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Activity patterns of some Namib Desert ants

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The activity patterns of eight epigaeic ant species from the Namib Desert were studied in summer and winter, and before and after a rainfall event. The patterns varied from unimodal to bimodal depending on species and season. Seven species exhibited seasonal changes in activity pattern, with a trend towards diurnalism in winter. One diurnal species exhibited similar activity in both seasons. Interspecific differences in activity pattern were greater in summer than winter. Activity levels increased significantly after rain, owing to an increase in foraging and nest construction. Multiple linear regression analysis indicated that surface temperature influenced ant activity more than vapour pressure deficit but a substantial amount of variation was not attributable to these two variables. Critical thermal limits were similar for all eight species irrespective of their normal activity period and some species were active over virtually the entire thermal range that they could withstand physiologically. Interspecific differences in activity may have evolved to minimise interference interactions which occur between ant species. Other possibilities that could explain the observed differences include navigational constraints and different thermal preferenda and, hence, the coincidental partitioning of time.

Introduction

Most of the important interactions an animal has with its environment occur when the animal is active. It is while the animal is moving about its habitat that it is likely to encounter the resources and mates it requires, as well as various mortality factors such as predators and malentities (*sensu* Andrewartha & Birch, 1984). The spectrum of environmental factors that are encountered will depend, in part, on when the animal is active. The activity period therefore influences an animal's probability of survival and reproduction. Thus, activity has profound evolutionary and ecological consequences and information on activity patterns is fundamental to understanding an animal's ecology.

It has been suggested that the principal components of environment that determine activity patterns of desert ants are heat, moisture (Bernstein, 1974; Briese & Macauley, 1980; Gamboa, 1976; Greenaway, 1981; Sheata & Kaschef, 1971; Whitford & Ettershank, 1975; Whitford, Depree *et al.*, 1981) and wind (Briese & Macauley, 1980; Curtis, 1985; Sheata & Kaschef, 1971). Similar environmental factors have been shown to be important in non-desert ants (e.g. De Bruyn & De Bruyn, 1972; Sanders, 1972) but they are of particular relevance in deserts because microclimatic factors at the surface are subject to very large diel and seasonal fluctuations (Oke, 1978). Thermal conditions are of special importance because the activity of small ectothermic ants will be restricted to those periods

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when surface conditions permit physiologically tolerable body temperatures. Environmental factors such as predatory and competitive interactions with other animals may, however, prevent an ant species from using the entire activity period for which it is physiologically adapted (Melhop & Scott, 1983; Whitford, Depree *et al.*, 1981).

The present study documents activity patterns and thermal tolerances of eight common and little-known ant species in the central Namib Desert. Activity was monitored in summer and winter as well as before and after a rainfall event. The data thus present an opportunity to examine environmental and physiological determinants of activity in this desert ant assemblage.

Materials and methods

Field studies were conducted on the gravel plains near Ganab (28°08′S 15°37′E) on the eastern edge of the Namib Desert. The habitat is a uniform, flat plain that becomes a grassland after sufficient rain has fallen (*c.* 20 mm). During this investigation the habitat was devoid of photosynthetically active vegetation and the only visible vegetation comprised widely scattered grass stubble 2–10 cm high. Thirteen ant species occur sympatrically in this region (Marsh, 1985*a*) but only eight, all myrmicines, were sufficiently abundant to provide adequate data on activity patterns. All of these species live in subterranean nests and are epigaeic foragers.

Activity patterns

Activity patterns were studied in May (winter) and late November–early December (summer) 1982. Three nests of each species were observed at regular intervals over a 24-hour period. Twelve nests were observed simultaneously each day and the entire study of 24 nests spanned 2 consecutive days each season. In summer each nest was observed continuously for 10 minutes every hour from 0500h to 2100h solar time. Thereafter, 10-minute observations were made at 2-hourly intervals until 0500h. In winter, 10-minute observations were made every hour from 0700h to 2100h and every 2 hours thereafter until 0700h. *Ocymyrmex robustior* nests were observed for 15 minutes during each observation period because of low levels of activity. All ants that emerged from and returned to the nest entrance were counted. The nests of *Messor denticornis* and *Tetramorium rufescens* have multiple entrances and a nest entrance with a high level of activity was selected and observed throughout the 24-hour period.

