Temperature and water relations of the giant whip scorpion, *Mastigoproctus giganteus* (Lucas) (Arachnida, Uropygi: Thelyphonidae)

Fred Punzo* and **Sandra Olsen**
Department of Biology,
University of Tampa,
Tampa, Florida 33606, USA

Summary

Experiments were conducted to assess the effects of ambient temperature (T_A) and relative humidity (RH) on the duration of embryonic development, upper (ULT_{50}) and lower (LLT_{50}) lethal temperatures, critical thermal minimum (CTM_{min}) and maximum (CTM_{max}) temperatures, survival, and preferred temperature in the giant whip scorpion, *Mastigoproctus giganteus*. No embryos completed development under xeric conditions (12% RH), regardless of T_A. Embryonic development required 42–47 days at 15°C, compared with 37–39 days at 22°C and 27–32 days at 29°C, at RHs of 40 and 75%. ULT_{50} values ranged from 35.2–38.5°C and 38.3–41.1°C, for nymphal stages under xeric (12% RH) and mesic (75%) conditions, respectively, and 40.2–42.6°C for adults. LLT_{50} values ranged from 3.5–4.7°C and 3.3–4.5°C for nymphs under xeric and mesic conditions, and 3.3°C for adults. CTM_{min} values ranged from 4.72–7.54°C for nymphal and adult stages depending on acclimation temperature (10 or 30°C), while CTM_{max} values ranged from 37.3–41.9°C. Under xeric and mesic conditions, survival capacity was greatest between 25 and 30°C for nymphs and adults. Less than 10% of whip scorpions survived at 5°C, regardless of RH. No animals survived when exposed to a T_A of 45°C. Survival was low at a T_A of 40°C (5% for nymphs, 12–15% for adult males and females) under xeric conditions; under mesic conditions: 9% (nymphs); 31–36% (adult males and females). Seventy-six percent of nymphs chose a temperature range of 23–28.9°C in a linear temperature gradient apparatus, compared with 81% for adult males.

Introduction

Organisms that inhabit deserts are often confronted with a variety of physical problems including extremes

*To whom all correspondence should be addressed.

of ambient (T_A) and surface (T_s) temperatures, shortage or absence of standing water, low relative humidity (RH) regimes, and additional factors that can intensify these problems such as hard soils which make burrowing difficult, and strong winds which increase evaporative water loss (EWL). EWL can place an animal under osmotic stress and may result in desiccation and death. High T_A can cause an increase in body temperature (T_B) which may inhibit metabolic processes. Thus, the distribution and activity of terrestrial arthropods are strongly influenced by temperature and moisture regimes (see reviews by Edney, 1977; May, 1985; Punzo, 1998; Cloudsley-Thompson, 2001).

With respect to desert arthropods, there have been numerous studies on the effects of T_A and RH on survival (see reviews by Cloudsley-Thompson, 1975; Punzo, 2000a), thermal tolerance (Chew, 1961; Punzo, 2000a; Cloudsley-Thompson, 2001), resistance to cold (Kirchner, 1987), metabolic rate (Anderson, 1970; Cloudsley-Thompson, 1991), and behaviour (Cloudsley-Thompson, 1975; May, 1985; Punzo, 2000a). Most of this research has focused on insects, scorpions and spiders. In contrast, little information is available on temperature and moisture relations of desert whip scorpions (Arachnida, Uropygi).

The giant whip scorpion, *Mastigoproctus giganteus* (Lucas) is a common component of the arachnid fauna in desert regions of south-western USA and northern Mexico (Punzo, 2001). It is a relatively large arachnid (adults, 40–80 mm in length), primarily nocturnal in its foraging behaviour, and moves over the ground surface where it feeds on a variety of arthropods (Punzo, 2000b). This species is characterised by an egg stage, followed by four nymphal stages (proto, deuto-, trito- and tetranymph), and adults (Punzo, 2000a). Females produce between 30–47 eggs which are carried within a membranous sac under the female's abdomen (Weygoldt, 1971).

There have been few studies on the temperature and moisture relations of *M. giganteus*. Ahearn (1970) showed that water loss was exponentially related to

body weight in *M. giganteus*. In addition, there was a significant increase in EWL at 37.5°C, and smaller animals were more efficient at reabsorbing water from moist substrates than their larger counterparts. Crawford & Cloudsley-Thompson (1971) reported that adults of *M. giganteus* exhibit a significant increase in EWL at ambient temperatures above 26°C, even when exposed to RH values of 90–95%. These results indicated that the epicuticle of this species is not a particularly effective barrier against EWL, and the suggestion was made that the wax-layer might have been abraded by sand. The marked nocturnal activity patterns of these animals help them to reduce desiccation by avoiding the more extreme conditions of daylight temperatures.

