

# CRITICAL THERMAL LIMITS OF DESERT HONEY ANTS: POSSIBLE ECOLOGICAL IMPLICATIONS<sup>1</sup>

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Critical thermal maxima (CTMAX) and minima (CTMIN), approximate upper and lower lethal temperatures, and the temperature limits of activity were determined for workers of diurnal and nocturnal species of *Myrmecocystus*. The CTMIN of diurnal species were between 11.2 and 12.0 C, and that of the nocturnal species was -0.4 C. All species had CTMAX between 43.3 and 48.4 C. Lower lethal temperatures of individuals of all species exposed for 2 h were below -5 C, and upper lethal temperatures were between 40 and 45 C. Diurnal species were active at 13-46 C air temperature (Ta) and 13-60 C soil surface temperature (Ts), and the nocturnal species was active at Ta and Ts of 2-30 C.

## INTRODUCTION

Upper and lower lethal temperatures, which are known for many arthropods (Cloudsley-Thompson 1970), define physiological temperature-tolerance limits, that is, the temperature limits for survival when exposed to high or low temperatures for a fixed period of time (Fry 1967; Cloudsley-Thompson 1970). Unfortunately, data for different insects often cannot be compared because investigators have not used a single exposure time (Cloudsley-Thompson 1970). Lethal temperature studies require large numbers of animals and considerable time. Investigators studying reptiles and amphibians commonly use parameters known as critical thermal maxima (CTMAX) and minima (CTMIN) to

define ecological temperature-tolerance limits of their animals, that is, the temperature limits for escape from a hostile environment (Fry 1967). Animals are heated or cooled, usually at 1 C/min, until locomotion becomes impaired. Techniques that approximate those used with vertebrates have been employed in only a few studies of invertebrates. Temperature-tolerance limits equivalent to CTMAX and CTMIN have been determined for several large flying insects and referred to as threshold temperatures of cold or heat torpor (Heath et al. 1971; Heath, Wilkin, and Heath 1972; May 1976). Recently Schumacher and Whitford (1974), Whitford and Ettershank (1975), and Whitford, Kay, and Schumacher (1975) have measured CTMAX and CTMIN of several species of desert ants.

During our investigations, CTMAX and CTMIN were measured for five species of honey ants (*Myrmecocystus romainei* Cole, *M. depilis* Forel, *M. mimicus* Wheeler, *M. mexicanus* Wesmael, and *M. navajo* Wheeler) all commonly encountered in the deserts of southern New Mexico (Snelling 1976). Approximate upper and lower lethal

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temperatures of some species were obtained for comparison to critical thermal limits. In the field, determinations were made of the temperature ranges over which foraging occurred. We hoped to detect possible physiological adaptations that allow diurnal *Myrmecocystus* (*M. romainei*, *depilis*, and *mimicus*) to forage at the high temperatures characteristic of their desert environments and to investigate the physiological correlates of nocturnality of some species (*M. mexicanus* and *navajo*).

#### MATERIAL AND METHODS

All ants were collected on the New Mexico State University Experimental Ranch, 30–40 km NNE of Las Cruces, Doña Ana County, New Mexico. Worker ants for laboratory studies were aspirated from the soil surface at their nest entrances. Males and alate queens were aspirated from galleries less than 20 cm beneath the soil surface. The insects were transported and maintained in plastic boxes on moist paper toweling. The laboratory remained at about 24 C and 20% relative humidity throughout the investigations.

#### FIELD OBSERVATIONS

Observations of workers entering and leaving nests of *M. romainei*, *M. depilis*, *M. mimicus*, and *M. mexicanus* were made at intervals during a 24-h period. With each observation of nest activity, air temperature ( $T_a$ ) at 0.5 cm above the substrate and soil surface temperature ( $T_s$ ) were measured using a telethermometer with a thermistor probe. Soil surface temperature was measured with the probe placed on the soil surface and covered with a thin layer of soil. Studies were repeated at about 2-wk intervals from August 1972 to August 1973.

#### LETHAL TEMPERATURES

Lethal temperature studies were conducted in October 1972 on workers of *M. romainei*, *M. depilis*, and *M. mexicanus*. Ten workers of a species were placed in each of 24 30-cc vials on brass screening. Twelve vials contained moist sand below the screening to humidify the air, and 12 contained anhydrous silica gel below the screening as a drying agent. Four vials of each species (two containing moist sand and two containing silica gel) were placed in a controlled-temperature incubator at one of six temperatures: -5, 5, 15, 35, 40, or 45 C. After 2 h the vials were removed from the incubators and the ants were given a 1-h period for recovery. The number of living and dead ants in each vial was then recorded.

