MICROCLIMATIC FACTORS INFLUENCING FORAGING PATTERNS AND SUCCESS OF THE THERMOPHILIC DESERT ANT, *OCYMYRMEX BARBIGER*

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SUMMARY

Ocymyrmex barbiger is a diurnal scavenger of arthropods in which the number of successful foraging excursions per colony per day increases with daily vapour pressure deficit. It appears that the ants make use of prey items which succumb to thermal and desiccation stress. Running speed is a function of surface temperature but progressively less time is spent searching for prey beyond a critical surface temperature with the result that the optimal search temperature for individual foragers is about 52°C. Maximal foraging activity of colonies occurs at surface temperatures corresponding to this optimal search temperature.

ZUSAMMENFASSUNG

Der Einfluss Mikroklimatischer Faktoren auf das Verhalten und den Erfolg bei der Nahrungssuche der thermophilen Wuesten Ameise
Ocymyrmex barbiger

Bei der *Ocymyrmex barbiger*, einem aasfressenden, tagaktiven Gliederfuessler, nehmen die erfolgreichen Nahrungsexkursionen, innerhalb einer Kolonie und eines Tages, mit dem taeglichen Dampfdruckabfall zu. Es hat den Anschein, als wuerden die Ameisen bei der Beutesuche von den Tieren Gebrauch machen, die den Temperaturen und der Austrocknung erlegen sind. Die schnelle Fortbewegung ist von der Oberflaechentemperatur abhaengig und sobald ein Grenzwert der Oberflaechentemperatur ueberschritten ist, wird zunehmend weniger Zeit fuer die Nahrungssuche aufgebracht. Die optimale Temperatur fuer die Nahrungssuche der einzelnen Ameise liegt bei ungefahr 52°C. Die maximale Aktivitat der nahrungssuchenden Ameisen einer Kolonie tritt bei Oberflaechen temperaturen ein, die dieser optimalen Temperatur entsprechen.

INTRODUCTION

Optimal foraging theory predicts that animals should forage in such a manner that their net rate of food intake is maximized (SCHOENER, 1971 ; KREBS & McCLEERY, 1984). This suggestion is both intuitively sensible and consistent with the theory of natural selection. It is, however, surprising that organisms should subject themselves to near-lethal temperatures in order to maximize their intake of food (WHITFORD et al., 1980). Nevertheless, there are situations where animals tolerate high thermal loads in their quest for food. For example, DREISIG (1980) has shown that the optimal foraging temperature of predatory tiger beetles, Cicindela hybrida, is close to their upper tolerance limit. This is a consequence of prey availability being greatest at such temperatures. In the Chihuahuan desert, the ant Novomessor cockerelli will forage under near-lethal thermal loads if the amount of proteinaceous food is increased artificially (WHITFORD et al., 1980).

In the Namib desert, workers of the ant Ocymyrmex barbiger regularly forage on barren ground until the surface temperature approaches 67° C. During these foraging excursions the ants are exposed to near-lethal thermal loads, where failure to locate thermal refuges at frequent intervals can be fatal (MARSH, in press). The present paper is concerned with the adaptive value of occupying this unusual thermal niche. To examine this problem, the diet and foraging behaviour of O. barbiger have been studied in relation to environmental conditions.

MATERIALS AND METHODS

The foraging ecology of O. barbiger was studied in the dry Kuiseb river bed, near the Namib Research Institute at Gobabeb (23°35 S ; 15°03 E). The river bed is sandy and supports numerous Acacia spp trees. Between the trees there are large patches of barren sand which receive direct insolation throughout most of the day. Foraging ants regularly spend their entire period of surface activity in these patches.

The ants live in small colonies in subterranean nests which are situated typically at the base of some living or dead vegetation, particularly grass clumps (Eragrostis spinosa), or in dry mud beds. Four nests that were excavated contained from 160 to 240 individuals. Ocymyrmex barbiger workers are monomorphic and have a live mass of 4.1 ± 1.2 mg (X ± sd, n = 30). Nests were located by following ants from a grid of bait. The distance from each nest to its nearest neighbour was measured.

