Activity of the Namib Desert dune ant, *Camponotus detritus*

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The activity of the ant *Camponotus detritus* was studied in the dunes of the central Namib Desert. Activity was divided into two components: transit activity and honeydew collection. Temperature governed both forms, but light controlled the initiation and termination of transit activity, which was bimodal in warm conditions and unimodal in cool conditions. No transit activity occurred at night. Ants were active over a surface temperature range of 10 – 55°C. Owing to a steep thermal gradient above the sand surface during the day in summer, the temperatures which the ants' bodies experienced at 5 mm above the sand were 10 – 15°C lower than surface temperatures; well within the ants' physiological limits. Winds of about 16 km h^{-1} inhibited activity which ceased when wind speeds reached about 25 km h^{-1}. In summer, the number of ants collecting honeydew was negatively correlated with air temperature while in winter it was positively correlated.

S. Afr. J. Zool. 1985, 20: 41 – 48

Die bedrywighede van die mier *Camponotus detritus* is in die duine van die sentrale Namibwoestyn bestudeer. Bedrywigheid is in twee komponente verdeel: rondbeweging en versameling van heuningdou. Temperatuur het albei bedrywighede bepaal maar lig beheer die aanvang en terminering van rondbeweging wat onder warm toestande bimodaal kon wees maar op koel dae slegs een piek het. Geen rondbeweging het snags voorgekom nie. Miere was oor 'n oppervlaktemperatuurbereik van 10 – 55°C bedrywig. Die skerp temperatuurgradient bo die sandoppervlak bedags in die somer het tot gevolg dat die temperatuur waaraan die mier se liggaam 5 mm bo die sand blootgestel was, 10 – 15°C laer as die oppervlaktemperatuur was; goed binne die mier se fisiologiese perke. By 'n windsterkte van ongeveer 16 km h^{-1} is bedrywigheid geïnhibeer en by omtrent 25 km h^{-1} is dit gestaak. In die somer was die aantal miere wat heunigdou versamel het, omgekeerd eweredig aan lugtemperatuur terwyl dit in die winter eweredig was.

S.-Afr. Tydskr. Dierk. 1985, 20: 41 – 48

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Received 23 November 1984; accepted 18 December 1984

The factors governing activity of any species are important since they determine the foraging time available to that species. Light is the controlling factor for activity of a number of ant species, particularly forest dwellers which experience fairly constant temperatures and humidities (Lévieux 1975; Lévieux & Louis 1975). Among desert species, however, temperature is more important (Délye 1968; Whitford, Depree, Hamilton & Ettershank 1981).

Many desert arthropods are nocturnal, avoiding high daytime temperatures. Of those which forage diurnally, most cease activity when surface temperatures reach a certain critical maximum. The diurnal harvester ants of North American deserts are active over a range of surface temperatures from 4 – 57 °C, depending on the species (Bernstein 1979). The meat ant, *Iridomyrmex pupureus*, of arid Australia is active over a narrower range, 14 – 43,5 °C (Greenaway 1981). Honeydew collectors may be active among the foliage for longer periods than surface foragers, but do not cross the ground when surface temperatures exceed a critical maximum (Greenaway 1981).

Camponotus detritus Emery is a large (7 – 16 mm) honeydew-feeding ant living in the sand dunes of the central Namib Desert in SWA/Namibia. Nests, ranging in size from 200 to 15 000 workers, are excavated among the roots of the sparse perennial vegetation on the dune slopes. Workers collect honeydew from scale insect-infested plants, sometimes walking as far as 200 m across bare sand from their nest to do so. Usually workers leave the nest individually, although occasionally groups of ants following a leader may be seen. No fixed trails are used but all workers move in the same general direction towards their foraging grounds (Curtis, B.A. 1983, unpublished M.Sc. thesis).

The Namib is a long, narrow desert on the west coast of southern Africa. The cold Benguela Current and south Atlantic anti-cyclone are responsible for the regular occurrence of advective fog. In summer (November to February), south-westerly winds off the coast help to lower the temperatures. In winter (May to August) hot easterly winds from the interior raise temperatures, with the result that the Namib does not experience marked climatic changes.

The term 'activity' refers to the state of moving of an animal. Most authors, when referring to ant activity, are referring to those ants entering or leaving the nest, usually along well-defined trails or tracks (eg. De Bruyn & Kruk-De Bruin 1972; Sanders 1972; Whitford & Ettershank 1975). They often equate this activity with foraging intensity. The term 'activity' can be somewhat misleading, however, since ants involved in maintaining the nest are 'active' yet are not

Similarly, not all *C. detritus* workers leaving the nest in search of food. Many may be going to a sister nging to the same colony. When visible activity on surface ceases, foragers may still be 'active' on the ered plants.

