TEMPERATURE TOLERANCES IN THE NAMIB DESERT DUNE ANT, *CAMPONOTUS DETRITUS*

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Abstract—The mean preferred temperature of workers and brood of *Camponotus detritus* was 35°C at 100% r.h. and 31–33°C at 30% r.h. The critical maximal temperature of workers was 53°C at both 100% r.h. and 30% r.h. while the critical minimal temperature was 4.57°C at 100% r.h. Workers tolerated −1°C and 95% r.h.; 45°C and 95% r.h. and 45°C and 45% r.h. for 24 h.

INTRODUCTION

Camponotus detritus Emery is a honeydew-feeding ant species found commonly in the sparsely vegetated sand dunes of the central Namib Desert in Namibia. Nests are constructed at the base of the perennial vegetation and sometimes workers walk 100–200 m across the bare sand from the nest to a scale insect-infested plant. Being predominantly diurnal, these ants are often exposed to high temperatures and low humidity. Workers also remain out of the nest throughout the night, when air temperatures in winter may drop to nearly 0°C (Curtis, 1985).

Honeydew-feeding ants of the genus *Myrmecocystus* from the American deserts have a physiological range of temperature tolerance of about 11–48°C (Kay and Whitford, 1978) while the range of the harvester ants, *Pogonomyrmex*, is from about 5–53°C (Whitford and Ettershank, 1975).

A series of laboratory experiments was performed to answer the following questions about *Camponotus detritus*: What is the preferred temperature of the workers and the brood? What is the workers' critical maximal and minimal temperatures? For what length of time can the workers withstand extremely high or low temperatures?

MATERIALS AND METHODS

Ants were collected from the dunes near Gobabeb (23° 32′S; 15° 04′E) in October 1981 and flown to Cape Town, where they were housed in plastic containers in the laboratory at 25 ± 3°C and maintained on a diet of sugar water.

Preferred temperatures

A temperature-gradient chamber was constructed after Kay (1978). The plexiglass chamber was 980 mm long, 5.5 mm wide and 4.8 mm high, with a removable lid and an aluminium floor. Brass rods under the floor extended beyond both ends of the chamber. One end of the rods was immersed in a water bath cooled by a refrigerated coil. The other end was buried in a container of dune sand heated on a hotplate. The chamber was placed in a masonite box insulated with vermiculite. With this apparatus a linear gradient of 18–50°C could be maintained. The chamber walls were lined with polytetra-fluoroethylene (FLUON) to prevent the ants escaping. The lid was covered with red cellophane and observations were made with the aid of a torch. This was found to be less disturbing to the ants than daylight. Lines were drawn on the lid, so that the number of ants per 50 mm could be counted. The floor was covered with 5 mm of dune sand. Thermocouples 2 mm above the sand surface measured the temperatures at 50 mm intervals along the approximate temperature range 29–44°C. Along the remainder of the chamber thermocouples were at 200 mm intervals. The entire apparatus was kept in a walk-in constant temperature room, with an ambient temperature of 22 ± 2°C and 30 ± 4% r.h.

At the start of all experiments groups of 20 ants were distributed evenly within the chamber and left to settle for an hour. As it was impossible to control the temperature gradient thermostatically, a certain amount of temperature change occurred. This caused the ants to move as their preferred temperature shifted. For this reason five observations were made per group at approximately hourly intervals and the mean number of ants per temperature interval calculated. Six such groups were examined on dry sand [r.h. 30 ± 5%] and six groups on moist sand [r.h. 100%] (humidity was measured with a Vysala humidity probe). A few ants persisted in trying to escape from the cold end of the chamber. These were excluded from the calculations and only those ants in a resting position were considered.

To determine the temperature chosen by the workers for the brood, larvae and pupae were placed in the chamber with the ants. This procedure was replicated twice on moist sand and three times on dry sand.

Critical maximal and critical minimal temperatures

Each experiment was replicated with 30 ants using the method of Schumacher and Whitford (1974). Groups of 5–10 ants were placed in a 100 ml beaker

in a water bath. The beaker contained a 10 mm layer of dune sand, above which was a ring of FLUON. Thermocouples recorded the temperature on the sand surface and 10 mm above the sand. In order to keep the air in the beaker saturated the sand was dampened, a moist ball of cottonwool suspended in the beaker and a layer of plastic placed over the beaker. For critical maximal temperatures the water bath was heated at a rate of 1°C min^{-1}. As each ant reached this maximum (regarded as that temperature at which the ants lost co-ordination) it was removed from the beaker. To determine whether high humidity affected this maximum, the experiment was repeated with the ants on dry sand, without cottonwool and plastic cover. For critical minimal temperatures the water bath was cooled with the aid of an immersion cooler at a rate of 0.07°C min^{-1}. Critical minimal temperature was regarded as that temperature at which ants were incapable of righting themselves when turned onto their backs, even though they were still capable of movement.

Significant differences in preferred and critical temperatures were determined using the appropriate Student's t-test.

