

Forager abundance and dietary relationships in a Namib Desert ant community

A.C. Marsh

Desert Ecological Research Unit, SWA/Namibia and Department of Zoology, University of Cape Town, Cape Town

Thirteen ant species coexist on a barren gravel plain habitat in the central Namib Desert. Numerical density of foragers of all species fluctuated considerably over a 17-month period. Peaks in abundance correlated to rainfall events and hence primary production pulses. The majority of foragers were nocturnal in summer and diurnal in winter. The community was dominated in terms of species, forager abundance and biomass by myrmicine, seed-harvesting ants. There was considerable intra- and interspecific variation in diet through time and no consistent patterns were apparent. Diet niche breadth and overlap also exhibited considerable variation between species at any one time and within a species through time. There was no consistent relationship between ant size and the size of food particle utilized. Namib Desert ants are highly opportunistic and the lack of consistent patterns suggests that interspecific competition for food is not likely to be of major importance in this community.

S. Afr. J. Zool. 1985, 20: 197–203

Dertien spesies miere hou op dieselfde onvrugbare gruisvlakte in die sentrale Namibwoestyn. Die getalsterkte van die voerzoekers het oor 'n ondersoekperiode van 17 maande aanmerklik gewissel. Hoogtepunte in getaldigtheid het saamgeval met reënvalperiodes en dus die primêre voedselaanbod. Die meerderheid voerzoekers het in die somer snags voer gesoek en in die winter bedags. Die gemeenskap is met betrekking tot spesies, die getalsterkte van voerzoekers, en biomassa gedomineer deur myrmicine, saad-insamelende miere. Daar was 'n aanmerklike intra- en interspesievariasie in dieet met verloop van tyd, maar geen duidelike vaste patroon kon vasgestel word nie. Dieetnisbreedte en -oorvleueling vertoon aansienlike wisseling tussen spesies op 'n bepaalde tydstip of binne 'n spesie oor 'n periode van tyd. Daar was geen konsekwente verhouding tussen die grootte van die miere en die grootte van die kosdeeltjie wat gebruik is nie. Miere in die Namibwoestyn is baie opportunisties en die gebrek aan 'n konsekwente patroon dui daarop dat interspesie-mededinging om voedsel waarskynlik nie van groot belang is in hierdie gemeenskap nie.

S.-Afr. Tydskr. Dierk. 1985, 20: 197–203

A.C. Marsh

Present address: Department of Zoology, University of the Witwatersrand, 1 Jan Smuts Avenue, Johannesburg, 2001 Republic of South Africa

Received 14 May 1985; accepted 26 June 1985

Ants are major components of desert ecosystems (Pisarski 1978; Crawford 1981) yet there are few studies which have satisfactorily determined the relative abundances of species within any community. Various techniques have been used for obtaining relative abundance data but most rest on untested assumptions or disregard potentially important biases. Measures based on colony density (Briese & Macauley 1977; Whitford 1978a; Bernstein 1979) invariably lack details on colony size; counting ants visiting baits (Chew 1977; Davidson 1977; Morton 1982) assumes that bait is equally attractive to all species and introduces other potential sources of variation related to providing an unnaturally concentrated food source such as interference interactions and different foraging modes; pitfall trapping (Greenslade & Halliday 1983) assumes equal capture probabilities for all species and periodic hand collections (Greenslade & Halliday 1983) assume that collections coincide with similar activity phases of all species despite well-documented interspecific differences in diel activity patterns that occur in desert ant communities (Bernstein 1974; Whitford & Ettershank 1975; Briese & Macauley 1980; Whitford, Depree, Hamilton & Ettershank 1981). Furthermore, the structure of desert ant communities cannot be accurately assessed at one point in time (Chew 1977; Whitford 1978a) and therefore the value of some studies (e.g. Davidson 1977; Morton 1982) may be reduced.

With these limitations in mind, an attempt was made to quantify the relative abundances of ant species in a Namib Desert community. A study of the efficaciousness of pitfall trapping indicated that this technique would not provide reliable, biologically meaningful data (Marsh 1984). Similarly, quantitative colony excavations were not feasible owing to edaphic factors. Finally, a study of diel activity (Marsh 1985) revealed substantial interspecific differences in activity patterns with some species having very short periods when surface activity occurred. To overcome these difficulties, a technique involving continuous censusing of surface active foragers for a minimum of 24 consecutive hours was devised. This paper reports the results of such a study over a 17-month period. The trophic relationships of the most common species in the community were also documented. The following specific questions were posed: How robust is the structure of the forager community? How stable are the dietary relationships between species at any given time and within a species through time?