:udy was undertaken to determine the factors gover- activity of *Camponotus detritus* and to establish the ure range over which activity of these ants occurs. ' was divided into two components: 'transit activity' neydew collection'. The former term refers to those ıls leaving the nest area altogether, or returning from e of at least 300 mm, whether it be to forage, to enter nest belonging to the same colony or to collect material for the nest. The terms 'honeydew n', 'tending' and 'foraging' have been used inter- ɔly to refer to those workers present on scale-infested

ls and Methods

:rvations were made in the dunes near Gobabeb ;/15°04′E) in the central Namib Desert.

activity

tions were made on 40 separate days and 20 nights sts over the period July 1979 to July 1982. A circle wn in the sand, or marked with string, around the rance 200 – 300 mm from the hole. The number of ssing the line, whether on their way into or out of was counted over a 5-min period every 15 or 30 min. t had more than one entrance on opposite sides of nd, a circle was drawn around the entire mound and into segments. Numbers of ants crossing the line were for 1 min per segment, and the total from all the s expressed as the number of ants active per minute hat observation period.

)-climatic data were recorded concomitantly: sand temperature was measured with either a Yellow Instruments telethermistor probe or a thermocouple 3ailey BAT 4; air humidity was measured at 1,5 m sling psychrometer. During the last 15 observation temperature of the air at ant body height (5 mm ne sand surface) was measured with a thermocouple ailey BAT 4. All wind speeds were recorded with a cht wind totalizer at a height of 1 m. Since wind speed s with height, the wind speed which the ants experience n above the ground would be less than that recorded wind totalizer. The simplest expression of the rela- between wind speed and height is

$$= a \log z + \log u$$

$=$ wind speed at height z (expressed in metres), nd speed at 1 m, and a = a variable which depends speed, temperature and ground surface (Geiger 1973

ve occasions simultaneous recording of wind speed n and 1 m were compared and a mean value of 0,114 ed for a. This value was used in the above equation ert wind speed at 1 m to wind speed at 5 mm. All eeds presented in the Results have been thus converted speed at 5 mm.

lew collection

nber of workers present per unit area of plant was hourly during the day and every two hours at night, concurrently with transit activity observations. As movement of ants on the plant was slight it was possible to count the number of ants in a small area at one time. Night observations were made using a fluorescent torch. Air temperature at 0,5 m, sand surface temperature, wind speed and humidity were recorded as before. To determine the lengths of time which individual ants spent foraging, 40 and 17 ants were marked with a spot of Humbrol enamel paint on the thorax and their position noted every half hour for 29 and 48 h respectively.

Differences between the number of ants collecting honeydew at night and during the day were tested using Student's *t* test. Correlations between the number of honeydew collectors and micro-climatic data were determined using the Product Moment correlation coeffecient.

Results

Transit activity

Transit activity was never observed at night but was very conspicuous during the day. This activity pattern was either bimodal or unimodal depending on the time of year. During the summer months [mean maximum surface temperature 61 °C (Seely & Stuart 1976)] activity peaks occurred during the morning and afternoon with a cessation of activity during the hottest part of the day (Figure 1). Sometimes, when heavy fog during the morning prevented midday surface temperatures from exceeding about 50 °C, activity continued through midday; nevertheless the pattern remained bimodal. During the winter months, [mean maximum surface temperature 44,2 °C (Seely & Stuart 1976)] transit activity was generally unimodal with no marked activity peaks and no midday cessation of activity (Figure 2). Occasionally, when surface temperatures approached 50 °C during a period of hot east winds, a bimodal activity pattern with decreased midday activity was again observed. Activity patterns during the intervening months, March, April, September and October, varied depending on the midday surface temperatures.

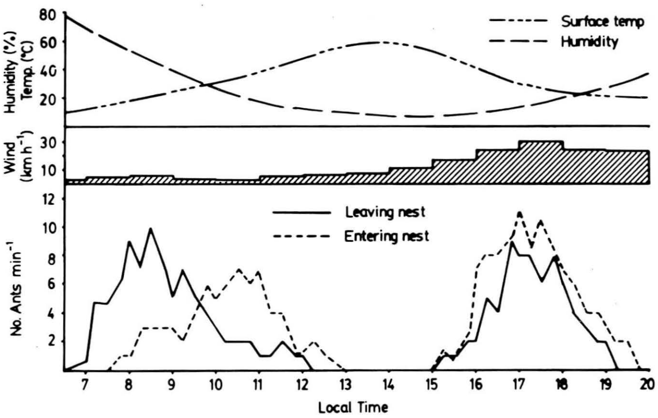

Figure 1 The effect of micro-climate on transit activity in summer observed at a *Camponotus detritus* nest on 7 November 1980. Local time precedes sun time by one hour.