Pianka's (1973) measure of overlap was used to quantify similarities in activity patterns between species:

$$O_{ij} = \sum_{a}^{n} P_{ai} P_{aj} \bigg/ \sqrt{\sum_{a}^{n} P_{ai}^2 \sum_{a}^{n} P_{aj}^2}$$

where P_{ai} and P_{aj} are the proportions of the *a*th time period used by the *i*th and *j*th species, respectively. Overlap values can range from zero for no overlap to unity for identical activity patterns.

Immediately after every 10–15-minute observation period the following microclimatic factors were measured: wind speed, at an elevation of 1 m, using a mechanical totalising anemometer; wet- and dry-bulb ambient temperatures at 1 m elevation, using a sling psychrometer; soil surface temperature; and air temperature at 1 mm, 3 mm and 5 mm elevation above the soil surface. All temperatures were measured using copper–constantan thermocouples and a digital thermometer (Bailey Instruments, Model BAT12). Air temperatures were unshaded, black-body temperatures and were measured using thermocouples built up with epoxy resin to approximate ant size and painted matt black. Black-body temperatures were used to obtain an approximation of the body temperatures that surface-active ants were likely to experience. The degree of cloud cover was estimated visually.

To determine the relationships between ant activity and surface temperature and vapour pressure deficit, the response curves of activity versus surface temperature and activity versus vapour pressure deficit for each species were linearised using a parabolic transformation (Forsythe & Loucks, 1972) and the data analysed using multiple linear regressions.

On 1 December, one day after the summer observations ended, 1·3 mm of rain fell on the study site and activity counts were repeated for two nests per species one day after the rainfall event.

Thermal limits

Ants were collected in the field and their critical thermal maxima (CT_{max}) and minima (CT_{min}) were determined within 12 hours of capture. Individuals were placed into 250-ml Erlenmeyer flasks, and the ambient temperature in the flask at ant height was raised or lowered at a rate of 1°C/minute. Temperatures were measured using copper–constantan thermocouples and a digital thermometer. Temperatures were raised by partly immersing the flask in water above a heating element, and lowered by suspending the flask in a freezer unit. The critical thermal limits were considered to have been reached when the ants were incapable of locomotion (*see* Marsh, 1985*b*). Each individual was used once only, either for a CT_{max} or a CT_{min} determination.

Results

Microclimate

Microclimatic conditions prevailing on the 5 study days are shown in Table 1. Minimum and maximum surface temperatures were lower in winter than in summer except on the day after rainfall, when cloud cover reduced surface heating. The higher minimum surface temperature on 30 November, relative to 29 November, is attributable to cloud cover which retarded re-radiation at night. Thermal conditions and vapour pressure deficit were similar for the 2 days in winter. Similarly, summer daytime thermal and humidity conditions varied little over the period of observation. The principal differences between summer and winter concerned day length and wind. There were 3 hours more daylight in summer than in winter and there was substantially more wind during the summer period (Table 1). The principal differences between the pre-rain summer and post-rain summer periods were a reduction in maximum surface temperature and maximum vapour pressure deficit after rain, both attributable to an increase in cloud cover and evaporative cooling of the damp surface.

Activity patterns

The activity patterns of the eight ant species, together with pertinent microclimatic conditions during winter and pre-rain summer, are shown in Fig. 1. Except for *O. robustior*, winter and summer patterns differed within each species, with a marked trend towards increased diurnalism in winter. *Messor denticornis, Monomorium viator* and *O. robustior* exhibited unimodal activity patterns in both seasons; the former two species are primarily nocturnal and the latter strictly diurnal with activity confined to the hottest period of the day. *Tetramorium sericeiventre* exhibited bimodal activity in summer and