Study site

The study was conducted within a 16-ha plot on the gravel plains of the central Namib Desert near Ganab (28°08'S/

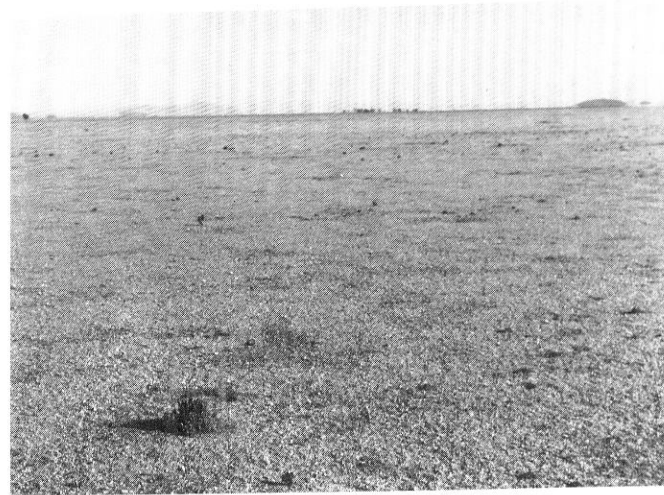


Figure 1 The study site in January 1984 showing small clusters of grass stubble.

15°37'E). For most of the study there was no photo-synthetically active vegetation in the habitat, the only indication of plant life being scattered clumps of grass stubble (Figure 1).

Two rainfall events occurred during the study period. In 1982, 97.2 mm fell in the area, most of it during March and April. This resulted in a flush of plant growth and production of seed. The majority of plant species were grasses (Marsh 1985). No effective rain fell in 1983 and 15.8 mm fell during the first half of 1984 with the majority in March. This resulted in plant growth and seed set. However, whereas perennial and annual grasses grew and set seed in 1982, only perennial grasses responded in 1984. The amount of vegetation was visibly less in 1984 and the numerical density of seeds of some of the dominant grass species was substantially lower (Marsh 1985).

Methods

The presence of ant species was determined using a variety of techniques. Ants were sampled at bait points using cheese, seed and sugar-water as baits, in pitfall traps using ethylene glycol as a preservative and during visual censuses. Representatives of all species were identified by B. Bolton of the British Museum (Natural History), London. The genus *Monomorium* is currently being revised and it is not possible to assign specific names to certain species. These species have been given alphabetical code names and reference specimens are lodged at the British Museum.

Monthly estimates of ant abundance were obtained during visual censuses of surface active foragers. Each census was conducted for 24 or 48 consecutive hours. Observers lay face-down on a pedal-powered vehicle (Figure 2) and collected all ants that were encountered between two antennae, placed 50 cm apart, attached to the vehicle. Transects were randomly orientated within the 16-ha plot and the length of each 24-h transect was measured on an odometer. A fluorescent lamp facilitated nocturnal observations. Censuses were conducted for 17 consecutive months between January 1983 and May 1984 inclusive. For each month the census data were expressed as the number of ants/ha that were encountered in a 24-h period. Biomass of foraging ants/ha/24 h was determined for each species by multiplying numerical density with mean dry mass of foragers. For polymorphic species, 100 foragers were collected at random, dried at 60 °C for 24 h and weighed.



Figure 2 Vehicle used to census foraging ants. Note the two antennae demarcating a 50 cm wide transect.

For monomorphic species 20 individuals were dried and weighed. The relative importance of each species was expressed in terms of numerical abundance and biomass. Kendall's coefficient of concordance (Siegel 1956) was used to test the degree of association between the 17 sets of species importance data.

Food items were collected from foragers returning to their nests in January and August 1982 and May 1984. These sample periods were selected because ants were moderately active then and assistance was available thus ensuring that samples could be collected for all species within a one-week period. Forage was taken from eight common species only. A minimum of four nests/species/collecting period was sampled. Food items were sorted into one of four categories: grass seed, dicotyledon seed, non-seed plant matter and arthropod.

Dietary niche breadths were calculated using the inverse of Simpson's (1949) diversity measure:

$$B = 1/\sum p_i^2$$

where p_i is the proportion of the i th food category in the sample. For these calculations three food categories were used: seed, non-seed plant matter and arthropod. Dietary niche breadth can range from one to three. Niche overlap between any two samples was calculated using Pianka's (1973) measure of similarity:

$$O = \frac{\sum p_i q_i}{\sqrt{\sum p_i^2 \sum q_i^2}}$$

where p_i is the proportion of the i th food item in one sample and q_i is the proportion of the i th food category in the second sample. Values of niche overlap range from zero to one. Kendall's coefficient of concordance (w) was calculated to test for the degree of association in rank order of species pair overlap values between the three samples.

The volume of each item of forage was estimated using the technique of Chew & De Vita (1980): The shape of the object was determined, most objects conforming to one, or a combination of two, of the following shapes: cylinder, truncated cone, sphere, triangular solid, rectangular solid. Critical dimensions of each object were then measured to 0.1 mm under a stereoscopic microscope and the volume calculated using geometric formulae. A Mann-Whitney U test was used to detect interspecific differences in food particle size. Dry body mass was regressed against food particle volume to determine whether there was a correlation between

body size and food particle size. Species were ranked according to mean size of food particle for each of the three sample periods and Kendall's coefficient of concordance (w) was calculated to test for the degree of association in species rank order.