Initiation of transit activity

Table 1 summarizes the micro-climatic data recorded at the start of transit activity. Light and temperature appeared to be the major factors responsible for initiation of activity, which never commenced before first light, even on occasions when pre-dawn surface temperatures were above 20 °C. Often ants were observed standing outside the nest entrance, or

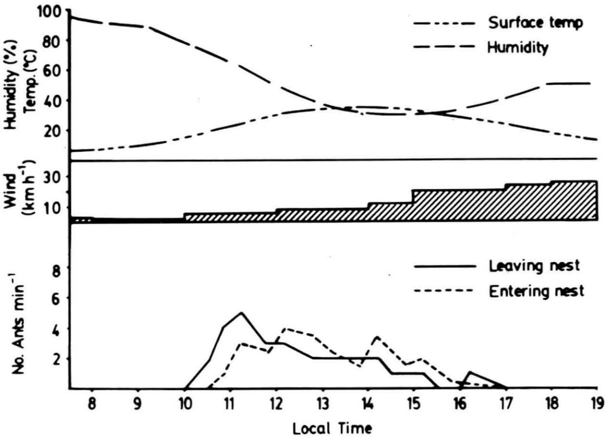

Figure 2 The effect of micro-climate on transit activity in winter observed at a *Camponotus detritus* nest on 29 June 1981. Local time precedes sun time by one hour.

rearranging detritus above the nest before dawn, but they only left the nest area when it became light. In contrast, winter activity often began an hour or two after sunrise when the mean surface temperature was 10 °C. During the warm east wind periods, however, when both air and surface temperatures were higher, winter activity began at sunrise. The presence of low fog appeared to have no effect upon transit activity except when surface temperatures were below about 10–15 °C, at which point activity was delayed.

The large standard deviation in relative humidity at the start of transit activity suggests that there is no causal effect between humidity and onset of transit activity. For example, activity was observed to commence during a fog when humidity was as high as 90–100% and during an east wind when humidity was only 10%.

Termination of transit activity

The micro-climatic data recorded at the termination of transit activity are shown in Table 2. Both in summer and winter, surface temperatures at the end of transit activity were 10–11 °C higher than those at the start of activity. This may be purely coincidental, since surface temperatures at sunset are usually higher than they are at sunrise and the onset of darkness may be the only causal factor for terminating activity. However, in winter activity always ceased either before or at sunset, and not at the onset of total darkness as in summer. An exeption to this was activity during east wind periods, when winter activity sometimes terminated with darkness, and surface temperatures were about 28 °C. This again suggests that temperature, as well as light, controls the temination of activity. The inhibiting effect of darkness on transit activity was seen on very hot days when surface temperatures were above 30 °C, yet all transit activity ceased by the time darkness fell. Darkness did not mean a total cessation of all activity, however. Surface nest maintenance continued throughout the night, both in summer and winter, when surface temperatures

Table 1 Micro-climatic conditions prevailing at the start of *Camponotus detritus* transit activity

	Time of sunrise	Time activity commences		Surface temp. (°C)			Ambient rh (%)			Nest temp. (°C)		
Season	(range)	range	*N*	*x̄*	S.D.	*N*	*x̄*	S.D.	*N*	*x̄*	S.D.	*N*
Summer												
Nov – Feb	06h12 – 06h45	06h00 – 07h30	12	15,9	2,8	8	81,6	9,8	11	26,5	4,5	12
Intervening months												
Mar, Apr, Sept, Oct	06h45 – 07h15	07h00 – 08h00	11	15,2	1,9	9	75,2	23,0	11	–	–	–
Winter												
May – Aug												
East wind	07h15 – 07h40	07h00 – 08h30	6	17,5	4,6	6	10,7	2,9	6	25,3	1,5	3
Non-east wind	07h15 – 07h40	08h15 – 09h30	11	10,3	3,1	10	68,1	29,3	11	15,7	2,2	6

Table 2 Micro-climatic conditions prevailing at the termination of *Camponotus detritus* transit activity

	Time of sunset	Time activity ceases		Surface temp. (°C)			Ambient rh (%)			Nest temp. (°C)		
Season	(range)	range	*N*	*x̄*	S.D.	*N*	*x̄*	S.D.	*N*	*x̄*	S.D.	*N*
Summer												
Nov – Feb	19h15 – 19h45	19h40 – 20h30	11	26,1	3,6	11	40,8	15,6	11	34,0	5,6	12
Intervening months												
Mar, Apr, Sept, Oct	18h45 – 19h15	17h00 – 19h30	9	26,1	2,5	9	32,8	19,6	11	–	–	–
Winter												
May – Aug												
East wind	18h20 – 18h45	18h00 – 18h50	4	28,2	2,9	6	7,8	5,6	6	28,3	2,1	3
Non-east wind	18h20 – 18h45	17h00 – 18h45	11	21,3	4,3	10	36,3	14,6	9	23,0	3,1	6

were above 10 – 15 °C. Honeydew collection too, continued throughout the night.

As during the start of activity, humidity at the termination of activity was very variable and unlikely to have had a causal effect.

Midday quiescence

Mean surface temperatures and humidities at the start and end of the period of midday inactivity are shown in Table 3. Both temperature and humidity were variable. On some occasions activity ceased when surface temperature was 40 °C while on others a few individuals were active at 60 °C. In general, it appeared that the ants were active at higher midday surface temperatures in summer than during the intervening months. Generally, no periods of total inactivity occurred in winter, except sometimes when surface temperatures were above 40°C.