Prey items were removed from ants as they approached their nest, and placed individually into sealed vials. The items were identified under a dissecting microscope, weighed, and then dried at 60°C for 24 h to determine moisture content. A minimum of 20 food items was collected every day, for six consecutive days, in October 1983. During this period microclimatic conditions varied considerably so that food collected during cool-moist days could be compared with that collected during hot-dry days. Food items were also collected in January and February 1982. During each collecting period, food was taken from ants as they returned to each of three nests.

Nests were observed for 10 min every 30 min from sunrise to sunset, and the number of ants that returned from foraging excursions was recorded. The total number of foraging excursions per day was computed by interpolation. Prior to each observation period, the following microclimatic data were noted: wet and dry bulb temperature at 1 m elevation using a sling psychrometer, and sand surface temperature using a copper-constantan thermocouple and digital recorder (BAILEY Instruments, Model BAT-12). The wet and dry bulb temperatures were used to calculate vapour pressure deficits, a measure of the drying power of the air. By interpolation, vapour pressure deficit was summed between 10h00 and 17h00 (the period when most ant activity occurred) and this value was considered to be an index of the physiological stressfulness of that day.

Ocymyrmex barbiger workers were easy to follow and observe, and showed no signs of being disturbed by an observer at a distance of 2-4 m Forty individual foragers were followed for entire foraging excursions and the following data collected for each excursion: the time that the ant spent on the sand surface relative to the total time it was out of he nest, the radius from the nest to the position where an item of food was located. Sand surface temperature was measured before and after each foraging excursion.

The speed of locomotion was determined for a range of sand surface temperatures by measuring the time ants took to move 1 m. To facilitate these observations, ants were lured to bait and only those ants which ran without hesitation toward the bait were included in the analysis.

RESULTS

Ocymyrmex barbiger is principally a scavenger of arthropods (table I). Of 242 items of food 95 % were insects, 2.4 % spiders and the remaining 2.6 % plant matter, specifically fruits. With the exception of two termites, all prey items were dead on arrival at the nest and many were fairly desiccated. The mean wet mass of prey items was 2.4 mg (range 0.12-24.7 mg) and the mean moisture content per item of forage was 19.1 %. The composition of the diet was similar during spring (October) and summer (January and February), the most notable difference being the greater importance of coleopterans in October (table I).

Despite the considerable range in maximum air temperature (24.3-37.3° C) and vapour pressure deficit (0.59-1.46 kPa) that occurred during the six days of sampling in October, there were no detectable differences in taxonomic composition of diet from day to day. The dry mass of food particles also did not differ from day to day (p > 0.05, t-test).

The activity patterns of ants from one nest on three different days are shown in figure 1. Day 1 was a cool-moist day, characterized by low vapour pressure deficits and surface temperatures. Days 2 and 3 were hot-dry days, characterized by high vapour pressure deficits and surface temperatures. Day 3 was exceptionally stressful in that, although the temperature profile was similar to that of Day 2, the vapour pressure deficit started off higher and remained higher throughout the day than Day 2. On the hot-dry days, foraging activity was bimodal, with morning and afternoon peaks

Table I. — Taxonomic composition of the diet of *O. barbiger*. The data are expressed as percentage of the total number of dietary items collected (n = 107 for the January/February sample and n = 135 for the October sample).

Tabelle I. — Taxonomische Zusammensetzung der Nahrung von *O. barbiger*. Die prozentualen Angaben beziehen sich auf das gesammelte Gesamtnahrungsgut (n = 107 Proben im Januar/Februar und n = 135 Proben im Oktober).