Results

Community structure

Thirteen ant species, the majority myrmecines, were collected in the study area (Table 1). There was considerable inter-specific variation in body size. *Messor denticornis* and the two *Camponotus* species exhibited continuous size polymorphism, *Pheidole tenuinodis* was dimorphic with minor (TL 2.5–2.6 mm) and major workers (TL 4.5–4.9 mm) and the remaining species were monomorphic. *Monomorium* sp. D was found on one occasion only, it was restricted to a relatively large clump of grass stubble and was apparently not epigeal. The other species were epigeal. Eleven of these species were discovered before the census study began using a combination of bait and pitfall traps. *Tetramorium peringueyi* was only discovered during the census. The cumulative species curve (Figure 3) reached a plateau after eight 24-h censuses and

Table 1 Total length and body mass of ant species occurring on the gravel plains at Ganab

Species	Total length (mm) range	Dry mass (mg)	
		\bar{X}	sd
Myrmicinae			
<i>Messor denticornis</i>	5,5 – 11,0	2,96	2,30
<i>Pheidole tenuinodis</i>	2,5 – 4,9	0,11	0,03
<i>Ocymyrmex barbiger</i>	6,7 – 7,2	1,44	0,16
<i>Tetramorium sericeiventris</i>	3,3 – 4,4	0,32	0,08
<i>Tetramorium rufescens</i>	4,0 – 5,1	0,72	0,11
<i>Tetramorium grandinode</i>	5,0 – 5,3	0,80	0,10
<i>Tetramorium peringueyi</i>	4,4 – 5,7	0,90	0,12
<i>Monomorium viator</i>	3,5 – 3,9	0,22	0,10
<i>Monomorium</i> sp. B	2,7 – 3,1	0,11	0,05
<i>Monomorium</i> sp. C	2,2 – 2,6	0,04	0,02
<i>Monomorium</i> sp. D	1,3 – 1,5	no data	
Formicinae			
<i>Camponotus maculatus</i>	7,7 – 12,0	2,80	1,60
<i>Camponotus mystaceus</i>	7,0 – 15,0	2,00	1,00

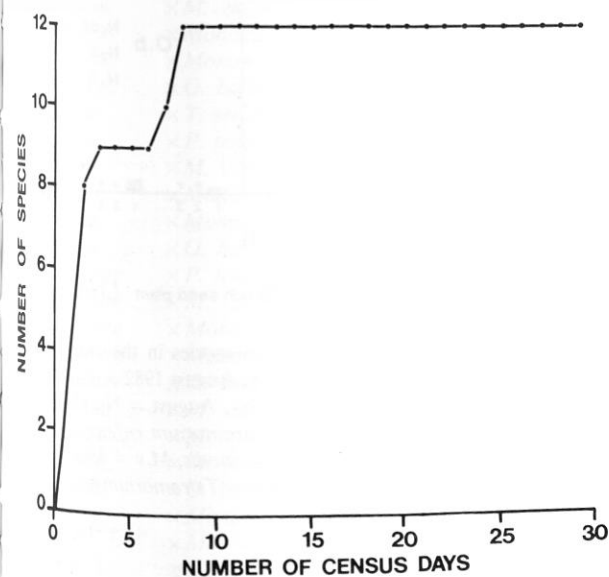


Figure 3 The relationship between cumulative species and cumulative census periods.

remained constant for the remainder of the study period suggesting that all species occurring in the study plot were sampled.

The numerical density of foragers of all species fluctuated markedly during the study period (Figure 4). Forager density peaked in April in 1983 and 1984 and was very low between July 1983 and February 1984. The 1984 peak in forager density was considerably lower than that of 1983 and only spanned two months, March and April. In contrast, forager density remained high for at least five months in 1983, January to May, and a trial-run census in December 1982 also revealed high densities of foragers. The majority of foragers were nocturnal in summer (December to April/May) and diurnal in winter (Figure 5).

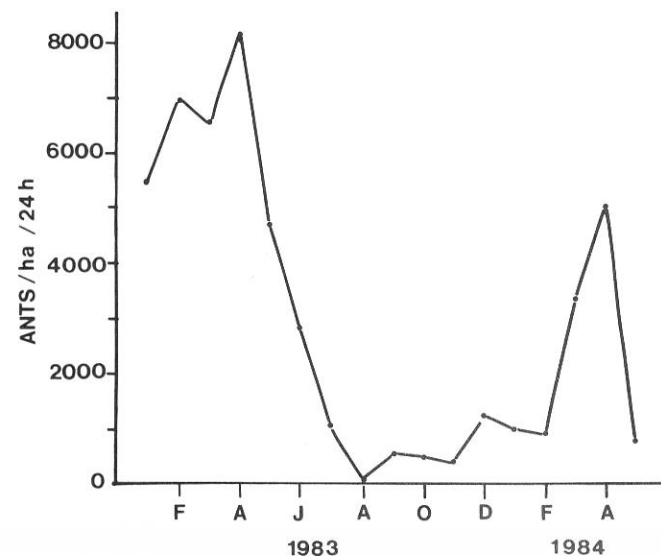


Figure 4 Numerical density of foraging ants (No./ha/24 h) during 1983 and early 1984.