#### CRITICAL THERMAL LIMITS

The apparatus used during measurements of critical thermal limits consisted of a 250-ml beaker containing an 8-mm layer of white gypsum sand. A thermistor probe and telethermometer were used to measure the temperature at about 1 mm above the sand surface. It was not possible to measure the temperature of the individual ants because of their small size and high activity, but the  $T_a$  measured was the temperature to which the ants were exposed. During measurements of CTMIN the beaker was cooled in a container of chipped ice and water (diurnal *Myrmecocystus* spp.) or chipped dry ice (*M. mexicanus*). An electric heating mantle (flask warmer) with a variable rheostat was used to heat the beaker during measurements of CTMAX.

At the beginning of each measurement period, five ants were placed in the beaker at room temperature, and the beaker was heated or cooled at about 1 C/min. Each ant was observed until locomotion became impaired. The tem-

perature at which locomotion of each ant ceased but before all movement ceased was considered to be the CTMIN or CTMAX of that individual. Pilot studies using *M. depilis* workers had shown that the rate of temperature increase was an important consideration since the CTMAX of ants heated at 2 C/min averaged 2 C lower than that of ants heated at 1 C/min. During critical thermal minimum experiments, a ring of cardboard 1 cm high was placed against the sides of the beaker because contact with the cold glass caused the ants to immediately become torpid.

In April, June, and July 1973, measurements of seasonal effects on CTMAX and CTMIN were made on small, medium, and large workers of five species of *Myrmecocystus*. Experiments were performed within 1–2 h of collection. In April 1973, experiments were conducted to examine acclimation of the CTMAX of workers of *M. depilis*. Ants were held in the laboratory for about 12 h and then placed in controlled-temperature incubators at 0, 5, 15, 25, or 35 C on moist sand in plastic containers with dilute honey as food. Ants were removed from the incubators after 0, 12, 25, 30, or 35 h exposure, and CTMAX were measured.

Means and .95 confidence intervals were calculated for all data sets. The  $t'$ -statistic was used to examine differences between means with unequal variances (Steel and Torrie 1960). The .05 probability level was used for tests of significance.

## RESULTS

### FIELD OBSERVATIONS

Workers of *Myrmecocystus romainei*, *M. depilis*, and *M. mimicus* were seen above ground at Ta of 13–46 C and Ts of 13–60 C throughout a day. At Ts above about 50 C workers remained on

the soil only a few seconds, climbing every object encountered as they moved between the nest and the plants on which they were foraging. Diurnal ants did not forage at night but often engaged in activities related to nest maintenance. Workers of *M. mexicanus* were active at Ta and Ts of 2–30 C. *Myrmecocystus mexicanus* usually ceased activity at dawn and resumed activity at dark, but occasionally on rainy days a few workers were above ground 1–2 h after dawn or 0.5–1 h before dark. Activity of all species decreased as temperatures approached the upper and lower activity limits. All species except *M. romainei* foraged throughout the year when temperatures permitted. *Myrmecocystus romainei* ceased activity in mid-October and resumed activity in mid-March.

### LETHAL TEMPERATURES

After exposure for 2 h to temperatures between 5 and 35 C, two *M. romainei* workers and one *M. depilis* worker were dead. No pattern in the deaths could be detected related to either temperature or humidity, so the deaths were probably the result of injuries. After 2 h at –5 C, about 15% of the ants of all species were dead in dry air, but about 25% of the ants were dead in wet air, probably because water condensed and froze on the ants at high humidities. After 2 h at 40 C death rates were 0% for *M. depilis* in both wet and dry air, 0% for *M. romainei* in wet air and 25% in dry air, and 15% for *M. mexicanus* in wet air and 70% in dry air. Ants of all species were weakened by the 40 C exposure in dry air (but not in wet air), and many died later, probably as a result of dehydration. A plastic box of wet sand containing *M. depilis* workers was maintained at 40 C for 12 h without casualties. At 45 C all ants died in 2 h. Therefore, the lower lethal temperatures

(defined as the temperature resulting in 50% mortality) of all species were below  $-5^{\circ}\text{C}$  when exposed in either wet or dry air for 2 h. The upper lethal temperatures were between 40 and 45  $^{\circ}\text{C}$  for all species in wet air and for all species except *M. mexicanus* in dry air.