Table 3 Micro-climatic conditions prevailing during the midday quiescence of *Camponotus detritus*

	Summer Nov – Feb			Intervening months Mar, Apr, Sep, Oct		
	$\bar{x}$	S.D.	*N*	$\bar{x}$	S.D.	*N*
Start of quiescence						
Surface temperature (°C)	55,8	5,2	11	46,6	5,6	5
Ambient humidity (%)	29,5	8,8	10	17,8	6,9	5
Nest temperature (°C)	29,8	5,9	11	–	–	–
End of quiescence						
Surface temperature (°C)	52,3	6,4	11	51,4	3,4	5
Ambient humidity (%)	24,1	7,9	10	12,4	7,7	5
Nest temperature (°C)	34,5	6,2	11	–	–	–
Length of quiescence	Range			Range		
Days without fog (h)	1,8 – 5,0		9	0 – 4,5		7
Days with fog (h)	0 – 4,0		3	0 – 1,5		3

Saturation deficit, which is a measure of the dryness of the air, appeared to have little effect on the length of midday quiescence. It is likely, however, that a combination of factors, such as surface temperature, saturation deficit and wind speed, control the behaviour of *C. detritus* during the midday heat, with threshold temperatures being the major factor.

Peak transit activity

The time of peak transit activity varied considerably depending upon the prevailing micro-climatic conditions (Table 4). Although peak activity occured over a fairly wide range of surface temperatures, activity patterns of neighbouring nests observed simultaneously were similar. Summer morning peaks always occured at lower temperatures and higher humidities than afternoon peaks (Figure 3). Sometimes in winter there were four of five small activity peaks, rather than one or two distinct peaks.

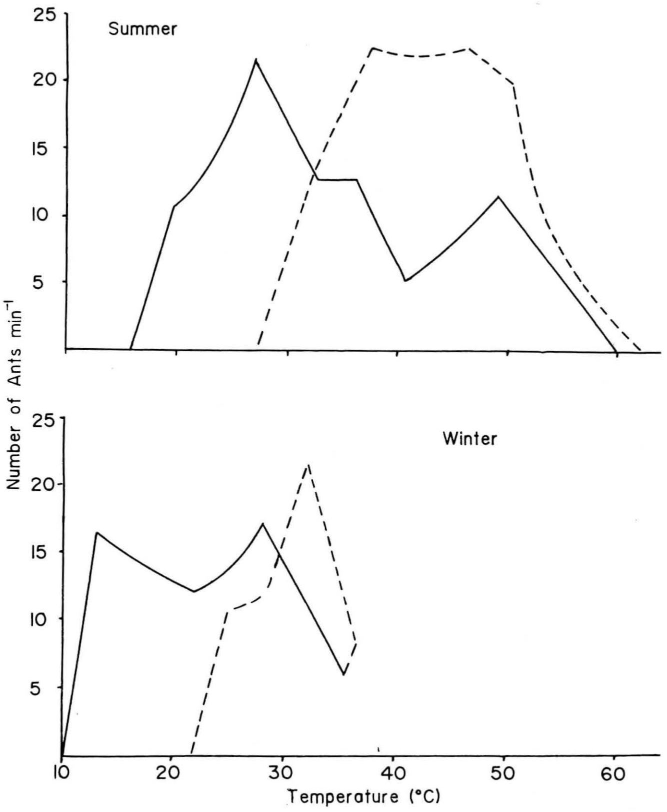

Figure 3 An illustration of the difference between morning (sunrise to noon) (solid lines) and afternoon (noon to sunset) (broken lines) transit activity (ants entering and leaving the nest) as related to surface temperature.

Thermal gradients

Myrmecologists studying terrestrial species generally only measure surface temperature (eg. Whitford & Ettershank 1975; Whitford *et al.* 1981) as most ant species have short legs and their bodies are almost at ground level. Since *C. detritus* is a species with relatively long legs for an ant (length

Table 4 Micro-climatic conditions prevailing during *Camponotus detritus* activity peaks

	Morning peak						Afternoon peak					
	Surface temp. (°C)			Ambient rh (%)			Surface temp. (°C)			Ambient rh (%)		
Season	$\bar{x}$	S.D.	*N*	$\bar{x}$	S.D.	*N*	$\bar{x}$	S.D.	*N*	$\bar{x}$	S.D.	*N*
Summer												
Nov – Feb	30,6	9,9	11	56,4	15,2	10	37,2	5,3	13	31,6	13,8	13
Intervening months												
Mar, Apr, Sept, Oct	28,7	8,6	12	57,2	17,2	12	40,2	5,7	9	26,7	14,6	9
Winter												
May – Aug												
Non-east wind	25,7	9,3	10	50,3	20,9	12	32,8	8,1	5	22,0	16,0	4