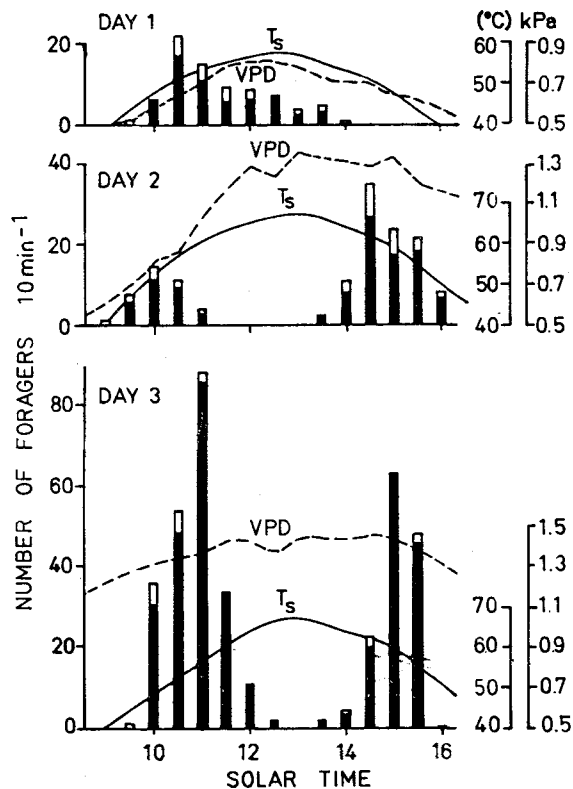| Food category	January/February (%)	October (%)
Lepidopteran larvae	20.6	27.4
Hymenoptera	34.6	14.8
Coleoptera	1.9	14.8
Hemiptera	9.3	13.3
Diptera	2.8	6.7
Isoptera	7.5	3.7
Thysanura	4.7	3.7
Neuropteran larvae	1.9	1.5
Insect remains	12.0	8.9
Araneae	4.7	0
Plant matter	0	5.2

Fig. 1. — Foraging activity patterns of an *O. barbiger* colony on three separate days in relation to meteorological conditions. Activity is expressed as the number of ants returning to the nest in 10 min. Shaded areas correspond to successful foragers. T_s = surface temperature (°C), VPD = vapour pressure deficit (kPa).

Abb. 1. — Verhalten bei der Nahrungssuche einer Kolonie von *O. barbiger* an drei verschiedenen Tagen in Beziehung zu Klimatischen Bedingungen. Als Aktivitaet wird die Anzahl der Ameisen angegeben die waehrend einer Beobachtungszeit von 10 Minuten zum Nest zurueckkehrten. Schattierte Areale beziehen sich auf die erfolgreichen Nahrungssucher. T_s = Oberflaechentemperater (°C), VPD = Dampfdruckabfall (kPa).

and a cessation of activity at midday. In contrast, on the cool-moist day foraging activity was unimodal. Similar patterns were exhibited from numerous other nests. The morning activity peaks on all three days occurred at surface temperatures between 52.0 and 56.5°C, whereas the afternoon peaks in activity on the two hot days occurred at a surface temperature of about 60° C. Despite similar surface temperature conditions, foraging activity ceased for about 180 min on Day 2 as opposed to 60 min on Day 3. The differences between the foraging activity on these three days are best illustrated by considering the total number of foraging excursions made during each day. Despite the relatively mild conditions on Day 1 only 232 foraging excursions occurred, whereas 423 occurred on Day 2, and on Day 3, the most stressful day, 1086 foraging excursions took place ; foraging activity increased with increasing environmental stress. Foraging efficiency, the number of ants returning with food relative to the total number returning to the nest, was similar on all three days (figure 1).

The relationship between the number of successful foraging excursions per day (excursions in which ants retrieved prey items) and summed daily vapour pressure deficit is presented in figure 2. These data were obtained over a period of 18 months from five different colonies and there is a significant correlation between environmental stress and the number of ants returning to the nest with food items ($p < 0.05$, t-test). Two of the five nests were observed for three to four days respectively (in the latter case observations were on consecutive days) and the relationship also held.