## CRITICAL THERMAL LIMITS

In July the CTMIN of workers of the nocturnal *M. mexicanus* (mean live weight =  $9.2 \pm 1.1$  mg) was much lower than that of diurnal *M. mimicus* ( $4.7 \pm 1.5$  mg), *M. depilis* ( $3.6 \pm 0.6$  mg), or *M. romainei* ( $3.2 \pm 0.7$  mg) (table 1). Workers of the largest diurnal species, *M. mimicus*, had the lowest CTMIN, and workers of the smallest species, *M. romainei*, had the highest CTMIN. Larger workers of a species usually had slightly lower CTMIN than smaller workers (*depilis*, mean CTMIN =  $2.5^{\circ}\text{C}$  lower; *mimicus*,  $2.4^{\circ}\text{C}$  lower; *romainei*, not measured; *mexicanus*,  $0.3^{\circ}\text{C}$  higher). Queens of *M. romainei* had a significantly lower CTMIN than workers.

The CTMAX of workers of the two nocturnal species, *M. mexicanus* and *M. navajo*, were not significantly different. Of the diurnal species, workers of the largest species, *M. mimicus*, had the highest CTMAX, and workers of the

smallest species, *M. romainei*, had the lowest CTMAX. Larger workers of a species usually had slightly higher CTMAX than smaller workers (*depilis*, mean CTMAX in July =  $1.8^{\circ}\text{C}$  higher; *mimicus*,  $1.5^{\circ}\text{C}$  higher; *romainei*,  $0.3^{\circ}\text{C}$  higher; *mexicanus* and *navajo*, not measured). Queens of *M. romainei* had a significantly higher CTMAX than workers. Males of *M. depilis* had a lower CTMAX than workers, but not significantly so.

The CTMAX of workers of *M. romainei* and *M. depilis* (but not *M. mimicus* or *M. mexicanus*) were significantly higher in July than in April. Workers of all diurnal species, except *M. romainei* in April, had higher CTMAX than workers of nocturnal species. During the high temperature exposures, workers of diurnal *Myrmecocystus* spp. elevated their bodies from the substrate, moved rapidly, and tried to climb every object encountered. Nocturnal workers did not display this behavior pattern.

The CTMAX of temperature-acclimated workers of *M. depilis* are shown in table 2. The mean of the measurements made at the beginning of the acclimation periods (acclimation time = 0) was considered as the control value.

TABLE 1

CRITICAL THERMAL MAXIMA AND MINIMA OF FIELD-ACCLIMATIZED ANTS OF THE GENUS "MYRMECOCYSTUS"

FORAGING AND SPECIES	CASTE	SPRING		SUMMER			
		CTMAX	N	CTMAX	N	CTMIN	N
Diurnal:							
<i>M. romainei</i> . . . .	Worker	$43.3 \pm .8a$	31	$46.1 \pm .4b$	26	$12.0 \pm .3e$	20
<i>M. romainei</i> . . . .	Queen			$47.2 \pm .6c$	10	$8.4 \pm .6$	10
<i>M. depilis</i> . . . . .	Worker	$46.2 \pm .8b$	35	$47.4 \pm .7c,d$	26	$11.6 \pm .5e,f$	20
<i>M. depilis</i> . . . . .	Male			$42.5 \pm 6.2a,b,c,d$	5		
<i>M. mimicus</i> . . . . .	Worker	$48.4 \pm .9d$	25	$47.7 \pm .9c,d$	20	$11.2 \pm .5f$	20
Nocturnal:							
<i>M. mexicanus</i> . . .	Worker	$44.7 \pm 5.0a,b,c,d$	3	$44.2 \pm .9$	20	$-0.4 \pm .7$	18
<i>M. navajo</i> . . . . .	Worker	$43.7 \pm 2.2a$	5				

NOTE.—CTMAX = mean critical thermal maximum  $\pm$  .95 confidence interval in  $^{\circ}\text{C}$ ; CTMIN = mean critical thermal minimum  $\pm$  .95 confidence interval in  $^{\circ}\text{C}$ . Means followed by the same letter are not significantly different ( $P < .05$ ).