Table 1. *Summary of microclimatic conditions on activity monitoring days*

Date	T_s (°C)		VPD (kPa)		Wind			Sun	Cloud cover	
(1982)	Minimum	Maximum	Minimum	Maximum	Mean (km/h)	Maximum (m/s)	>6 m/s (hours)	(hours)	(%)	(hours)
18 May	7·1	40·6	1·2	3·9	3·6	2·7	0	10·5 d	0	
19 May	6·4	44·2	1·0	4·1	4·3	3·6	0	10·5 d	50	5
29 Nov	14·6	52·6	0·6	3·5	9·8	7·2	2	13·5 d	0	
30 Nov	19·8	53·9	1·0	3·4	11·3	8·8	3	13·5 d	90	4
2 Dec	18·8	37·0	0·6	2·2	13·4	6·7	2	13·5 id	100	24

T_s, surface temperature (°C); VPD, vapour pressure deficit (kPa). Number of hours with mean wind speed >6 m/s given after one-hour maximum wind speed. Sun, hours of sunshine (d, direct; id, indirect). Number of hours with cloud are given after percentage cover.

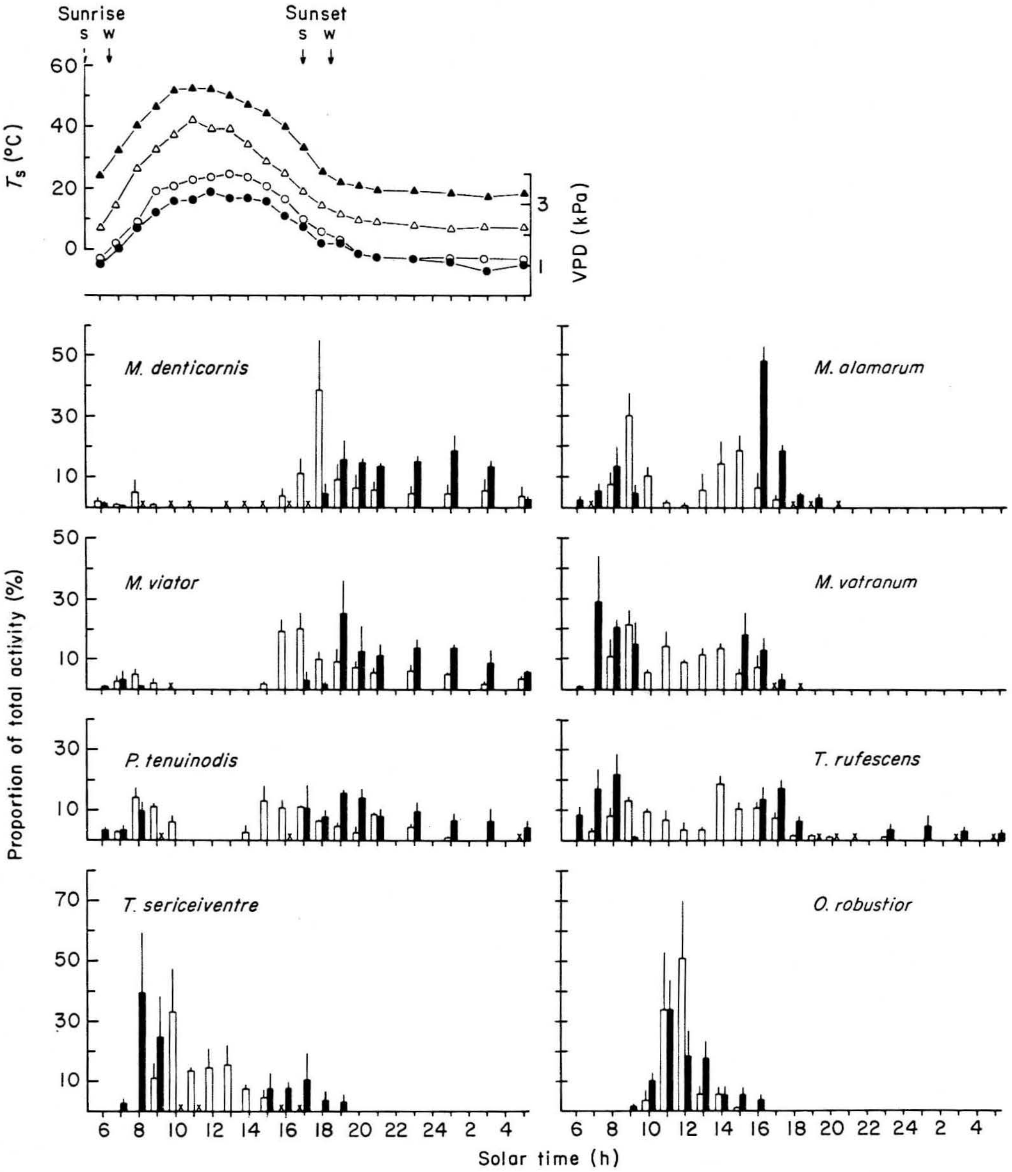

Figure 1. Activity patterns of ants in winter and pre-rain summer. The data are expressed as percentages of the total number of exits and entrances that occur in a 24-hour period. The length of each bar represents the mean and one standard error of three nests (clear, winter; shaded, summer). Values less than 1% are represented by ×. The sand surface temperatures (T_s) and vapour pressure deficits (VPD) indicated represent hourly means over the 48-hour observation period. s, Summer; w, winter. ▲, Summer T_s; △, winter T_s; •, summer VPD; ○, winter VPD.

unimodal activity in winter. The other four species exhibited bimodal activity patterns. *Pheidole tenuinodis* was inactive during the middle of the day; the inactive period was substantially shorter in winter. The other bimodal, diurnal species remained active throughout the day in winter although activity was reduced during the