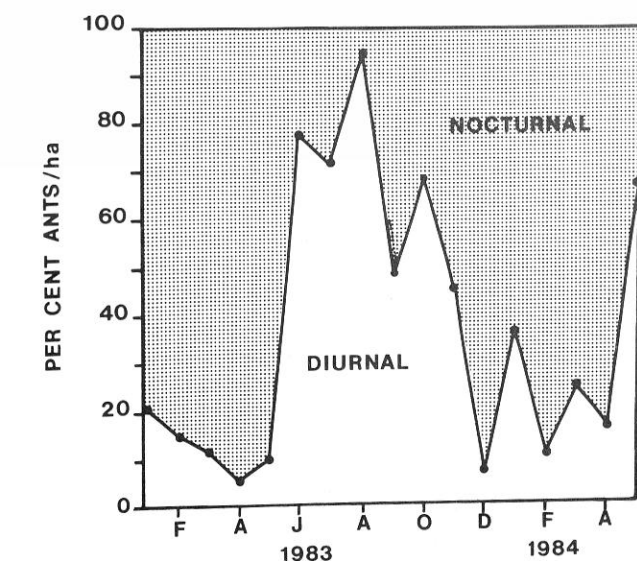


Figure 5 The proportion of foraging ants (% of numerical density/24 h) that were diurnally and nocturnally active over a 17-month period.

The rank order of species depended on whether species importance was based on numerical density or biomass per unit area (Table 2). For both criteria the top three species were *M. denticornis*, *T. rufescens* and *M. viator*, although the order

Table 2 Rank sequence of ant species based on numerical density and biomass. Data are expressed as numbers and mass (mg) of ants per hectare per day and as a per cent of the total numbers or biomass of the community. The data are from 17 pooled monthly censuses. Where species had identical densities or biomass their rank position was decided using the data extended to three decimal places

Numerical density				Biomass		
Rank	Species	No./ha	%	Species	mg/ha	%
1	<i>T. rufescens</i>	1096	41,52	<i>M. denticornis</i>	1438	57,95
2	<i>M. viator</i>	555	21,03	<i>T. rufescens</i>	789	31,80
3	<i>M. denticornis</i>	486	18,41	<i>M. viator</i>	122	4,92
4	<i>P. tenuinodis</i>	265	10,04	<i>C. maculatus</i>	46	1,85
5	<i>Monomorium</i> sp. C	88	3,33	<i>P. tenuinodis</i>	33	1,33
6	<i>T. sericeiventris</i>	71	2,69	<i>T. sericeiventris</i>	23	0,93
7	<i>Monomorium</i> sp. B	41	1,55	<i>T. grandinode</i>	13	0,52
8	<i>C. maculatus</i>	16	0,61	<i>Monomorium</i> sp. B	5	0,20
9	<i>T. grandinode</i>	16	0,61	<i>O. barbiger</i>	4	0,16
10	<i>O. barbiger</i>	3	0,11	<i>C. mystaceus</i>	4	0,16
11	<i>C. mystaceus</i>	2	0,08	<i>Monomorium</i> sp. C	4	0,16
12	<i>T. peringueyi</i>	0,5	0,01	<i>T. peringueyi</i>	0,5	0,02

within this group depended on the criterion used. These three species comprised 81,0% of the total forager community in terms of numerical density and 94,7% in terms of biomass. Rank order of species within the community varied from month to month but overall patterns were fairly stable. Kendall's coefficient of concordance was highly significant using numerical density data ($w = 0,79$, $p < 0,001$) and biomass data ($w = 0,64$, $p < 0,001$), indicating that the relative ranking of species within the community was stable through time.

Dietary relationships

There was considerable intra- and interspecific variation in diet (Figure 6). *Tetramorium sericeiventris* alone had a reasonably consistent diet over all samples. Intraspecific variability in diet made it difficult to assign species to a definite trophic group. In a broad sense all species were omnivorous. *Messor denticornis*, *T. rufescens*, *Monomorium* sp. C, *M. viator* and *P. tenuinodis* occasionally harvested and stored large quantities of seed and are probably best regarded as granivores. *Ocymyrmex barbiger* predominantly took arthropod carrion during the one sample period when the ants were sufficiently active to collect their forage. As this species consistently took arthropod carrion in a more detailed study in the Kuiseb River bed (Marsh in press a) it can, with reasonable confidence, be regarded as an arthropod scavenger. The remaining two species, *Monomorium* sp. B and *T. sericeiventris*, regularly took a diversity of food items, never took large quantities of seed and are best assigned to an omnivore category. The proportion of grass seed relative to dicotyledon seed also varied between samples in most species. Incidental observations on the remaining four species, at the study area and elsewhere in the central Namib Desert, revealed that the two *Camponotus* species were predominantly honeydew feeders and the two *Tetramorium* species were predominantly granivorous (Marsh in press b).