Long-term tolerance to extreme temperatures

Two groups of 20 ants were placed in 1000 ml beakers. One beaker contained dry sand and the other moist sand. Because FLUON vapourizes at high temperatures and high humidity, and prolonged exposure to these fumes kills the ants, a gauze lid was placed 20 mm above the sand. Damp cottonwool and a plastic covering were used as for the previous experiment. The beakers were immersed in a water bath maintained at 45 ± 2°C for 24 h, and the per cent mortality observed after 12 and 24 h. Long-term tolerance to low temperatures was examined in a similar manner for 30 ants at −0.5 ± 1°C and 95% r.h. for 24 h.

RESULTS

Preferred temperature

The temperatures chosen by the workers for the brood were the same as those they chose for themselves (Fig. 1), with workers of different size classes showing the same temperature preferences. Temperature preference at 100% r.h. was significantly higher than that at 30% r.h. for both the workers (34.7 ± 1.9°C and 31.3 ± 2.4°C respectively) and the brood (34.8 ± 0.9°C and 32.7 ± 1.4°C respectively) ($P < 0.001$).

Critical maximal and minimal temperatures

The critical maximal temperature of C. detritus was found to be 52.8 ± 0.9°C at 100% r.h. and 53.8 ± 0.9°C at 55% r.h., but there was no statistically significant difference between the results obtained at the two humidities. The critical minimal temperature, determined only at 100% r.h., was 4.6 ± 0.5°C. There was no difference in the critical temperatures between workers of different sizes. The behavioural response of C. detritus workers to different temperatures in the laboratory was similar to that in the field. Below 10°C their movements were very slow, but as temperatures
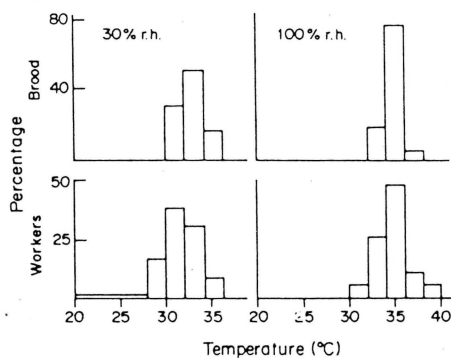

Fig. 1. Preferred temperatures of *Camponotus detritus* workers and brood at two different humidities ($N = 120$ workers and 40 brood).

increased, so did the speed of movement. At surface temperatures of about 45°C and above, the ants ran very rapidly over the sand, elevating their bodies as far off the ground as possible and lifting their legs higher than usual before replacing them.

Long-term tolerance to extreme temperatures

The ability of C. detritus workers to tolerate 45°C for up to 24 h was not affected by humidity. No mortality occurred after 12 h and only 20–25% after 24 h. No mortality occurred at −0.5 ± 1°C after 12 h, and only 3% after 24 h.

DISCUSSION

The range of temperature preferences shown by C. detritus workers was unusually low, considering that these ants are active over a range of surface temperatures in the dunes from 10–55°C (Curtis, 1985) and even their peak activity periods range from 20–42°C surface temperature in summer. In contrast, Kay (1978) found that the ranges of temperature choice of the desert honey ants, *Myrmecocystus* species, in the laboratory were similar to the ranges over which they were active in nature. As was the case among C. detritus workers of different sizes, Kay (1978) found no difference in temperature preference between species of different sizes. The range of temperatures over which C. detritus workers are active in the field encompasses a variety of ambient humidities and wind speeds and it was found in the temperature-choice chamber that changes in humidity affected the preferred temperature of these ants.

Since water loss is minimal at 100% r.h. (Curtis, unpublished) both workers and brood were possibly able to tolerate higher temperatures at high humidities. At lower humidities the increase in desiccation rate may have resulted in a lower temperature preference. Kay (1978) found a similar decrease in temperature preference with a decrease in humidity for the desert honey ant, *Myrmecocytstus romainei*, which she also interpreted as a response to desiccation. As temperature and humidity are never high simultaneously in the Namib Desert, the lower temperature preference of 31°C at 30% r.h. was perhaps a more realistic value.

The preferred temperature for the brood corresponded with the mean nest temperature in summer (32 ± 3°C), but the range of temperature choice was unexpectedly narrow since nest temperatures are not constant, but fluctuate considerably with depth and time of day (Curtis, unpublished). It is apparently not essential that the brood be maintained at their preferred temperature in the nest, since brood were found throughout the nest.

The preferred temperatures of the North American honey ants, *Myrmecocystus* spp, are lower than *C. detritus*, being 19–27°C (Kay, 1978). These ants, however, spend most of their time in the vegetation and are unlikely to experience the high temperatures which *C. detritus* experiences on the dune surface. Délye (1968) on the other hand, found that *Cataglyphis* and *Acantholepis* species from the Sahara have temperature preferences between 36–40°C. These predominantly diurnal species live and forage on the bare sand or gravel and probably experience higher temperatures than *C. detritus* (mean annual absolute maximal air temperature at Beni Abbés, Sahara is 47.5°C (Délye, 1968) and at Gobabeb it is 42.5°C (Seely and Stuart, 1976)). The nocturnal Saharan *Camponotus thoracicus* has a preference of 26–28°C. Délye (1968) found that, in general, Saharan species had higher temperature preferences than their mesic congeners.