Ocymyrmex barbiger workers typically searched for and retrieved food items independently. Recruitment was, however, observed on numerous occasions. The recruiting ant emerged from the nest, with her gaster directed downwards in a typical trail laying posture, followed immediately by up to 10 recruits. The recruiter advanced at a relatively slow pace making frequent pauses, often appearing to pause until bumped by one of the recruits. The recruits darted rapidly from side to side, advancing less directly than the recruiter, but frequently overtaking her. Often, after a few metres, some recruits lost contact with the recruiter but invariably some were successfully directed to a prey item. For example, five recruits were successful in locating a large lepidopteran larva 40 m from the nest. Typically, recruitment occurred when an item of prey, too large for an individual to retrieve, was located. Cooperative retrieval of the intact prey items did not occur, instead the ants bit the prey into pieces that individuals could carry.

Foraging excursions lasted for up to 35.6 min (= 2134 s), and ants travelled up to 50 m from their nests in search of food. The distance covered on foraging excursions varied with microclimatic conditions. On a cool-moist day (maximum air temperature 30.0° C, surface temperature 57.0° C, vapour pressure deficit 0.70 kPa) the mean radius from the nest to the location of food particles was 31 ± 9 m ($\overline{X} \pm$ sd, n = 16), whereas, on a
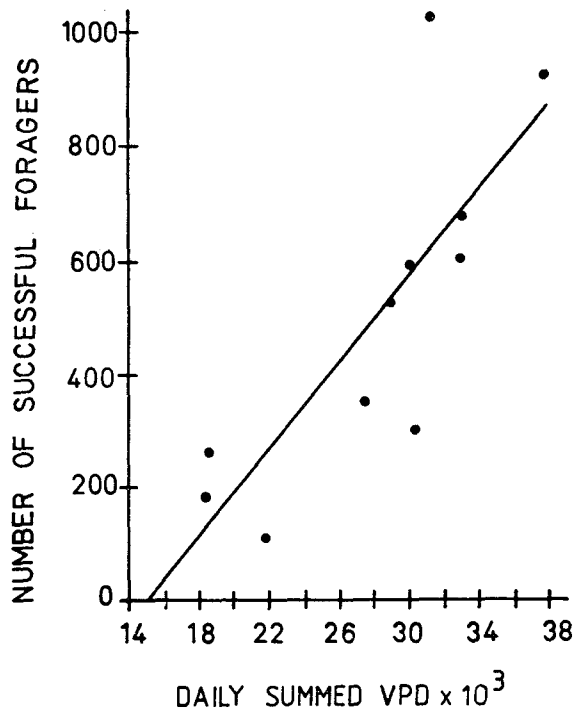
Fig. 2. — Relationship between the number of successful foraging excursions from one colony per day and summed daily vapour pressure deficit (kPa). y = —595.9 + 0.04×; r² = 0.64.

Abb. 2. — Verhaeltnis von der Anzahl der erfolgreichen Nahrungssucher einer Kolonie pro Tag, zum taeglichen Gesamt- Dampfdruckabfall (kPa). y = —595.9 + 0.04×; r² = 0.64.

hot-dry day (maximum air temperature 40.2° C, surface temperature 68.0° C, vapour pressure deficit 1.43 kPa) foraging distance was only 16 ± 9 m (n = 19). These values are significantly different (p < 0.05, MANN-WHITNEY U-test).

Relative to foraging distance, inter-nest distance was small (X̄ 32.2 m, range 13-50 m, n = 17). Thus colonies probably have overlapping foraging areas. This was confirmed by the frequent occurrence of ants from two to three colonies at the same bait point. Also, in the course of following foragers, there were occasions when an individual passed within a few cm of another colony's nest entrance.

Typically prey items were located on the exposed sand surface (n = 50 observations) and not in shaded areas. However, at surface temperatures greater than 51° C foraging ants make periodic retreats into thermal refuges, such as in the shade or by climbing up objects such as grass stalks (MARSH, in press), where food does not occur. With increasing sand surface temperatures beyond 51° C the effective time ants spent searching for prey, relative to the total time away from the nest, decreased progressively (fig. 3).

