Forager abundance and dietary relationships in a Namib Desert ant community

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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.

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Dertien spesies miere hou op dieselfde onvrugbare gruisvlakte in die sentrale Namibwoestyn. Die getalsterkte van die voersoekers het oor 'n ondersoekperiode van 17 maande aanmerklik gewissel. Hoogtepunte in getaldigtheid het saamgeval met reënvalperiodes en dus die primêre voedselaanbod. Die meerderheid voersoekers het in die somer snags voer gesoek en in die winter bedags. Die gemeenskap is met betrekking tot spesies, die getalsterkte van voersoekers, 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.

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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/

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 myrmicines, 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 epigaeic. The other species were epigaeic. 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 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).

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

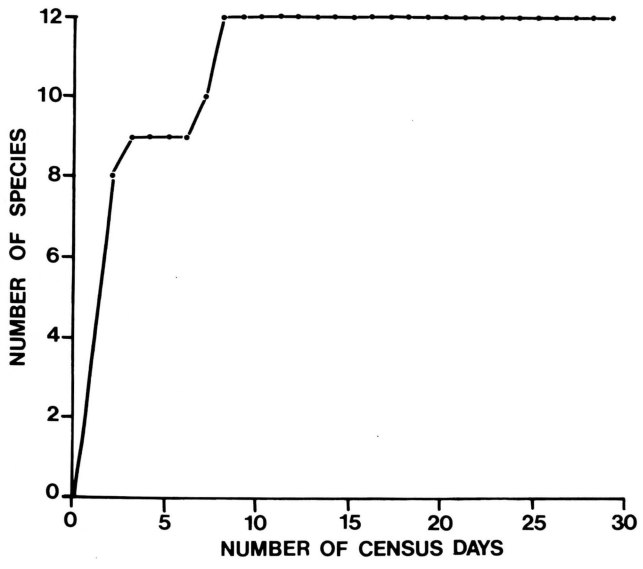

Figure 3 The relationship between cumulative species and cumulative census periods.

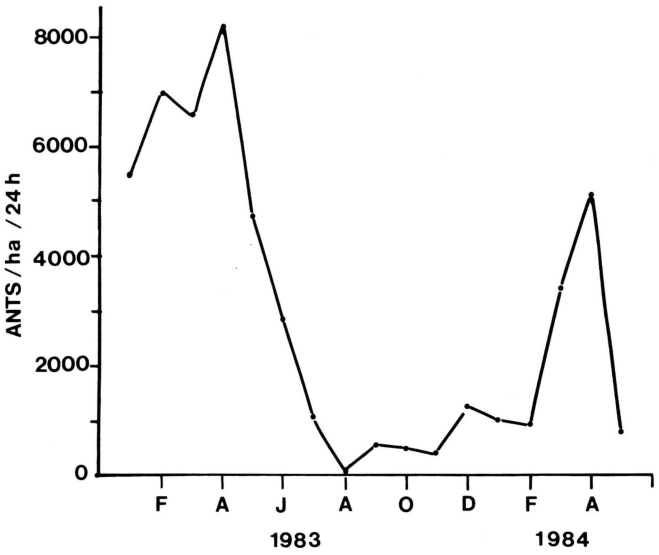

Figure 4 Numerical density of foraging ants (No./ha/24 h) during 1983 and early 1984.

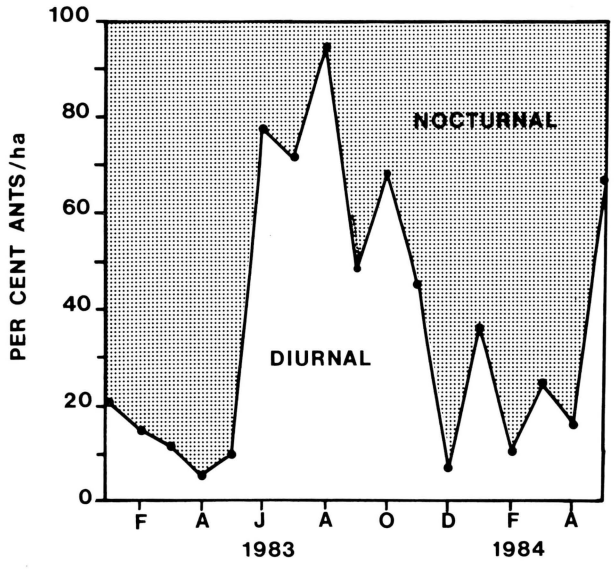

Figure 5 The proportion of foraging ants (% of numerical density/24 h) that were diurnally and nocturnally active over a 17-month period.

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 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	
M. denticornis	1,99	1,00	1,90	33,7
T. rufescens	3,00	1,28	2,09	40,6
T. sericeiventre	2,16	1,92	2,24	8,1
P. tenuinodis	2,30	–	2,86	15,5
M. viator	1,94	1,63	2,56	23,0
Monomorium sp. B	2,43	2,39	2,51	2,5
Monomorium sp. C	1,28	1,88	2,23	26,7
O. barbiger	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. sericeiventre*, thus confirming the impression obtained from 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. sericeiventre* 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 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
M. denticornis	0,59	0,89	0,89
T. rufescens	0,49	0,79	0,60
M. viator	0,31	0,48	0,94
T. sericeiventre	0,94	0,98	0,99
Monomorium sp. B	0,72	0,75	0,97
Monomorium sp. C	0,79	0,89	0,80
P. tenuinodis	–	0,77	–

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

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

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*
M. denticornis	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
T. rufescens	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
T. sericeiventre	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
P. tenuinodis	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
M. viator	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
Monomorium 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
Monomorium 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
O. barbiger	Jan	4,77	5,67	0,06	28,96	50

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