Compared with other desert arthropods, for example beetles and locusts, *C. detritus* had a fairly low preferred temperature (Hafez and Ibrahim, 1964; El Rayah, 1970). The behaviour of the species must also be taken into account, however. The diurnal Namib Desert tenebrionid beetles, for instance, forage on the bare sand where temperatures increase extremely rapidly. These beetles actually maintain elevated body temperatures (37–40°C) for extended periods by means of behavioural thermoregulation (Hamilton, 1975; Henwood, 1975). *Camponotus detritus* workers on the other hand, forage among the vegetation where temperatures are lower, and only walk across the sand intermittently. Moreover, the tenebrionid beetles are more resistant to desiccation than *C. detritus* (Edney, 1971).

The term "critical temperature" may lead to some confusion and should be clearly defined. Some define the term "critical temperature" as the transitional temperature at which the lipid molecules in the cuticle apparently lose their orientation, resulting in a rapid and marked increase in cuticular water loss (Hadley, 1974). The ecological significance of this value is doubtful since these temperatures are often higher than upper lethal temperatures (Hadley, 1974), some being as high as 99–101°C (Louw and Seely, 1982). Others use the term to refer to the temperature at which the animal's locomotor ability is so reduced that it loses the ability to escape from thermal conditions which would lead to its death (Bartholomew, 1977). This is an ecologically more meaningful value than the former.

Highly mobile insects such as ants are unlikely to be confined to extreme conditions for long periods, but may be exposed briefly to temperatures above the conventional "upper lethal". For this reason I have used the second definition of critical temperature, which has also been used by Whitford and his colleagues (Schumacher and Whitford, 1974; Whitford and Ettershank, 1975; Kay and Whitford 1978) in their work on North American desert ants.

The results of the present study are directly comparable with those of North American species since the same methods were used. The critical maximal temperature of *C. detritus* was similar to that of the soil-surface foragers, *Pogonomyrmex* and *Novomessor* species in North America, but higher than those of the other species, which forage predominantly on plants (Whitford and Ettershank, 1975; Kay and Whitford, 1978). Although *C. detritus* workers were seen foraging primarily on plants, they walk long distances across the sand (up to 200 m) and would thus be exposed to high surface temperatures. The critical minimal temperature of *C. detritus* was also similar to that of *Pogonomyrmex* and *Novomessor* species. No direct comparisons can be made with the Saharan species since different methods were used for determining critical temperatures (Délye, 1968). Nevertheless, the maximal temperatures tolerated by most Saharan species appear to be a few degrees lower than those of *C. detritus*. An exception is *Cataglyphis* species which are able to tolerate temperatures similar to the critical maximal temperature of *C. detritus*.

Not only did *C. detritus* have a higher preferred temperature than *Myrmecocystus* spp, but was also able to withstand longer periods at 45% r.h. and 45°C (Kay and Whitford, 1978). *Camponotus detritus* was not as tolerant of high temperatures as the Saharan *Cataglyphis* sp, however, since the former died within minutes at its critical maximal temperature of 53°C, while the latter were able to withstand 55°C for 10–20 min (Délye, 1968).

It is difficult to compare temperature tolerance with other desert arthropods since different techniques have been used. The maximal voluntarily tolerated body temperature of Namib Desert tenebrionids ranges from 42.5–43.8°C (Hamilton, 1975). This would presumably be somewhat lower than their critical maximal temperature. Hafez and Makky (1959) performed an experiment in which desert beetles, *Adesmia bicarinata*, were gradually heated (1°C every 10 min) until the onset of "heat stupor" at 53°C, which is comparable with the 53°C critical maximal temperature of *C. detritus*. Upper lethal temperatures for other desert invertebrates seem to vary between 40–50°C. For example, the beetle *Pimelia grandis* withstood 43°C and 10% r.h. for 24 h whereas the solifuge *Galeodes granti* survived 50°C and 10% r.h. for 24 h (Cloudsley-Thompson, 1962).

Most animals avoid excessively high temperatures, but not all avoid cold, and invertebrates are sometimes trapped and immobilized by low temperatures (Cloudsley-Thompson, 1970). The critical minimal temperature of an insect determines the lower limits of its activity, but does not necessarily reflect the lower lethal temperature. For example, *C. detritus* became completely immobile at about 5°C but survived up to 24 h at −1°C with no apparent ill effects. On cold winter nights when air temperature dropped below 5°C, ants outside the nest became immobile and often fell from the scale insect-infested plant. When temperatures increased in the morning however, they resumed their normal activity.

Thus *C. detritus* showed a wide range of physiological temperature tolerance, but a narrow range of preferred temperature. Both critical maximal temperature and the preferred temperature were fairly high for an ant, although not as high as those of *Cataglyphis* spp or other desert arthropods. The critical maximal temperature was higher than that likely to be experienced by a worker in the dunes under normal conditions. Certainly no ant would experience temperatures as high as 45°C for 12 h. Temperatures in the Namib may often drop below critical minimal temperature but seldom below freezing (Seely and Stuart, 1976). Therefore although ants may be temporarily immobilized by cold, they are unlikely to be killed by low temperatures.

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