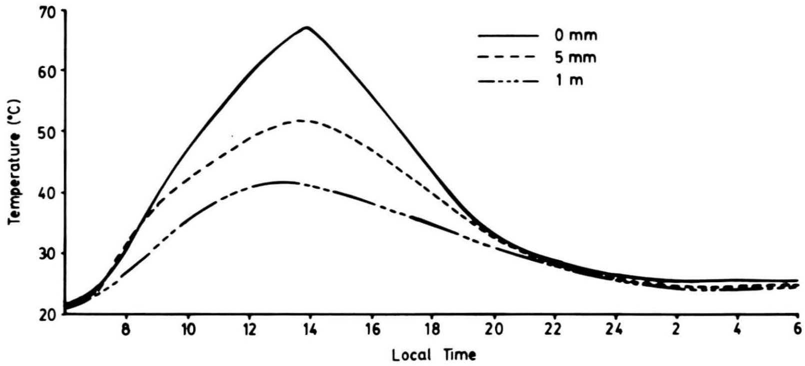

Figure 4 Thermal gradient above the sand surface in the dunes of the Namib Desert in summer (6 February 1982). Local time precedes sun time by one hour.

of tibia and tarsus 5,04 ± 0,58 mm, 20 workers of all sizes), the temperature to which an ant's body is exposed is the temperature of air 5 mm above the ground. At night and in the early morning, air temperatures at 5 mm were the same as surface temperatures, but in summer, as surface temperatures increased, a steep thermal gradient developed above the sand surface until at midday, temperatures at 5 mm were sometimes as much as 10 – 15 °C lower than surface temperatures (Figure 4).

During midday in summer when surface temperatures were 50-55 °C, the temperatures to which the ants' bodies were exposed were only 40 – 45 °C. These temperatures were within the physiological limits of the ants as determined in the laboratory (Curtis, in prep.). Since peak transit activity occurred when surface temperatures were between 30 °C and 43 °C with a mean of 37 °C, the ants would have experienced air temperatures of 25 – 38 °C at 5 mm, with a mean of about 31 °C. This corresponds with the preferred temperature of *C. detritus* workers held at 30% rh in the laboratory (Curtis, in prep.).

Numbers of workers entering and leaving the nest during transit activity

In summer, the number of ants leaving or entering the nest during the day was initially low (one or two per minute), thereafter increasing rapidly to a peak with a mean number of 16,1 ± 8,0 S.E. (N = 12) ants min^{-1} (Figure 1). The peak number of ants leaving the nest often occurred slightly earlier than that of ants returning to the nest, but during the afternoon, numbers of ants entering and leaving the nest were usually similar.

The number of ants active during peak transit activity varied considerably from nest to nest, however, as well as from one month to another in the same nest. Sometimes 30 – 40 ants were active per minute during peak activity; at other times only 6 – 10 ants. The mean number of ants active throughout the day was similarly variable, with an overall summer mean of 6,2 ± 2,9 S.E. (N = 11) min^{-1}. This appeared to be associated to a certain extent, although not entirely, with surface temperature.

In winter, activity peaks were less marked than in summer, having a mean of 10,3 ± 3,6 S.E. (N = 11) min^{-1}, but the mean number of ants active throughout the day was not significantly different from that of summer, 5,1 ± 2,5 S.E. (N = 11) min^{-1}. A few nests became completely inactive in winter. During the intervening months mean peak activity was 17,2 ± 16,0 S.E. (N = 10) ants min^{-1} and the daily mean was 5,5 ± 5,3 S.E. (N = 9) ants min^{-1}.

The number of hours per day that ants were active was 10 – 11 h in summer and 9 – 10 h in winter. Longer daylight hours and higher morning surface temperatures in summer were counteracted by the midday quiescence. The total number of ants estimated to leave a nest during a day varied from about 700 to as many as 5 000. This does not necessarily reflect the number of individuals leaving the nest since a single ant may leave and re-enter the nest many times.

Effects of rain on transit activity

On the three occasions when rain fell for 10 min or more all transit activity ceased. Inintially, however, as the rain started to fall and immediately after a shower the numbers of ants leaving the nest to drink water from the damp sand rose markedly.

Effect of wind on transit activity

Moderate winds, up to 8 or 11 km h^{-1} at a height of 5 mm did not appear to inhibit transit activity. Small workers were blown off-course by 8 km h^{-1} winds, and yet they continued walking against the wind. At about 16 km h^{-1} and above, wind appeared to have a marked inhibiting effect upon activity. Figure 5 shows the effect of an east wind on the activity of two nests in the same area. The entrance of nest C faced east, while the entrance of nest B was on the west side of a large mound and was relatively protected from the wind. As workers from nest B left the lee of the mound they were blown off-course by the wind and about 90% of them returned to the nest after walking 1 – 3 m away from the nest. During each 3 min observation period at nest C, from two to six workers came out of the nest briefly, but turned back again.

The general pattern of transit activity during an east wind appeared to follow the strength of the wind. As mentioned previously, the increased surface temperature caused transit activity to start at sunrise. Gradually, as both temperature and wind speed increased, transit activity decreased and finally ceased when the wind was gusting up to about 25 km h^{-1} and above. In the afternoon, when the wind dropped, the ants resumed transit activity.