Running speed was a function of temperature, showing a linear increase between sand surface temperatures of 27-62° C (fig. 4). The maximum re-
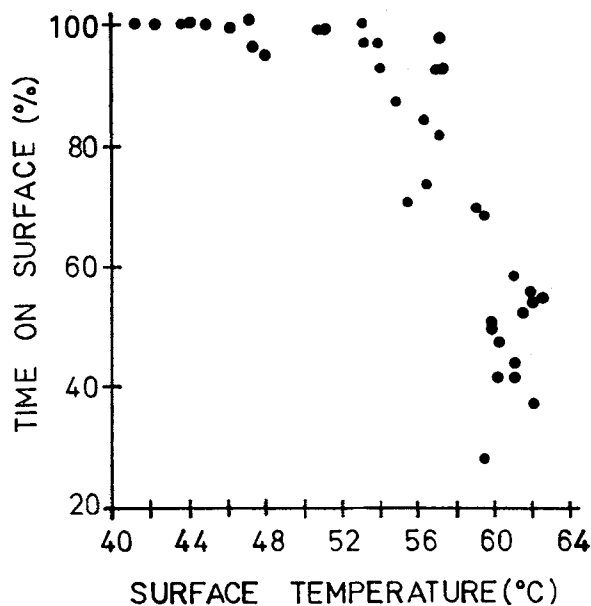
Fig. 3. — Relationship between
sand surface temperature
and the amount of time
foragers spent on the in-
solated sand surface rela-
tive to the total time
spent away from the nest.
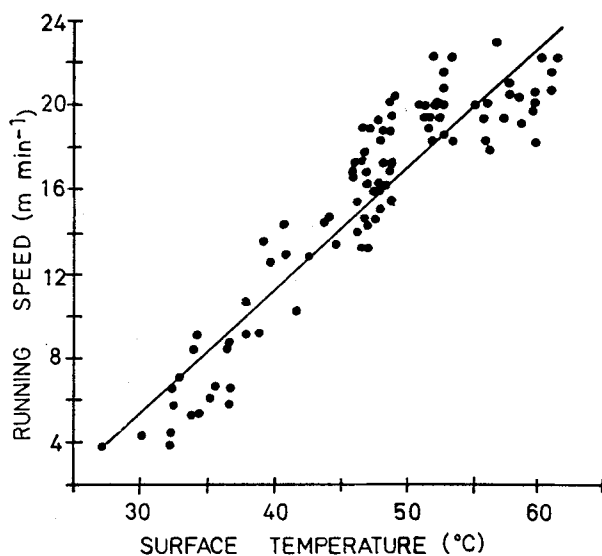
Fig. 4. — Relationship between
running speed and sand
surface temperature. y =
—11.79 + 0.58×; r^2 =
0.86.

corded speed was 23 m min^{-1}. At the lowest recorded temperature, when
the first individuals emerged to forage, ant movements were erratic and
uncoordinated, relative to locomotion at higher temperatures. There were
no apparent impairments to coordination at the highest recorded tempera-
tures.

DISCUSSION

The present study indicates that *O. barbiger* is a scavenger of arthropods. Furthermore, less detailed observation on *O. turneri* and *O. velox*, in the Namib desert, and on *O. velox* and an unidentified congener in the Etosha National Park, SWA/Namibia, indicate that these species are also primarily insectivorous (unpubl.). All of these observations have been in arid habitats and are in marked contrast to the observations of Prins (pers. comm.) who, in less arid regions of southern Africa (Cape Town and Namaqualand), has collected large amounts of seed from the nests of *O. barbiger*. Furthermore, Prins (pers. comm.) has made similar observations on *O. weitzeckeri* in the Kruger National Park, South Africa and these observations have led to the generalization that all members of the genus *Ocymyrmex* are highly granivorous (PRINS, 1963 ; 1965). From the available evidence it thus appears that *O. barbiger*, and other members of the genus, are capable of switching their diet depending on locality but more detailed data from localities other than the Namib desert are required to confirm this tendency. Furthermore, numerous seed-harvesting ants preferentially take insect prey when they are available (WHITFORD, 1978) and especially when seeds are scarce (MARSH, unpubl.).

