	Apr	3,26	0,51	45	0,37	0,07	46	0,001
1983	May	1,92	0,53	46	0,91	0,47	50	0,01
1983	Jun	1,96	0,64	33	1,20	0,98	46	NS
1983	Jul	2,59	0,56	44	0,75	0,10	43	0,001
1983	Aug	no data			0,81	0,12	27	−
1983	Sep	3,07	0,49	50	1,13	0,11	44	0,001
1983	Oct	2,49	0,49	50	0,43	0,06	26	0,001
1984	Mar	2,21	0,86	41	0,37	0,05	51	0,001

Table 4 Means and standard errors of the numbers of ants from control nests (unmanipulated throughout) and experimental nests (food added to environment after activity counts of Day 1) $N = 10$ nests per species per treatment group

	Species			
	T. rufescens		*M. denticornis*	
	\bar{X}	SE	\bar{X}	SE
Control				
Day 1	4,4	0,9	17,1	4,8
Day 2	2,1	0,5	6,4	3,5
Experimental				
Day 1	4,5	0,7	20,6	3,0
Day 2	14,8	2,8	36,5	7,1

period (Figure 5). Food abundance increased for the first few months, peaked in November 1982 and thereafter declined rapidly. For 15 consecutive months levels of food abundance were very low, finally showing a slight increase in May 1984. The large standard errors about each mean reflect the variability in food particle dispersion.

Discussion

The two species exhibited very similar patterns of activity during the study period, suggesting similar responses to the same environmental factors. One factor that could affect activity levels is food availability. In the present study, when food was scarce activity was depressed but could be enhanced by artificially increasing food abundance (Table 4, Figures 1 & 5). A correlation between food availability and activity has also been documented for harvester ants in North American deserts (Whitford & Ettershank 1975; Whitford, Depree & Johnson 1980) and in a semi-arid region in Australia (Briese & Macauley 1980).

Forager activity did not track food availability closely for most of the study. For example, activity peaked five months
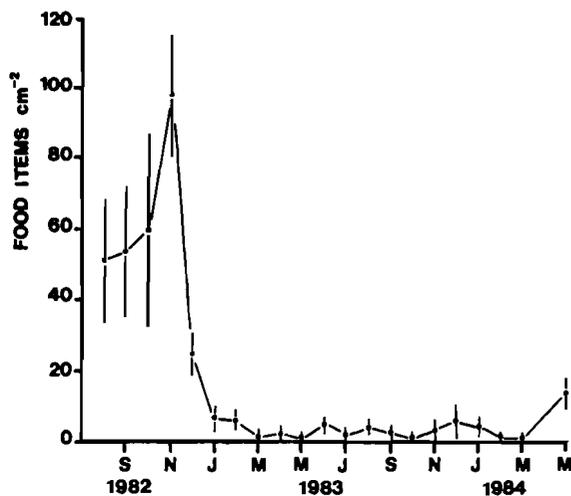
Figure 5 Temporal changes in environmental food density, expressed as one standard error about the mean.

after food availability had peaked; occurring at a time when food levels were already substantially reduced. The delay in the peak of ant activity probably reflects the time lag between the collection of food and a resultant increase in the ant population. It thus appears that food was superabundant for several months following seed set and that the ants collected and stored the major portion of food during this period. A similar situation has been noted for North American harvester ants (Whitford 1978).

Once the granaries of colonies are replete the pressure to forage should relax. Food retrieved during the period of environmental food scarcity would supplement the diet and retard the rate of seed store depletion but may not be essential to survival. At least for *M. denticornis*, although seed stores must have been reduced, they were not depleted during the study period. Colonies of *M. denticornis* are polydomous (pers. obs.) and throughout the study, even after 20 months without effective rain, surface active ants were seen carrying food between nests; although this internest traffic of food was not analysed quantitatively the observations indicated that aerial *Enneapogon* seeds predominated in the food stores. The observations that food appears to be superabundant imply that interspecific competition for food is unlikely between Namib Desert harvester ants.

Although harvester ants are considered by some biologists to be food specialists (e.g. Brown *et al.* 1979; Petal 1978), dietary flexibility, reflecting the opportunistic character of a generalist have been noted for many species. Whitford (1978) reviewed information on the forage of North American ants and indicated that numerous genera, including *Veromessor* (synonomized with *Messor* by Bolton 1982), prey heavily upon termites when they are present on the surface; termites constituting up to 50% of the forage during such circumstances. Furthermore, *Novomessor* and *Veromessor* regularly take up to 50% non-seed matter, including stems, leaves, floral parts, faecal matter and exoskeletons. In the Namib Desert, *M. denticornis* and *T. rufescens* exhibit similar but more extreme dietary flexibility. Of the two species *T. rufescens* is the least specialized; the apparently random fluctuations in its diet range reflecting opportunistic foraging behaviour. In contrast, *M. denticornis* exhibited more stable dietary patterns, continuing to collect considerable amounts of seeds long after seeds had become rare in the diet of *T. rufescens*. These patterns may be due to two factors. First, the data suggest

a better efficiency at locating seeds in *M. denticornis*; this may be related to its larger size, larger foraging range (unpubl. data) and hence increased probability of locating rich seed patches. Secondly, the patterns are largely due to the differential use of basal seeds by the two species and it is possible that basal seeds are less attractive to *T. rufescens* than to *M. denticornis*. The absence of data on food preferences prevents a more definite conclusion being reached.

In North American harvester ant assemblages, patterns of diet, dispersion, activity and body size are consistent with the notion that interspecific competition plays an important role in determining assemblage structure (see review by Brown *et al.* 1979). The Namib Desert harvester ant patterns are not, however, readily reconciled with competition theory. Despite large interspecific differences in body size there was a high degree of overlap in diet, particularly during the most important foraging period when storable seeds were available. When food was scarce both species responded opportunistically to transient resources, frequently taking identical prey types. No spatial segregation of foraging areas was apparent and both species were nocturnal. A less detailed study of dietary patterns in eight Namib Desert species, including *M. denticornis* and *T. rufescens*, supports the above data (Marsh 1985). The existence of patterns in North American harvester ant assemblages that are consistent with competition theory and the lack of clear-cut competitively determined patterns in the Namib Desert as well as the greater opportunism exhibited by Namib Desert ants is probably a reflection of differences in the seed resources; the Namib exhibiting greater uncertainty in terms of seed production and a lower diversity of seeds than the North American deserts.

Acknowledgements

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