hottest period of the day. In contrast, in summer these species had a period of total inactivity in the middle of the day. *Pheidole tenuinodis* was primarily nocturnal in summer and crepuscular to diurnal in winter. *Monomorium alamarum*, *M. vatranum*, *Tetramorium rufescens* and *T. sericeiventre* were primarily crepuscular to diurnal in summer and almost exclusively diurnal in winter.

Table 2. *Activity overlap values for the eight ant species for winter and pre-rain summer. Summer overlap values are on the upper right and winter values on the lower left of the matrix*

	MD	TR	TS	MVi	MVa	MA	PT	OR
MD	—	0·19	0·04	0·94	0·02	0·04	0·82	0·0
TR	0·19	—	0·67	0·22	0·72	0·69	0·54	0·03
TS	0·02	0·60	—	0·08	0·70	0·47	0·38	0·05
MVi	0·97	0·45	0·03	—	0·07	0·09	0·87	0
MVa	0·07	0·85	0·67	0·21	—	0·49	0·25	0·08
MA	0·08	0·85	0·54	0·23	0·82	—	0·27	0·07
PT	0·47	0·74	0·30	0·73	0·60	0·70	—	0·0
OR	0	0·30	0·55	0·0	0·50	0·10	0·02	—

MD, *M. denticornis*, TR, *T. rufescens*; TS, *T. sericeiventre*; MVi, *M. viator*; MVa, *M. vatranum*; MA, *M. alamarum*; PT, *P. tenuinodis*; OR, *O. robustior*.

Activity similarity values for the winter and pre-rain summer periods are presented as a symmetrical matrix in Table 2. Of the 28 species pair combinations, 19 show a decrease in similarity of activity pattern in summer relative to winter and two species pairs only, *P. tenuinodis–M. denticornis* and *P. tenuinodis–M. viator*, show marked increases in similarity of activity pattern in summer relative to winter. The binomial probability of obtaining 19 shifts in one direction from 28 independent trials is 0·026; thus, this trend is unlikely to be due to chance.