Intraspecific variability in dietary niche breadth was considerable (Table 3). Of the six species for which three samples were collected, only *Monomorium* sp. B and *T. sericeiventris* had relatively constant niche breadths through time as indicated by the low coefficients of variation obtained. The lowest niche breadth was that of *M. denticornis* in the August

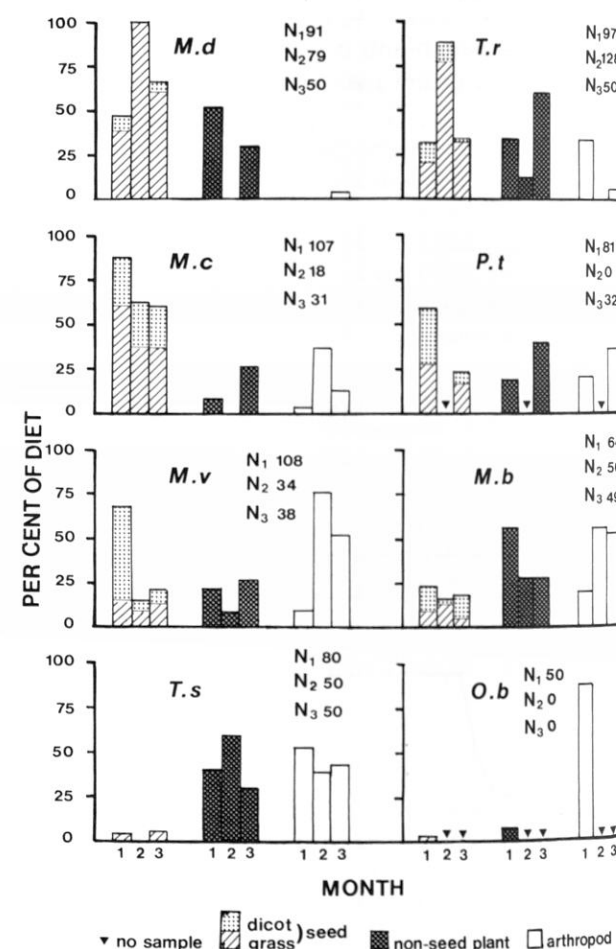


Figure 6 Proportion of three food categories in the diets of eight common ant species. January 1982 = 1, August 1982 = 2, May 1984 = 3. Sample sizes refer to: January = N_1 , August = N_2 , May = N_3 . *M.d* = *Messor denticornis*, *T.r* = *Tetramorium rufescens*, *M.c* = *Monomorium* sp. C, *P.t* = *Pheidole tenuinodis*, *M.v* = *Monomorium viator*, *M.b* = *Monomorium* sp. B, *T.s* = *Tetramorium sericeiventris*, *O.b* = *Ocymyrmex barbiger*.

sample when this species took seeds exclusively, primarily grass seed. The highest niche breadth was that of *T. rufescens* in the January sample when this species took approximately

Table 3 Dietary niche breadths and coefficients of variation (CV) in niche breadth of eight common ant species

Species	Month			C.V. (%)
	Jan 1982	Aug 1982	May 1984	
<i>M. denticornis</i>	1,99	1,00	1,90	33,7
<i>T. rufescens</i>	3,00	1,28	2,09	40,6
<i>T. sericeiventris</i>	2,16	1,92	2,24	8,1
<i>P. tenuinodis</i>	2,30	—	2,86	15,5
<i>M. viator</i>	1,94	1,63	2,56	23,0
<i>Monomorium</i> sp. B	2,43	2,39	2,51	2,5
<i>Monomorium</i> sp. C	1,28	1,88	2,23	26,7
<i>O. barbiger</i>	1,28	—	—	—

equal proportions of the three food categories (Figure 6).

Intraspecific variability in diet is reflected in between sample dietary niche overlap values (Table 4). The only species that exhibited high similarity in diet through time was *T. sericeiventris*, thus confirming the impression obtained from

Table 4 Between sample similarity of diet for seven common ant species (See text for explanation of similarity index)

Species	Sample comparisons		
	Jan × Aug	Jan × May	Aug × May
<i>M. denticornis</i>	0,59	0,89	0,89
<i>T. rufescens</i>	0,49	0,79	0,60
<i>M. viator</i>	0,31	0,48	0,94
<i>T. sericeiventris</i>	0,94	0,98	0,99
<i>Monomorium</i> sp. B	0,72	0,75	0,97
<i>Monomorium</i> sp. C	0,79	0,89	0,80
<i>P. tenuinodis</i>	—	0,77	—

Table 5 Interspecific dietary niche overlap values on three widely spaced occasions

