University of Florida Book of Insect Records Chapter 21 *Most Heat Tolerant*

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Desert-dwelling, scavenger ants are among the most thermophilic insects yet identified. Of these desert ants, Cataglyphis bicolor (Hymenoptera: Formicidae), an inhabitant of the Sahara Desert, is identified as the most thermotolerant. At least three genera of desert dwelling ants, Cataglyphis, Ocymyrmex, and Melophorus, from the Sahara, Namib and Australian Deserts, respectively, are known to forage in surface temperatures above 60°C. Current literature supports Cataglyphis as the most thermotolerant of these genera, with a critical thermal maximum of $55\pm1^{\circ}$ C recorded for Cataglyphis bicolor.

This paper attempts to identify the insect which is naturally occurring and active at the highest temperature. Highest temperature is considered in two ways, with both interpretations influencing the selection of a champion. First, it is the ambient temperature in which the insect naturally lives and completes its life cycle. Second, it is *heat tolerance*, often measured as the critical thermal maximum (CTM), that the insect can physiologically withstand in an active state (i.e., not egg or diapause). To determine CTM, organisms at their acclimation temperature are heated at a constant rate until they lose the ability to escape the increasing temperature by locomotion but are not killed. The temperature at which this endpoint occurs is recorded as the CTM (Moulton et al. 1993).

The scope of search was limited to active life cycles to give it more ecological relevance. There are many instances, for example, of extraordinary tolerances in specific stages. One such example, a fly larva (*Polypedilum*) from Nigeria and Uganda, can withstand a temperature of 102°C for 1 minute and still metamorphose successfully (Hinton 1960). While this thermotolerance is remarkable and may contain scientific discoveries yet unrevealed, it would probably never be encountered in a natural ecosystem.

Methods

Secondary literature, solicitation over the ENTOMO-L Bulletin Board, and queries of faculty at the University of Florida Entomology/ Nematology Department provided the initial candidates. A subsequent literature search of *Biological Abstracts* and *Zoological Record* narrowed the focus.

Results

There are at least three genera of ants, all desert scavengers, and each from a different desert around the world, that forage for the corpses of insects and other arthropods which have succumbed to the heat stress of their desert environment (Gehring & Wehner 1995). These genera include Cataglyphis (Formicinae) in North Africa, Ocymyrmex (Myrmicinae) of South Africa, and Melophorus (Formicinae) of Australia (Heinrich 1993). Among these thermophilic ants, Cataglyphis seems to emerge as the premier thermophile. It lives in the Sahara Desert and forages at a body temperature well above 50°C with surface temperatures of up to 70°C (Wehner et al. 1992). In laboratory tests, the critical thermal maxima were measured at 53.6±0.8°C (SD?, SE?) for C. bombycina and 55.1±1.1°C for C. bicolor

(Gehring & Wehner 1995). Although the other genera mentioned may forage at similar environmental temperatures, they are apparently not quite as thermotolerant. In laboratory tests, for example, the Namib Desert ant Ocymyrmex barbiger entered a heat coma in only 25 seconds when placed in a 55°C environment, whereas five Cataglyphis species exhibited symptoms after 10 to 25 minutes (Marsh 1985b). Perhaps the most serious challenger to C. bicolor is Melophorus bagoti from the central Australian desert. Greenaway (1981) reported that M. bagoti survived in lab tests for one hour at 54°C. In fact, the ants do not even emerge to forage in their desert environment until the surface temperature is a blistering 56°C.

Aquatic insects, principally those present in hot springs, were also examined. The physio-logical challenges presented by aquatic habitats are very different from those of terrestrial habitats, particularly with respect to thermoregulation. Due to the moderating effect of the heat capacity of water, aquatic insects must accept body temperatures equal to that of the pool. This limits the hot spring temperature they can accept. Pennak (1978) reported the upper limit for aquatic insects in an active state at around 50°C. Ward (1992) compiled a list of active aquatic insects occurring in hot springs at temperatures in excess of 40°C, the most thermophilic being Chironomus near tentans (Diptera: Chironomidae), at 49°C.

A variety of other insects were considered, including the desert cicada *Diceroprocta apache* (Homoptera: Cicadidae), beetles such as desert tenebrionids and cicindellids, termites, and social bees and wasps. All fell short of the accomplishments of the desert scavenging ants.

Discussion

No animal is known to live and carry out its complete life cycle at a temperature over 50°C (Schmidt-Nielsen 1990). It is probable, then, that desert scavenger ants are foraging at temperatures at or near the limit of animal potential. In field studies, it has been determined that these ants forage within a narrow internal heat band very near to their thermal maximum. As a typical case in point, the foraging activity of *C. bombycina* is compressed to a width of just 7°C (46.5°C to 53.6°C) (Wehner et al. 1992). They will forage until their body temperature reaches the CTM, at which time they must seek refuge. Failure to find respite from the heat in critical seconds will result in becoming a heat casualty themselves. One can assume that this small insect with a mean body weight of 9.7 mg would within seconds have a body temperature close to that of the environment, which often exceeds their CTM (Heinrich 1993).

There are basically three characteristics that adapt these thermophilic ants to exploit the hottest deserts of the world at the hottest times of the day. First, the ants are quite speedy, which minimizes sun exposure and may contribute to convective cooling. Wehner et al. (1992) clocked C. fortis and C. bombycina at 1 meter/second, which approaches the top speed of Onymacris plana, the Namib Desert tenebrionid which is possibly the fastest running arthropod ever recorded (Heinrich 1993). In addition, there is a direct correlation between running speed and surface tempera-ture (Marsh 1985a). Second, their long legs elevate them above the hot substrate. Tempera-tures 4mm above the ground (which is roughly "ant height") are some 6 to 7°C cooler than at the surface (Gehring & Wehner 1995). Third, they possess a foraging behavior of pausing on the stalks of dry vegetation where the lower temperatures can off-load excess body heat. On the hottest days, approximately 75% of their foraging time is spent in thermal refuges (Wehner et al. 1992).

Desert ants occupy a specific ecological niche and risk thermal death with each foraging expedition. In the case of *C. bombycina* in the Sahara Desert, foraging activity is limited to a small thermal window in the full midday summer sun. As other desert ants retreat to underground burrows at surface temperatures of 35 to 45°C, C. bombycina is only starting its foraging activity (Wehner et al. 1992). It is near this same temperature that a lizard predator, Acanthodactylus spp., also retreats underground. Ants experimentally released on the desert floor at temperatures lower than the natural foraging temperature fell victim to predation, often within 5 minutes. The narrow foraging window of C. bombycina, then, is defined by predation pressure at the low extreme and its CTM at the other (Wehner et al. 1992). By pushing their thermal limits to the extreme, they occupy a specialized ecological niche; effectively reducing competition from other, less thermotolerant, ants and neatly evading predation by desert vertebrates which must burrow to escape the intense heat.

This incredible adaptation to exposure to high temperatures exhibited by desert scaven-ger ants may be linked to heat shock protein (HSP) synthesis. Although the mechanisms are not fully understood, HSP studies conducted by Gehring & Wehner (1995) on *C. bombycina* and *C. bicolor* indicate the increased HSP synthesis observed in these species confers increased thermotolerance.

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