In summer, the activity patterns of *O. robustior* were quite distinct from all other species but in winter, reasonably high similarity values were recorded between *O. robustior* and *T. rufescens*, *T. sericeiventre* and *M. vatranum*. The two primarily nocturnal species, *M. denticornis* and *M. viator*, had very high similarity values in summer and winter. The activity of both species was dissimilar to all other species except for *P. tenuinodis*. The activity shift of *P. tenuinodis* from crepuscular–diurnal in winter, to primarily nocturnal in summer is reflected in the summer increases in similarity between it and *M. denticornis* and *M. viator*. Concomitantly, this change in activity pattern is reflected in the marked reductions in similarity between *P. tenuinodis* and *T. rufescens*, *M. vatranum* and *M. alamarum* in summer. *Tetramorium rufescens* exhibited moderately high similarity with *P. tenuinodis* and the three *Monomorium* species, and all showed a marked reduction in similarity from winter to summer.

The total number of exits and entrances that occurred in 24 hours was computed for each nest by interpolation. Two-way analysis of variance revealed significant interspecific differences in total daily activity ($p < 0{\cdot}005$) and activity duration ($p < 0{\cdot}001$) but no significant differences between winter and pre-rain summer (Table 3). However, in summer there were significant differences in total daily activity ($p < 0{\cdot}005$) and activity duration ($p < 0{\cdot}001$) before and after rain (Table 3). For most species total daily activity

Table 3. *Critical values of two-way analysis of variance tests of total daily activity and duration between seasons (winter versus pre-rain summer) and between pre-rainfall and post-rainfall summer periods*

	Total daily activity			Activity duration		
	F	d.f.	p	F	d.f.	p
Season						
Between species	12·268	7, 32	<0·001	23·450	7, 32	<0·001
Between seasons	2·011	1, 32	NS	0·812	1, 32	NS
Species × season	4·277	7, 32	<0·005	0·885	7, 32	NS
Rainfall						
Between species	4·517	7, 16	<0·01	50·541	7, 16	<0·001
Between pre- and post-rain groups	12·138	1, 16	<0·005	40·147	1, 16	<0·001
Species × rain	2·891	7, 16	<0·05	5·199	7, 16	<0·005

NS, not significant.

Table 4. *Comparison of daily surface activity before and after rainfall in summer*

		Number of ants per nest per day		Duration of activity (hours)	
Species	Nest	Pre-rain	Post-rain	Pre-rain	Post-rain
M. denticornis	1	31,278	74,178	16	24
	2	37,229	52,455	15	19
T. rufescens	1	6696	62,205	17	24
	2	10,886	205,860	18	24
T. sericeiventre	1	504	8580	5	10
	2	4776	29,610	6	10
P. tenuinodis	1	4185	20,295	18	24
	2	2964	10,605	16	22
M. viator	1	6111	77,100	13	22
	2	21,936	120,540	16	24
M. vatranum	1	756	1065	7	9
	2	570	1320	5	11
M. alamarum	1	810	2355	7	12
	2	1014	1650	9	6
O. robustior	1	376	152	6	1
	2	104	327	7	3

and activity duration increased after rainfall (Table 4). *Ocymyrmex robustior* showed a decrease in activity duration and conflicting patterns of change in total daily activity after rain.

The relative importance of surface temperature and vapour pressure deficit as determinants of ant activity, is represented by the standard partial regression coefficients in Table 5. The ratios of the standard partial regression coefficients suggest that, in general, surface temperature influenced activity more than vapour pressure deficit. The adjusted R^2 values imply, however, that a substantial amount of variation in activity is not explained by these two physical variables. Although the adjusted R^2 values were moderately low for most species (0·049–0·585), nine of them are significant ($p < 0·05$) and most of the remainder are close to significance. A Fisher's combined probability test (Sokal &

Table 5. *Relative importance, as measured by standard partial regression coefficients (c), of soil surface temperature T_s (°C) and vapour pressure deficit VPD (kPa) as determinants of ant activity*