TABLE 2  
CRITICAL THERMAL MAXIMA OF TEMPERATURE-ACCLIMATED WORKERS  
OF "MYRMECOCYSTUS DEPILIS"

HOURS <sup>a</sup>	ACCLIMATION TEMPERATURE (°C)							
	5			15		25		35
	CTMAX <sup>b</sup>	N	CTMAX	N	CTMAX	N	CTMAX	N
0.....	47.2±1.7	10	47.2±1.7	10	47.2±1.7	10	47.2±1.7	10
12.....	.....	.....	.....	.....	.....	.....	48.0±1.5	5
25.....	46.4±.8	10	48.0±.9	5	47.4±.9	10	49.2±.8 <sup>c</sup>	10
30.....	47.8±.5	5	47.8±.7	5	47.0±1.3	5	51.4±1.5 <sup>c</sup>	5
35.....	48.3±.7	5	47.2±1.2	10	49.2±1.7	5	51.9±1.5 <sup>c</sup>	5

<sup>a</sup> Hours of acclimation.

<sup>b</sup> Mean critical thermal maximum ± .95 confidence interval in °C.

<sup>c</sup> Significantly different from CTMAX at h = 0 ( $P < .05$ ).

Only CTMAX of workers at 35 C for 25 h or longer were significantly different from the control. At 35 C, the CTMAX increased with time in acclimation and appeared to stabilize after about 30 h.

#### DISCUSSION

Measurement of CTMIN and CTMAX proved to be a simple and ecologically meaningful method of obtaining temperature-tolerance limits of *Myrmecocystus* spp. The CTMIN of workers of diurnal and nocturnal species of *Myrmecocystus* were within 2 C of the minimum foraging temperatures, suggesting that the ants do not cease surface activity until the temperature drops to near the point at which locomotion would be impaired. However, light intensity apparently partially determined the type of activity in which diurnal workers engaged (foraging vs. nest maintenance). Lower lethal temperatures of *Myrmecocystus* spp. were much lower than foraging limits, supporting Delyé's (1968) hypothesis that lower lethal temperatures are of little ecological significance to desert ants. Mellanby (1940) found that an arctic ant, *Formica semirufa*, had a chill coma temperature of 1–3 C, comparable to the CTMIN of -0.4 C found for workers of *M. mexicanus*. None of the

diurnal or crepuscular desert ants studied by Schumacher and Whitford (1974) or Whitford and Ettershank (1975) had CTMIN below 3.6 C. The CTMIN of all of the ants that have been tested, but especially of *M. mexicanus*, are lower than the cold torpor temperatures of several large flying insects (Heath et al. 1971, 1972).

The CTMIN of diurnal *Myrmecocystus* spp. were 1.5–8.4 C higher than those of species of *Pogonomyrmex*, *Novomessor*, *Formica*, and *Trachymyrmex* studied by Schumacher and Whitford (1974) and Whitford and Ettershank (1975). Those investigators chose as the CTMIN (or CTMAX) that temperature at which all movement ceased. Bertram (1935) determined both a temperature of locomotor impairment and a temperature of cessation of movement for 49 different insects and found an average difference between the two temperatures of 4.1 C. We felt that the temperature of locomotor dysfunction was the temperature at which ants could no longer return to their nests, and therefore the temperature limit of ecological significance.

The upper temperature limits of activity of diurnal *Myrmecocystus* spp. were close to their CTMAX but slightly higher than their upper lethal tempera-

tures. However, the upper lethal temperatures represent 2-h exposures to constant temperatures. Workers of *M. mexicanus*, on the other hand, ceased surface activity at temperatures about 15 C below their CTMAX. Workers of the nocturnal species, *M. navajo*, in southern Utah were observed foraging only at temperatures lower than 25 C, about 19 C below their CTMAX (Fautin 1946). The upper temperature-tolerance limits probably determine the upper foraging limits of diurnal species but not of nocturnal species. Light intensity may be the most important factor controlling foraging of nocturnal species (Fautin 1946; Cazier and Statham 1962). Thus, nocturnal *Myrmecocystus* spp. probably are never exposed to dangerously high temperatures. This suggests that nocturnal species have not evolved the behavioral responses to high temperatures as noted for diurnal *Myrmecocystus* spp. during our experiments (elevation of the body and other attempts to escape from the hot environment).