Honeydew collection

Camponotus detritus workers were seen on scale-infested plants 24 h per day (Figures 6 and 7) with significantly more ants present at night than during the day in summer ($P <$ 0,05). This suggests that *C. detritus* is nocturnal as well as diurnal. However, during the day there was constant transit activity to and from the plants with a high change-over rate of foragers on the plants except during the heat of midday, while at night no movement occurred between plants or from

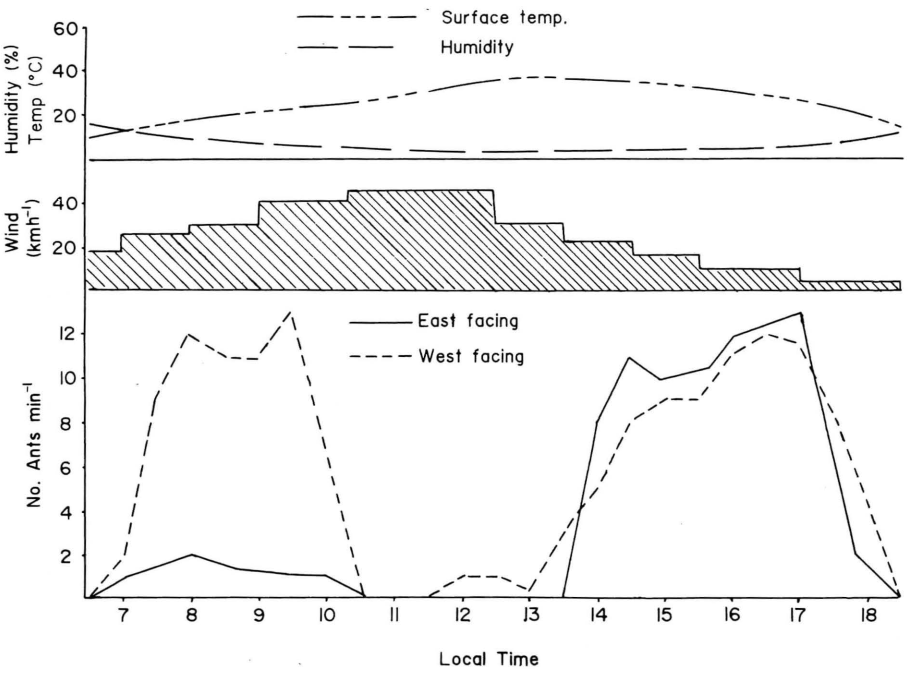

Figure 5 The effect of an east wind on the transit activity of *Camponotus detritus* observed on 14 July 1982. The lower graph shows the number of workers leaving two different nests, one with the entrance facing east, the other facing west (see text). Local time precedes sun time by one hour.

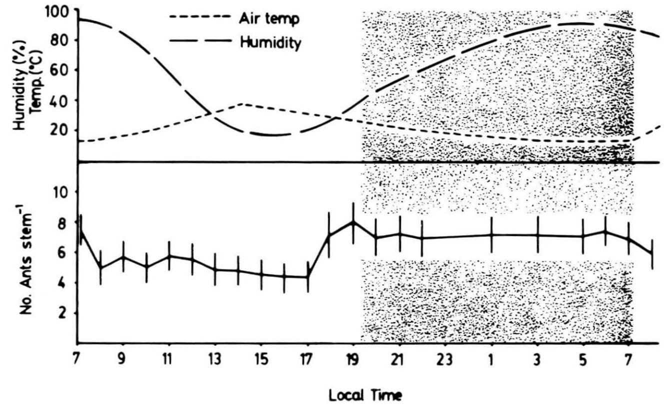

Figure 6 Summer honeydew collection activity of *Camponotus detritus* workers observed on 23 February 1982. Each point represents a mean of activity observed on 10 stems. Vertical lines indicate standard errors. Local time precedes sun time by one hour.

the plants to the nest. Only 38 ± 5 % of the individually marked ants seen during the day remained out at night, and all the ants present at nightfall remained on the same plant until dawn.

In summer the number of workers collecting honeydew was negatively correlated with ambient temperature ($P < 0,05$), with the lowest numbers of honeydew collectors occurring in the early afternoon (maximum air temperature) and maximum numbers just prior to sunset. Peak honeydew collection occurred at ambient temperatures (26 – 33 °C) similar to the experimentally determined preferred temperatures of workers (Curtis in prep.). Of the total number of foragers present at sunset, 87 ± 6 % remained on the plants throughout the night, the rest returned to the nest before darkness.