Species	Season	T_s (c_1)	VPD (c_2)	Ratio c_1:c_2	Adjusted R^2	p	n
M. denticornis	Summer	−0·431	−0·113	3·8:1·0	0·209	<0·05	33
	Winter	−0·095	−0·296	1·0:3·1	0·083	<0·10	34
M. viator	Summer	−0·306	−0·097	3·2:1·0	0·049	<0·25	31
	Winter	−0·511	−0·039	13·1:1·0	0·359	<0·005	42
P. tenuinodis	Summer	−0·030	−0·397	1·0:13·2	0·130	<0·05	39
	Winter	−1·351	0·627	2·5:1·0	0·585	<0·001	28
T. rufescens	Summer	−1·177	−0·575	2·1:1·0	0·444	<0·001	39
	Winter	−0·860	0·131	6·6:1·0	0·533	<0·001	45
M. alamarum	Summer	−0·277	0·421	1·0:1·5	0·352	<0·005	23
	Winter	−0·815	0·279	2·9:1·0	0·324	<0·01	25
M. vatranum	Summer	−0·761	0·490	1·6:1·0	0·246	<0·05	20
	Winter	−0·331	−0·261	1·3:1·0	0.106	<0·10	27
T. sericeiventre	Summer	0·132	−0·579	1·0:4·4	0·143	<0·10	21
	Winter	−0·378	−0·086	4·4:1·0	0·077	<0·25	21
O. robustior	Summer	0·378	−0·227	1·7:1·0	0·206	<0·10	19
	Winter	−0·485	0·083	5·8:1·0	0·113	<0·25	13

Table 6. *Field-determined upper (T_{max}) and lower (T_{min}) thermal limits for surface activity and the temperature coinciding with maximal activity (T_{pref}). Values are black-body temperature at ant height (°C)*

Species	Activity period*	T_{min}	T_{max}	T_{pref}	Temperature range	n†
M. denticornis	N	7	39	20–23	32	8
M. viator	N	7	42	19–24	36	8
P. tenuinodis	FN	7	41	19–23	34	8
T. rufescens	FD	7	42	31–36	35	8
M. alamarum	D	19	46	35–40	27	8
M. vatranum	D	20	46	39–42	26	8
T. sericeiventre	D	26	46	38–42	20	8
O. robustior	D	33	>49	46–48	22‡	8

* N, Nocturnal; FN, facultative but predominantly nocturnal; FD, facultative but predominantly diurnal; D, diurnal.
† Number of colony days from which the data were derived.
‡ Maximum value from a Kuiseb River population in the central Namib Desert (Marsh, 1985*b*).

Rohlf, 1981) reveals that the overall relationship between surface temperature, vapour pressure deficit and activity is significant ($\bar{x}$ = 120·9854; d.f. 32, $p < 0·05$).

All species were active over a wide thermal range, with the predominantly nocturnal and facultative species operating over the widest range of temperatures (Table 6). Despite the range of temperature over which activity occurred, all nests, irrespective of season, were maximally active (defined as the greatest number of ants emerging and returning to the nest in a 10- or 15-minute observation period) over a fairly narrow range of temperatures. The preferred temperatures of species that were most active during relatively cool conditions, were situated approximately midway between the minimum and maximum tolerated temperatures. In diurnal species there was a tendency for preferred temperatures to approach the upper tolerance limits.

Critical thermal limits

CT_{max} and CT_{min} were similar for all species irrespective of their activity period (Table 7). CT_{max} ranged from 42·9–51·5°C and CT_{min} from 8·5–13·3°C. Despite these similarities, individual variation within a species was small and most interspecific comparisons were significantly different. In general, CT_{max} values for the diurnal species were higher than for the more nocturnal species, with the most diurnal species, *O. robustior*, having the highest CT_{max}. Although *M. denticornis* is predominantly nocturnal, it had a high CT_{max}. The predominantly nocturnal and crepuscular–nocturnal species, *M. denticornis*, *M. viator* and *P. tenuinodis*, had the lowest CT_{min} values (all <10°C), whereas all diurnal species had CT_{min} >10°C.