It appears that *O. barbiger* foragers occupy their temporal/thermal niche in order to maximize the exploitation of dead arthropods. Although, in the short term, the size and type of prey remained the same irrespective of microclimatic conditions, recovered prey originated substantially closer to the nest during hot-dry periods than during cool-moist conditions. The most acceptable explanation for this observation is that prey density increases during hot-dry conditions.

In hot deserts high temperatures and desiccation could be important mortality factors for small arthropods. The apparent increase in prey availability and the increase in forager activity attending hot-dry periods supports this hypothesis. Furthermore, many of the soft-bodied arthropods taken by *O. barbiger* were visibly moist and therefore, had died that same day as dead insects dehydrate rapidly (EDNEY, 1977).

Studies, on the behavioural ecology of *O. velox* (WEHNER & MARSH, unpubl.) and the present investigation on *O. barbiger*, indicate that the genus *Ocymyrmex* (Subfamily Myrmicinæ) occupies the same ecological niche as *Cataglyphis* species (subfamily Formicinæ) occupy in the Sahara desert and southern Greece (HARKNESS & WEHNER, 1977 ; SCHMIDT-HEMPEL, 1983 ; WEHNER *et al.*, 1983). Both genera are primarily scavengers of arthropods, forage during the heat of the day, run very rapidly and are single prey loaders. Both genera are adapted to utilizing a low density, spatially unpredictable food source and occupy their thermal niche in order to take advantage of environmentally stressed prey.

One of the major differences between the two genera is colony size. While *Ocymyrmex* colonies comprise a few hundred individuals, *Cataglyphis* colonies are larger, frequently containing several thousand workers. Furthermore, recruitment behaviour does not occur in *Cataglyphis* species the workers of which exhibit life-long fidelity to specific foraging areas. In contrast, *Ocymyrmex* species have a well developed recruitment system and workers appear to have little fidelity for specific foraging areas (WEHNER & MARSH, unpubl. ; present study).

In the Australian arid-zone, members of the ant genus *Melophorus* occupy a similar thermal niche to that of *Ocymyrmex* and *Cataglyphis* species with some species foraging at surface temperatures just exceeding 65° C (MORTON, 1982). Some *Melophorus* species are, however, seed-harvester ants and thus the selective pressure which have resulted in thermophilic behaviour may be different in the African and Australian ants. It is also possible that similar selective pressures may have been in operation during the evolution of thermophilic behaviour with the *Melophorus* species radiating at a later stage into a harvesting role. Further studies of all three genera are necessary before any meaningful conclusions can be made.

The locomotory speeds measured reflect the maximum speeds that *O. barbiger* workers attained at different temperatures *(fig. 4)*. In practice the ants did not run continuously while on the insolated sand surface but occasionally paused, either to investigate a potential food item or for navigational purposes. On the plausible assumption that the frequency of such pauses is not related to temperature, searching speed should increase with thermal load. Beyond a critical temperature however the ants cannot remain continuously on the surface *(fig. 3)* and as prey items do not occur in thermal refuges (MARSH, in press), time spent in refuges reduces the amount of extranidal time available for farging *per se*. It follows that there should be a temperature at which the area searched by foraging ants per unit time is maximal and the time required to collect a single food item is least. This temperature can be regarded as optimal for foraging. By combining the information from *figure 3 and 4* it can be seen that the optimal searching surface temperature for an individual is about 52° C *(fig. 5)*. [In view of the foregoing discussion, the vertical scale on *figure 5* cannot be taken literally as it reflects a theoretical maximum, however, the pattern generated is valid and serves to identify the optimal searching temperature]. As temperature changes continuously throughout the day it would be unreasonable for ants to forage at this optimal temperature only. It would, however, be reasonable to predict that at the colony level foraging activity should peak at this temperature. The morning activity peak coincides closely with this temperature ($\overline{X}$ 53.5, range 51.8-56.3, n = 11), and on relatively cool days (maximum sand surface temperature 62° C) the afternoon peak in forager activity also occurs in this range ($\overline{X}$ 51.8, range 50.5-52.5,