Species pair	Month		
	Jan	Aug	May
<i>M. denticornis</i> × <i>T. rufescens</i>	0,76	0,98	0,82
<i>M. denticornis</i> × <i>T. sericeiventris</i>	0,53	0	0,45
<i>M. denticornis</i> × <i>P. tenuinodis</i>	0,71	—	0,62
<i>M. denticornis</i> × <i>M. viator</i>	0,56	0,12	0,45
<i>M. denticornis</i> × <i>Monomorium</i> sp. B	0,84	0,22	0,34
<i>M. denticornis</i> × <i>Monomorium</i> sp. C	0,68	0,65	0,90
<i>M. denticornis</i> × <i>O. barbiger</i>	0,10	—	—
<i>T. rufescens</i> × <i>T. sericeiventris</i>	0,92	0,13	0,76
<i>T. rufescens</i> × <i>P. tenuinodis</i>	0,85	—	0,81
<i>T. rufescens</i> × <i>M. viator</i>	0,64	0,14	0,56
<i>T. rufescens</i> × <i>Monomorium</i> sp. B	0,89	0,29	0,51
<i>T. rufescens</i> × <i>Monomorium</i> sp. C	0,54	0,69	0,81
<i>T. rufescens</i> × <i>O. barbiger</i>	0,71	—	—
<i>T. sericeiventris</i> × <i>P. tenuinodis</i>	0,60	—	0,97
<i>T. sericeiventris</i> × <i>M. viator</i>	0,38	0,64	0,91
<i>T. sericeiventris</i> × <i>Monomorium</i> sp. B	0,82	0,85	0,91
<i>T. sericeiventris</i> × <i>Monomorium</i> sp. C	0,19	0,36	0,61
<i>P. tenuinodis</i> × <i>M. viator</i>	0,90	—	0,94
<i>P. tenuinodis</i> × <i>Monomorium</i> sp. B	0,71	—	0,92
<i>P. tenuinodis</i> × <i>Monomorium</i> sp. C	0,82	—	0,77
<i>P. tenuinodis</i> × <i>O. barbiger</i>	0,47	—	—
<i>M. viator</i> × <i>Monomorium</i> sp. B	0,63	0,94	0,98
<i>M. viator</i> × <i>Monomorium</i> sp. C	0,65	0,74	0,65
<i>M. viator</i> × <i>O. barbiger</i>	0,21	—	—
<i>Monomorium</i> sp. B × <i>Monomorium</i> sp. C	0,36	0,71	0,60
<i>Monomorium</i> sp. B × <i>O. barbiger</i>	0,41	—	—
<i>Monomorium</i> sp. C × <i>O. barbiger</i>	0,11	—	—

inspection of Figure 6. Dissimilarities in diet were quite marked, the extreme being *M. viator* in which the diets in January and August showed an overlap of only 0,31. Over all species and samples, dietary niche overlap averaged 0,62 ($N = 64$, $SD = 0,26$). As a consequence of intraspecific variability, interspecific similarities varied considerably through time for all species pairs (Table 5). The greatest change in dietary similarity was that between the two *Tetramorium* species which had high similarity in January ($O = 0,92$) and high dissimilarity in August ($O = 0,13$). Interspecific overlap values ranged from complete dissimilarity (*M. denticornis* × *T. sericeiventris* in August) to almost complete similarity (*M. viator* × *Monomorium* sp. B in May). There was no concordance between overlap values over the three sample periods ($w = 0,49$, $p > 0,01$) indicating that shifts in dietary overlap were random with no tendency for changes to be directional between any two sample periods.

There was considerable intra- and interspecific variation in the size of food particles taken (Table 6). Using data from all samples most species took statistically distinct food particle sizes ($p < 0,05$ for 25 of 28 species pair comparisons, Mann-Whitney *U* test) although the large standard deviations reveal considerable overlap between species. The only species pairs that were not statistically different in food particle size utilization were *M. denticornis* × *O. barbiger* ($p = 0,11$), *T. rufescens* × *P. tenuinodis* ($p = 0,14$) and *M. viator* × *Monomorium* sp. C ($p = 0,32$). Despite this, however, no consistent relationship between body length and mean food particle size was apparent. Over all samples there was a positive relationship between body size and food particle size ($Y = -4,14 + 1,43X$; $r = 0,95$; $p < 0,01$; $n = 8$); In the January and May samples similar relationships existed (January: $Y = -6,11 + 2,01X$; $r = 0,95$; $p < 0,01$; $n = 8$;

Table 6 Estimated volumes (mm^3) of individual food particles collected by the eight most common ant species

Species	Sample	Mean	sd	Min	Max	n
<i>M. denticornis</i>	Jan	12,13	24,04	0,05	135,59	91
	Aug	0,28	0,04	0,17	0,44	97
	May	2,98	7,77	0,08	35,49	49
	All	8,93	20,35	0,05	135,59	237
<i>T. rufescens</i>	Jan	1,30	2,11	0,01	14,48	96
	Aug	0,46	0,76	0,03	4,99	128
	May	1,25	3,36	0,02	16,78	50
	All	1,28	2,59	0,01	16,78	274
<i>T. sericeiventris</i>	Jan	1,16	1,98	0,01	9,65	80
	Aug	2,98	4,37	0,06	21,74	50
	May	1,19	1,70	0,08	7,53	50
	All	1,68	2,90	0,01	21,74	180
<i>P. tenuinodis</i>	Jan	0,77	1,05	0,01	7,04	81
	May	0,59	0,88	0,01	3,62	32
	All	0,72	1,01	0,01	7,04	113
<i>M. viator</i>	Jan	0,48	0,53	0,002	3,77	108
	Aug	0,24	0,26	0,01	1,08	34
	May	0,26	0,27	0,01	3,40	38
	All	0,39	0,51	0,002	3,77	180
<i>Monomorium</i> sp. B	Jan	0,86	2,54	0,004	15,91	64
	Aug	0,30	0,64	0,003	3,06	48
	May	0,28	0,57	0,01	2,82	49
	All	0,52	1,69	0,003	15,91	161
<i>Monomorium</i> sp. C	Jan	0,39	0,31	0,002	1,32	107
	Aug	0,15	0,12	0,03	0,63	18
	May	0,32	0,49	0,01	2,27	31
	All	0,36	0,36	0,002	2,27	156
<i>O. barbiger</i>	Jan	4,77	5,67	0,06	28,96	50