Table 7. *Laboratory-determined critical thermal limits for eight common Namib Desert ant species: critical thermal maxima (CT_{max}) and critical thermal minima (CT_{min}) (°C)*

		CT_{max}			CT_{min}		
Species	Activity*	Mean	Standard error	*n*	Mean	Standard error	*n*
M. denticornis	N	47·5	0·2	15	8·6	0·3	15
M. viator	N	46·7	0·3	15	9·1	0·2	15
P. tenuinodis	FN	42·9	0·3	15	8·5	0·1	15
T. rufescens	FD	46·9	0·1	15	11·4	0·1	15
M. alamarum	D	49·0	0·2	10	13·3	0·2	8
M. vatranum	D	49·0	0·3	15	10·9	0·3	15
T. sericeiventre	D	47·9	0·2	15	11·6	0·1	15
O. robustior	D	51·5	0·2	15	12·1	0·2	15

* N, Nocturnal; FN, facultative but predominantly nocturnal; FD, facultative but predominantly diurnal; D, diurnal.

All species pair comparisons were significantly different (Mann–Whitney *U*-test, $p < 0.05$) except for *M. viator–T. rufescens, M. denticornis–T. sericeiventre, M. vatranum–M. alamarum* (CT_{max}) and *T. sericeiventre–O. robustior, T. rufescens–M. vatranum, M. denticornis–P. tenuinodis* (CT_{min}).

Discussion

A convenient way of looking at the determinants of activity is to assign them to two groups; stimulatory–inhibitory and regulatory (Briese & Macauley, 1980). Simulatory–inhibitory factors control absolute levels of activity whereas regulatory factors determine relative rates of activity. The most important biotic stimulatory–inhibitory factor, particularly for harvester ants, appears to be food availability (Briese & Macauley, 1980; Whitford & Ettershank, 1975), although this will be modified by colony hunger. Marsh (1985*c*) has shown that activity levels of *M. denticornis* and *T. rufescens* increase significantly with increases in food abundance. This relationship undoubtedly exists in the other Namib Desert species studied but data on the availability of food for these species is lacking. An important physical stimulatory–inhibitory factor is rainfall (Briese & Macauley, 1980; Schumacher & Whitford, 1976; Whitford, 1978; Whitford & Ettershank, 1975). The

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of desert ants may have evolved. Interspecific aggression is common among ants (Holldobler, 1974; Holldobler & Lumsden, 1980; Mabelis, 1979; Samways, 1983; Steyn, 1954; Whitford, Johnson *et al.*, 1976; Wilson, 1971) and temporal partitioning may reduce aggressive interactions (Briese & Macauley, 1980; Carothers & Jaksic, 1984; Chew, 1977; Hansen, 1978; Melhop & Scott, 1983; Schumacher & Whitford, 1976; Whitford & Ettershank, 1975; Whitford, Johnson *et al.*, 1976; Whitford, Depree *et al.*, 1981). However, although interspecific aggression does occur among the Namib Desert ants (Marsh, 1985*c*), data on the frequency of interspecific encounters and the severity of aggression are required before the notion that temporal partitioning enhances species persistence in a given habitat can be critically assessed. The seasonal shifts in activity patterns are best interpreted as responses to the physical environment. The reduction of temporal overlap among diurnal species in summer, for instance, probably reflects the longer daylight period and consequent broader spread of temperatures during this period.

Another possible explanation of interspecific differences in temporal activity periods is that different species have different navigational requirements. Two of the predominantly nocturnal species, *M. denticornis* and *P. tenuinodis*, are trunk-trail foragers (Marsh, 1984) and use pheromone trails to navigate between the nest and foraging area. Pheromone persistence may be enhanced during the comparatively cool and moist nocturnal period although there are diurnal ants in other hot environments that utilise trunk trails (Gamboa, 1976; Greenaway, 1981; Wheeler & Rissing, 1975). In the Namib Desert many diurnal species do not normally exhibit pheromone trail-laying behaviour (pers. obs.). These ants presumably rely on solar navigation and therefore could not forage at night.

Finally, it has been suggested that differences in activity patterns in ectotherms may merely reflect different thermal preferenda and that temporal partitioning is essentially an epiphenomenon (Carothers, 1983; Huey & Pianka, 1981, 1983). The above explanations for interspecific partitioning of time are also not necessarily mutually exclusive. All or some of them may be relevant; some could be the proximal reasons for the observed differences while others may be the ultimate reasons the interspecific differences have evolved.