At high temperatures, the temperatures of locomotor impairment of *Myrmecocystus* spp. were about 1 C below the temperatures of cessation of movement. Species of *Myrmecocystus* had CTMAX comparable with that of *F. perpilosa* (45.2 C), an ant in the same subfamily that also forages in the plant canopy (Schumacher and Whitford 1974), and 3.3–10.5 C lower than those of species of *Pogonomyrmex* and *Novomessor*, ants that forage primarily on the soil surface (Whitford and Ettershank 1975; Whitford et al. 1975).

It was impossible to determine whether small differences in CTMAX and CTMIN among workers of different sizes and among diurnal species of *Myrmecocystus* were the result of actual physiological differences or of differences in thermal inertia. These small ants

probably have thoracic temperatures very close to the temperatures measured, but we cannot rule out the possibility that the largest ants heated or cooled at slightly lower rates. Thermal inertia may also have accounted for the higher CTMAX and lower CTMIN of *M. romainei* queens, which had weights about 30 times those of workers. The slightly lower CTMAX of males of *M. depilis* (range, 37.1–47.7 C) could not be attributed to size differences because males were about the same size as medium-sized workers. Males die quickly in the laboratory, and those with low CTMAX may have been weakened or injured prior to experiments. The small effect of size on the temperature-tolerance limits of worker ants is probably of little ecological significance since smaller ants predominate in the foraging populations of most honey-ant species.

Seasonal effects on the temperature-tolerance limits have been demonstrated for only a few arthropods (Edney 1964; Cloudsley-Thompson 1969; May 1976). Seasonal changes in the CTMAX were small for all species of *Myrmecocystus* except *M. romainei* and probably of little ecological significance. The CTMAX of workers of *M. romainei* were lower in April, immediately following winter dormancy, than in July.

Exposures of 24 h or longer to sublethal high temperatures increase the upper lethal temperatures of many insects, but acclimation to lower temperatures usually has no effect (Cloudsley-Thompson 1970). The CTMAX of *M. depilis* workers responded to temperature acclimation in a similar way. We also found that the CTMAX of 15 workers of *M. romainei* that had been held at 0 C for 10 days was  $46.5 \pm 1.2$  C, not significantly different from the CTMAX of field-acclimatized workers in July. The CTMAX of field-acclima-

tized workers was never elevated (table 1), even though air temperatures often remained above 35 C while the ants were being transported to the laboratory. Foragers would not be exposed to temperatures of 35 C or above for more than 10 h in their natural environment, suggesting that acclimation to sublethal high temperatures seldom occurs in nature.

#### CONCLUSIONS

*Myrmecocystus mexicanus* can remain active at much lower temperatures than most desert ants (Delyé 1968; Schumacher and Whitford 1974; Whitford and Ettershank 1975). The low temperature-tolerance limit of this species probably reflects an adaptation to nocturnal foraging since temperatures below 15 C occur frequently at night in warm desert areas. The ability to forage at temperatures below 10 C allows *M. mexicanus* to be active at night throughout much of the year in southern New Mexico. In the Las Cruces area, the diurnal *Myrmecocystus* spp. can also forage throughout the year because midday temperatures are well above their CTMIN during most of the winter.

The upper temperature-tolerance limits of *Myrmecocystus* spp. are similar to

those of many insects that are not adapted to desert life (Cloudsley-Thompson 1970). Delyé (1968) found that most Sahara Desert ants do not have unusually high upper lethal temperatures. A few desert ants, notably species of *Cataglyphus* (Delyé 1968) and species of *Pogonomyrmex* (Whitford and Ettershank 1975), tolerate higher temperatures. Investigators have hypothesized that physiological differences among desert ants may be related to the "feeding guild" (Whitford et al. 1975) or foraging behavior (Delyé 1968) of the ants. For example, ants such as *Pogonomyrmex* spp. that collect seeds or other relatively dry food on the ground may have evolved physiological tolerances to higher temperatures and vapor-pressure deficits than ants such as *Myrmecocystus* spp. that spend much of their time in the plant canopy collecting nectar. Despite the fact that diurnal species of *Myrmecocystus* cannot tolerate unusually high temperatures, workers forage at midday in the summer when few other ants are active. Although high temperatures preclude activity on the soil surface, foragers can remain in the plant canopy during the hottest portion of the day and return to the nest when the temperature drops.

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