May: $Y = -1,06 + 0,49X$; $r = 0,96$; $p < 0,01$; $n = 8$); whereas, in August there was no relationship ($Y = 0,90 - 0,04X$; $r = 0,10$; $p > 0,05$; $n = 8$). Furthermore, there was no concordance through time between the relationship of species sequence to food particle size ($w = 0,61$; $p > 0,05$) indicating that species do not occupy the same position relative to one another in terms of the food particles utilized. For example, *Monomorium* sp. C did not consistently take smaller items than its two congeners. It did in two samples but it took larger items in one sampling period.

Discussion

From the results it is clear that a single survey of the community would not have provided a representative picture of structure. First, on the average only 70% of the species known to occur in the community were sampled in any one census. No single census sampled all species and only 2 of 17 censuses included 11 of the 12 species. Second, although community structure was reasonably robust through time, rank order was not the same at each census, not even for the three most abundant species. Thus to reasonably describe the structure of this community several censuses were necessary. This conclusion supports those of Chew (1977) and Whitford (1978a) on North American desert ant communities and that of Wiens (1981) for terrestrial vertebrates in general and North American bird communities in particular.

Food availability has a marked effect on the activity levels of foraging ants in arid environments (Bernstein 1974; Whitford & Ettershank 1975; Briese & Macauley 1980; Whitford, Depree & Johnson 1980; Whitford *et al.* 1981). During the present study two pulses of primary production, separated by a long period of food scarcity occurred and the availability of food for *M. denticornis* and *T. rufescens* peaked during these events (Marsh 1985). The first peak in food availability was considerably larger than the second. It is a reasonable deduction that similar patterns of food availability occurred for all ant species in the community, particularly for those species that utilized seeds, thus explaining the patterns of forager abundance (Figure 4).

Seasonal shifts in diel activity patterns have been noted for numerous desert ant species (Whitford & Ettershank 1975; Gamboa 1976; Whitford, Johnson & Ramirez 1976; Whitford 1978a) and these are normally thought to be in response to shifts in microclimatic conditions, especially temperature. In the present study, the shift from predominantly nocturnal to predominantly diurnal activity during winter reflects in part diel activity shifts in response to the thermal environment [see Marsh (1985) for details on the thermal environment at the study site]. Overall activity levels were also depressed during winter because of food scarcity and in certain censuses some of the usually dominant harvester species, including the nocturnal *M. denticornis* and *M. viator*, were almost completely inactive whereas the diurnal non-harvester species remained active. In August 1983, for example, *T. sericeiventris* was the dominant species numerically and in biomass and *M. denticornis* and *M. viator* did not occur in the transect.

Granivorous ants are typically the dominant (Chew 1977; Briese 1982) or codominant (Whitford 1978a) trophic group in desert ant communities. In the present study 7 of 12 species were harvester ants, 94,7% of all individuals were harvesters making up 96,7% of the total forager biomass. The overwhelming dominance of harvester ants is to be expected because they are predominantly primary consumers that rely on a relatively dependable and nutritious food resource which can be stored for extensive periods (Carroll & Janzen 1973;

Brown *et al.* 1979). The relative scarcity of other trophic groups is attributable to the absence of perennially green vegetation and hence honeydew-producing insects and to the fact that they are predominantly secondary consumers.

The large fluctuations in dietary niche breadth and overlap that were exhibited by most species in the present study reflect opportunism. Only omnivorous species, with broad generalized diets, did not show much dietary variation. Flexible feeding habits have been reported for many desert ant species (Whitford 1978b; Briese & Macauley 1981). Trophic flexibility facilitates survival in a variable environment where food is unpredictable in time and space. Furthermore, although food resources are partitioned according to size in certain North American desert ant communities with large species taking large food items and vice versa (Davidson 1977; Chew & De Vita 1980), this relationship is not clear cut in the Namib Desert community nor in a desert ant community in Australia (Morton 1982). The lack of clear patterns supports the notion that interspecific competition for food is not of major importance to ants inhabiting unpredictable arid environments (Briese & Macauley 1981).

Acknowledgements

I am indebted to M.K. Seely, J. Lighton, D. Boyer and the assistants from the Desert Ecological Research Unit who helped collect the field data. The manuscript was critiqued by M.K. Seely, G.N. Louw, S. Nicholson and R. Pietruszka. B. Bolton identified the ants and H. Kastner designed and built the census vehicle. The Department of Nature Conservation, SWA/Namibia gave permission and provided facilities to live and work in the Namib-Naukluft Park. The work was funded by the Transvaal Museum, the University of Cape Town, the C.S.I.R. and the Rossing Foundation.