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present study supports this notion, as activity increased substantially for most species after rain (Tables 3 and 4). Elevated activity levels were not only a consequence of an increased duration of the activity period, since at any given moment activity levels were considerably greater in most species. The increase in activity duration after rain may be a consequence, in part, of cloud cover and moist sand which reduced thermal and desiccation stress throughout the 24-hour sampling period. Observations on some nests indicated that the increased activity subsequent to rainfall is caused by an increase in both foraging effort and nest construction. The increase in foraging effort may be in response to an increase in availability of food, such as insect prey, but the principal food item for most of the ant species is seed (Marsh, 1985*a*), which could not have increased in abundance in the time available. Furthermore, it is unlikely that seed availability could have increased through uncovering of seeds, since the rainfall in question was very gentle (1·3 mm in 6 hours). In the absence of quantitative data on feeding habits and food availability on either side of a rainfall event, this remains speculative. Much of the increase in activity after rainfall is attributable to nest construction, particularly debris removal. It appears that rainfall stimulates ants to expand nest size, probably in anticipation of seed production and the resultant storage requirements and/or increase in colony size. Some of this activity may also be related to nest entrance expansion to facilitate the departure of reproductives which occurs typically after rainfall (Conway, 1980; Curtis, 1983; Delye, 1968; pers. obs.).

The absence of seasonal differences in the number of active individuals and activity duration was an unexpected result. This probably reflects the fact that similar prevalences of suitable microclimatic conditions exist for each species in summer and winter. That these conditions occur at different times in the diel cycle is reflected in the observed diel shifts in activity patterns.

In the present study, variations in the thermal and humidity environment explain a significant amount of the observed variation in activity, although a substantial amount of variation cannot be attributed to these two factors. Similar unexplained variation has been found in studies of ant activity in the Chihuahuan Desert (Whitford & Ettershank, 1975; Whitford, Depree *et al.*, 1981) and in semi-arid Australia (Briese & Macauley, 1980).

North American desert ants do not utilise the entire spectrum of thermal conditions available to them (Whitford & Ettershank, 1975; Whitford, Depree *et al.*, 1981). In general, nocturnal species approach their CT_{min} while foraging but cease activity considerably below their CT_{max}. Conversely, diurnal species typically commence surface activity when conditions are substantially hotter than their CT_{min} and forage until temperatures approach their CT_{max}. In contrast, some of the Namib Desert ant species were active over virtually the entire range of thermal conditions that they could withstand physiologically, for example *M. alamarum*, *M. viator*, *P. tenuinodis* and *T. rufescens* (Tables 6 and 7). Indeed, some species appeared to be active at temperatures less than their CT_{min} but this presumably indicates the difficulties involved in assessing locomotor dysfunction in response to increasing cold.

In general, the preferred temperatures of desert ants are lower in nocturnal than in diurnal species (Delye, 1968; Kay, 1978). Most species prefer temperatures between 20 and 30°C but values of 35–40°C have been reported for *Cataglyphis* spp. that exhibit extreme diurnalism (Delye, 1968). The Namib Desert ant species conform to these general trends, with predominantly nocturnal species preferring temperatures below 24°C and diurnal species preferring temperatures of *c.* 40°C.

Strong winds can inhibit ant activity (Briese & Macauley, 1980; Curtis, 1985; Sheata & Kaschef, 1971). Briese & Macauley (1980) suggest that wind speeds >8 m/s inhibited activity in an Australian ant assemblage. In the Namib Desert the critical wind speed was *c.* 6 m/s (pers. obs.). Above this speed ants were occasionally lifted up and blown off course. During the study period wind strength seldom exceeded this critical limit (Table 1) and thus wind *per se* probably had little effect on the overall results. Wind may, however, have had an indirect effect on ant activity by modifying the thermal environment.

There are several possible reasons why interspecific differences in the activity patterns

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