From about 20h00 – 24h00, 40 – 50% of the ants present were active while the rest remained motionless with their heads down and their legs close to their bodies. As the night progressed more and more ants became motionless. An hour

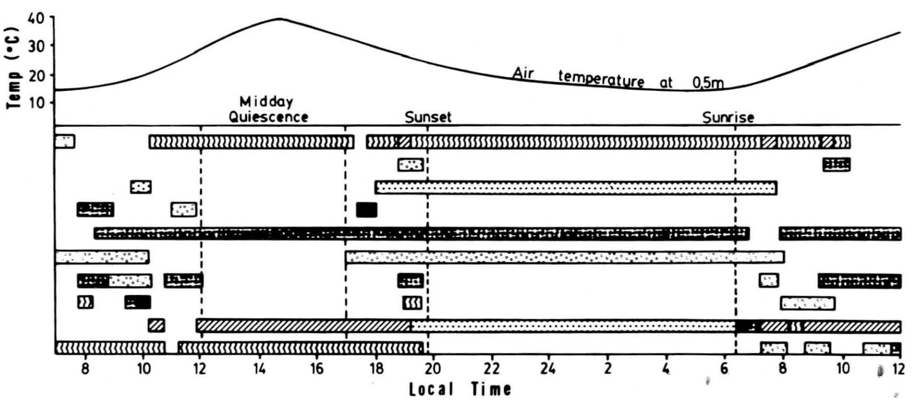

Figure 7 Honeydew collection activity of 10 individually marked *Camponotus detritus* workers observed on 23 and 24 February 1982. Each horizontal bar represents the activity of one ant. Shading indicates presence on different grass stems. Open areas indicate the absence of the ant, which was presumably in the nest at the time. Local time precedes sun time by one hour.

or two prior to sunrise about 10 – 30 % of the foragers had distended gasters and most of these foragers left the plants shortly after sunrise to return to the nest.

During the day individuals with distended gasters were also noticed on the plants, but in fewer numbers. There were considerable differences in the foraging time of individuals. Some of the marked ants foraged for only 30 min out of 48 h whereas others remained on one plant for as long as 26 out of 48 h.

In winter the pattern of activity was slightly different. There was a positive correlation between the number of ants collecting honeydew and ambient temperature ($P < 0{,}05$), with peak numbers in the late morning and minimum numbers at night. On warm winters nights (eg. after an east wind) the pattern of honeydew collection was the same as it was in summer but on cold nights all ants remained totally motionless. At temperatures below 8 °C some ants fell off the plants and remained on the sand until morning.

During an east wind the number of foragers was negatively correlated with wind strength and those ants that remained on the plants sheltered on the leeward side of the thicker stems. Only where scale insects were found on the leeward side of the stems did the ants continue to collect honeydew. There was no correlation between foraging intensity and relative humidity in either winter or summer.

Only two observations were made on honeydew collection during the intervening months. On both occasions the mean numbers of honeydew collectors were the same during the day and night, but the time of maximum and minimum numbers differed on each occasion.

Peaks in *C. detritus* transit activity did not correspond directly with peaks in the numbers of honeydew collectors present on the plants. The numbers of workers moving to and from the scale insect-infested plants however, showed a similar pattern to that of overall transit activity. Not all workers leaving the nest (i.e. transit activity) went to scale-hosting plants. Some went to other nests belonging to the same colony while others collected building material for the nest or scavenged for dead arthropods.

Discussion and Conclusion

Temperature, the major factor controlling the activity of *Camponotus detritus*, determined whether the ants were able to be active outside the nest, while light determined whether that activity took on the form of transit activity or simply nest maintenance and honeydew collection. Light, in conjunction with temperature, controls activity among American desert species (Kay & Whitford 1978). For *Pheidole* species which switch from noctural or crepuscular activity in summer to diurnal activity in winter, temperature is a more important activity cue than light (Whitford *et al.* 1981). Similarly, temperature governs activity of many Saharan ant species (Délye 1968).

Many ant species from vastly differing habitats exhibit a bimodal pattern of diurnal activity with a midday period of total inactivity when surface temperatures reach a certain threshold (eg. Délye 1968; De Bruyn & Kruk-de Bruin 1972; Lévieux 1977; Whitford, Depree & Johnson 1980; Whitford *et al.* 1981). Like *C. detritus,* the North American harvester ants, *Pogonomyrmex occidentalis, P. californicus* and *Myrmecocystus kennedei* cease surface activity at 54, 54, and 57°C respectively (Bernstein 1979). Individuals of the Saharan *Cataglyphis bombycina* have been seen active at a surface temperature of 58 °C (Délye 1968), while *Ocymyrmex barbiger* of the Namib is only active when temperatures are fairly high and has been observed moving across the sand at a surface temperature of 65°C (Marsh, A.C. 1983, pers. comm.). Like *C. detritus* however, most ants may be exposed only very briefly to surface temperatures above 50°C (Délye 1968; Whitford & Ettershank 1975; Kay & Whitford 1978).

Steep thermal gradients similar to those found in the Namib occur above the sand surface in the Sahara Desert and it is significant that those species which are active at high surface temperatures i.e. *Cataglyphis* species, also have long legs (Délye 1968). Species with short legs whose bodies are close to the ground eg. *Messor aegyptiacus* cease activity when surface temperature is 39°C.