References

- BERNSTEIN, R.A. 1974. Seasonal food abundance and foraging activity in some desert ants. *Am. Nat.* 108: 490–498.
- BERNSTEIN, R.A. 1979. Relations between species diversity and diet in communities of ants. *Insect. Soc.* 26: 313–321.
- BRIESE, D.T. & MACAULEY, B.J. 1977. Physical structure of an ant community in semi-arid Australia. *Aust. J. Ecol.* 2: 107–120.
- BRIESE, D.T. & MACAULEY, B.J. 1980. Temporal structure of an ant community in semi-arid Australia. *Aust. J. Ecol.* 5: 121–134.
- BRIESE, D.T. & MACAULEY, B.J. 1981. Food collection within an ant community in semi-arid Australia, with special reference to seed harvesters. *Aust. J. Ecol.* 6: 1–19.
- CARROLL, C.R. & JANZEN, D.H. 1973. Ecology of foraging by ants. *Annu. Rev. Ecol. & Syst.* 4: 231–257.
- CHEW, R.M. 1977. Some ecological characteristics of the ants of a desert-shrub community in southeastern Arizona. *Am. Midl. Nat.* 98: 33–49.
- CHEW, R.M. & DE VITA, J. 1980. Foraging characteristics of a desert ant assemblage: functional morphology and species separation. *J. Arid Env.* 3: 75–83.
- CRAWFORD, C.S. 1981. Biology of desert invertebrates. Springer-Verlag, New York.
- DAVIDSON, D.W. 1977. Species diversity and community organization in desert seed-eating ants. *Ecol.* 58: 711–724.
- GAMBOA, G.J. 1976. Effects of temperature on the surface activity of the desert leaf-cutter ant, *Acromyrmex versicolor versicolor* (Pergande) (Hymenoptera: Formicidae). *Am. Midl. Nat.* 95: 485–491.
- GREENSLADE, P.J.M. & HALLIDAY, R.B. 1983. Colony dispersion and relationships of meat ants *Iridomyrmex purpureus* and allies in an arid locality in South Australia. *Insect. Soc.* 30: 82–99.
- MARSH, A.C. 1984. The efficacy of pitfall traps for determining the structure of a desert ant community. *J. Entomol. Soc.*

- South. Afr.* 47: 115–120.
- MARSH, A.C. 1985. Aspects of the ecology of Namib Desert ants. Ph.D. thesis, University of Cape Town.
- MARSH, A.C. In press a. Thermal responses and temperature tolerance in a diurnal desert ant, *Ocymyrmex barbiger*. *Physiol. Zool.*
- MARSH, A.C. In press b. Ant species richness along a climatic gradient in the Namib Desert. *J. Arid. Env.*
- MORTON, S.R. 1982. Granivory in the Australian arid zone: diversity of harvester ants and structure of their communities. In: Evolution of the flora and fauna of arid Australia, (eds) Barker, W.R. & Greenslade, P.J.M. Peacock, Adelaide, pp. 257–262.
- PIANKA, E.R. 1973. The structure of lizard communities. *Annu. Rev. Ecol. & Syst.* 4: 53–74.
- PISARSKI, B. 1978. Comparison of various biomes. In: Production ecology of ants and termites, (ed.) Brian, M.V. Cambridge University Press, Cambridge, pp. 326–331.
- SIEGEL, S. 1956. Nonparametric statistics for the behavioural sciences. McGraw-Hill, New York.
- SIMPSON, E.H. 1949. Measurement of diversity. *Nature* 163: 688.
- WHITFORD, W.G. 1978a. Structure and seasonal activity of Chihuahua Desert ant communities. *Insect. Soc.* 25: 79–88.
- WHITFORD, W.G. 1978b. Foraging by seed-harvesting ants. In: Production ecology of ants and termites, (ed.) Brian, M.V. Cambridge University Press, Cambridge, pp. 107–110.
- WHITFORD, W.G. & ETTERS HANK, G. 1975. Factors affecting foraging activity in Chihuahuan Desert harvester ants. *Environ. Entomol.* 4: 689–696.
- WHITFORD, W.G., DEPREE, D.J., HAMILTON, P. & ETTERS HANK, G. 1981. Foraging ecology of seed-harvesting ants, *Pheidole* spp. in a Chihuahuan Desert ecosystem. *Am. Midl. Nat.* 105: 159–167.
- WHITFORD, W.G., DEPREE, D.J. & JOHNSON, P. 1980. Foraging ecology of two Chihuahuan Desert ant species: *Novomessor cockerelli* and *Novomessor albigaster*. *Insect. Soc.* 27: 148–156.
- WHITFORD, W.G., JOHNSON, P. & RAMIREZ, J. 1976. Comparative ecology of the harvester ants *Pogonomyrmex barbatus* (F. Smith) and *Pogonomyrmex rugosus* (Emery). *Insect. Soc.* 23: 117–132.
- WIENS, J.A. 1981. Single sample surveys of communities: are the revealed patterns real? *Am. Nat.* 117: 90–98.