n = 6). In contrast, on exceptionally hot-dry days (maximum surface temperature > 67° C) foraging activity is apparently maximal at high, suboptimal temperatures ($\overline{X}$ 59.0, range 57.0-62.0, n = 3) but more data is required to confirm this tendency.
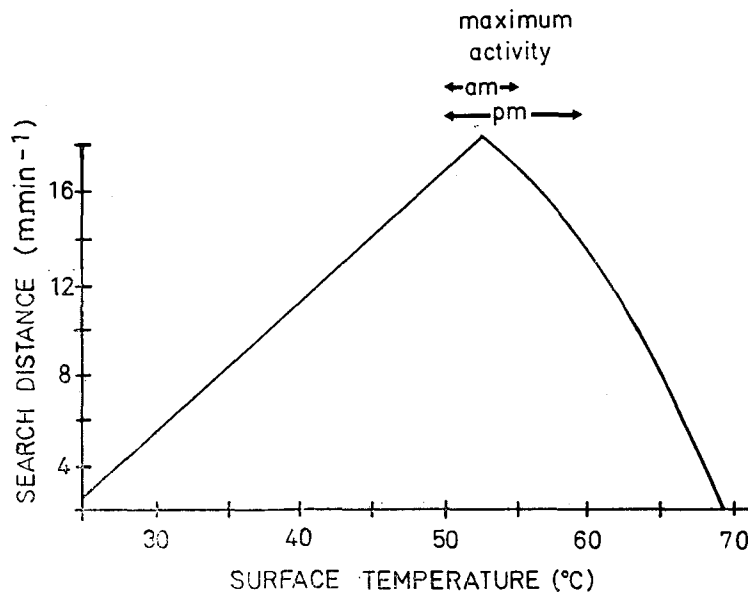

Fig. 5. — Relationship between search distance per unit time and sand surface temperature. " am " and " pm " indicate the range of temperatures over which colony activity peaked during the morning and afternoon activity periods respectively.

Abb. 5. — Verhaeltnis von bei der Nahrungssuche, zurueckgelegten Entfernung einer Ameise pro Zeiteiheit, zur Sandoberflaechen temperatur. Der Temperaturbereich fuer die Hauptaktivital einer Kolonie am Vor — bzw. Nachmittag wird mit " am " bzw. " pm " angegeben.

Although there will be a loss of foraging efficiency at temperatures greater than optimum, provided prey density is higher during such conditions than at the optimal searching temperature, the reward per unit time can still be greater. For example, the prey retrieval rate would be the same at 64° C and at the optimal temperature provided prey density was double that at the optimal temperature. The evidence provided here suggests that changes in prey density of this magnitude do occur and that they are related to the fluctuating thermal environment.

For a number of reasons foragers of social insects may be able to tolerate higher thermal loads than other insects, before incurring reduced fitness. Workers are sterile and contribute only indirectly to producing the next generation (WILSON, 1971). The death of a forager would reduce, but not prevent, the reproductive output of a colony. Of the various physiological

functions, reproduction in insects is most readily affected adversely by temperature extremes (BURSELL, 1964). Because foraging is usually performed by old workers (WILSON, 1971 ; OSTER and WILSON, 1978 ; PORTER and JORGENSEN, 1981 ; WEHNER et al., 1983) the loss, or incapacitation, of a forager that has progressed through various other work roles, is likely to be less detrimental to the ergonomic efficiency of a colony than that of a younger worker.

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