Camponotus detritus had an unusually wide surface temperature range for activity: from 10 – 55 °C. *Pogonomyrmex occidentalis, P. californicus* and *Myrmecocystus kennedei* cease activity at surface temperatures similar to *C. detritus,* but only begin activity at surface temperatures of 27, 32 and 36 °C respectively (Bernstein 1979). *Messor aegyptiacus* and *Pogonomyrmex owyheei* which begin activity at 10 and 13 °C respectively, cease activity when surface temperatures reach 39 and 40 °C respectively (Dèlye 1968; Bernstein 1979). *Camponotus detritus* is the only ant species in the dunes at Gobabeb and the dominant dune species further east. Apparently for this reason it is able to utilize the full thermal range available to it, unlike species of the North American deserts, where interspecific competition has led to temporal partitioning of food resources (eg. Bernstein 1974; Schumacher & Whitford 1974; Whitford & Ettershank 1975; Davidson 1977).

Seasonal differences in activity patterns occur among a wide range of ant species. Like *C. detritus*, the temperate species *Formica polyctena* alternates between a bimodal and a unimodal activity pattern depending upon surface temperature (De Bruyn & Kruk-De Bruin 1972). Low winter temperatures result in a total cessation of all activity among many temperate species (eg Brian 1965; Sanders 1972; Mabelis 1979). Among three *Camponotus* species of the boreal forests the factors governing activity appear to vary seasonally (Sanders 1972).

The Australian *Iridomyrmex purpureus* also has two activity peaks in summer, one commencing at dawn and one late afternoon with a total of 6,8 h activity time. In winter, activity begins well after sunrise and ends late afternoon with a total of 7,4 h (Greenaway 1981). This is in contrast to *C. detritus* where total activity in summer is longer than that in winter. This may be explained by the fact that *I. purpureus* workers cease activity at lower surface temperatures (43,5 °C) than *C. detritus*.

Forage availability and quality greatly affect many desert species, particularly the seed harvesters, resulting in marked seasonal differences in foraging activity (Whitford, Johnson & Ramirez 1976; Bernstein 1979; Briese & Macauley 1980; Whitford *et al.* 1981). Colony satiation also plays an important role in regulating the activity of harvester ants (Whitford & Ettershank 1975).

The lack of seasonality in foraging intensity, the absence of food reserves within the nest and the presence of brood throughout the year suggest that *C. detritus* has a fairly constant food supply (Curtis in prep.). This food supply is maintained by the relatively uniform climatic conditions prevailing in the central Namib dune-field. Within a particular area, however, the amount of food available may vary, resulting in local activity differences. Thus certain nests were found to become completely inactive in winter, but this was the exception rather than the rule.

Although temperature appeared to be the major factor regulating honeydew collection by *C. detritus* workers, this may have been indirect, since the pattern of honeydew excretion by scale insects would influence the activity of ants, and may itself be either directly or indirectly influenced by temperature. Peak numbers of ants tending scale insects may reflect maximum daily honeydew production. Kawai & Tamaki (1969) found that maximum and minimum frequency of honeydew excretion by the scale insect, *Ceroplastes pseudoceriferus*, occurred between 18h00 – 20h00 and 06h00 – 08h00 respectively. A similar maximum peak of honeydew excretion by scale insects in the Namib during summer may by responsible for the increased numbers of ants on scale-infested plants just prior to sunset. Honeydew excretion may be higher at night than during the day as a result of the translocation of photosynthates in the plant at night, thus resulting in the presence of more ants at night. On the other hand, Myers (1957) found that the foraging rhythm of *Anoplolepis steingroeveri* was not correlated with the rate of honeydew production, but was correlated with ambient temperature. These plant/scale insect/ant interactions would provide very interesting and worthwhile possibilities for future research.

Like *C. detritus* the nearctic species *C. noveboracensis*, which collects honeydew excreted by a membracid, tends the membracid 24 h per day, but most activity between the nest and foraging grounds occurs during the day. At night and at low temperatures both ants and membracids remain motionless. In autumn when the numbers of membracids decrease, the numbers of foraging ants also decrease (Gotwald 1968).

Camponotus detritus may be described as a predominantly diurnal ant species whose activity appeared to be governed by a combination of temperature and light. Because of its long legs and the steep thermal gradient above the sand during the day and because it foraged off the ground among the foliage, this species was able to be active over a wide range of temperatures. Its status as the only or dominant ant species allowed it to utilize the full thermal range available to it. Seasonal changes in activity were reflected only in the pattern of activity and not in intensity. Since activity was not restricted by food production, as occurs among harvester species, these ants were able to maintain brood throughout the year, contributing to their success in the sand dunes of the Namib Desert.

Acknowledgements

This paper forms part of an M.Sc. thesis submitted to the University of Cape Town. My thanks to: Professor G.N. Louw and Dr M.K. Seely for supervision of the thesis; the Desert Ecological Research Unit (D.E.R.U.), Gobabeb, funded by the C.S.I.R. and Transvaal Museum, for use of vehicles, equipment and other research facilities; the Department of Agriculture and Nature Conservation, South West Africa/Namibia for use of facilities and permission to work in the Namib-Naukluft Park; the C.S.I.R. for a post-B.Sc. (Hons) bursary for two years; the University of Cape Town for a Twamley post-graduate bursary for one year and other financial support; D.E.R.U. technicians for help with field work and Dr M.K. Seely for reading the manuscript.

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