The purpose of this study was to investigate in more detail the effects of T_A and RH on *M. giganteus*. Specifically, we analysed the effects of temperature and RH on upper and lower lethal temperatures, critical thermal minimum and maximum temperatures, and survival capacity, as well as determining the preferred temperature range for this species.

Methods

Habitats, experimental animals, and husbandry techniques

Adult male and female whip scorpions were collected during April through June 2000, at several locations in Big Bend National Park (BBNP; Brewster County, Texas), which lies within the northern region of the Chihuahuan Desert. These locations are listed in Table 1. They are characterised by low precipitation (<250 mm/year), low RH (10–25% at ground surface), and high summer air temperatures that range from 24.3–30.4°C at night, and 37.9–47.3°C at midday. They also contain hard adobe soils with numerous rocks and sparse plant cover. The dominant vegetation consists of sotol (*Dasylirion leiophyllum*), creosote (*Larrea divaricata*), lechuguilla (*Agave lechuguilla*), ocotillo (*Fourquieria splendens*), and mesquite (*Prosopis glandulosa*). Adults and nymphs of *M. giganteus* occur throughout these sites, where they are typically found within abandoned rodent burrows, within rock crevices, or under plant debris.

All animals used in these experiments were captive-bred, comprising various developmental stages (protonymphs, deutonymphs, tritonymphs and tetranymphs) as well as adult males and females, depending on their availability at the time of testing. They were descendants of gravid females originally collected at the sites described above (Table 1). The whip scorpions were maintained individually in plastic cages (nymphs: $15 \times 15 \times 8$ cm; adults: $25 \times 20 \times 9$ cm) and provided with water *ad libitum*. These cages contained sterilised sand as a substrate, and were placed in Precision Model 816 environmental chambers (22 ± 0.2°C; 65% RH; 10L:14D photoperiod regime; Central Scientific, Chicago, Illinois). Protonymphs and deutonymphs were fed twice per week on a diet of fruit flies (*Drosophila melanogaster* and *D. mojavensis*) and second-instar nymphs of crickets (*Acheta* spp.). Tritonymphs, tetranymphs and adults were fed adult crickets (*Acheta* spp.), cockroaches (*Periplaneta americana*), and mealworm beetle larvae (*Tenebrio molitor*).

Duration of embryonic development

Thirty-two females that were observed to mate with males were housed individually in plastic cages ($18 \times 18 \times 9$ cm). These were placed in Freas Model 805 environmental chambers (Chicago, Illinois), maintained at one of three test temperatures (15, 22 or 29°C), one of three RHs (12, 40 or 75%), and a 10L:14D photoperiod regime. These temperature and RH values were chosen because the whip scorpions had been collected from burrows exhibiting values within these ranges (Punzo, unpubl. data). Those females that became gravid ($n=21$) were maintained under these conditions during the period when eggs were enclosed in a membranous sac under their abdomen and throughout embryonic development. The time that elapsed between the appearance of eggs in the membranous sacs and the hatching of protonymphs was used to define the duration of embryonic development. Twenty eggs, randomly selected from each of 9 females ($n=180$ eggs), were used for data analysis, with 20 eggs also being randomly assigned to each of the 9 test conditions (3 temperatures and 3 RHs). Data were arc-sine transformed and analysed using an analysis of variance (ANOVA) and Tukey's tests for comparisons between treatment means (Sokal & Rohlf, 1995).

Lethal temperatures and critical thermal minimum/maximum determinations

Experiments to determine upper (ULT_{50}) and lower (LLT_{50}) lethal temperatures, critical thermal minimum (CTMmin) and maximum (CTMmax), and survival under various combinations of temperature and RH were conducted on various nymphal stages as well as on adults (depending on availability), according to methods described by Punzo & Rosen (1984). The various life cycle stages and associated morphometric data for the experimental animals are listed in Table 2. All experiments were conducted in Percival environmental chambers.

To determine lethal temperatures, 35 whip scorpions from each of the four nymphal stages, as well as 25 adult males, were placed individually in glass containers for

Location	Coordinates	N	Distance from previous location
Boquillas Canyon	29°12′N, 102°55′W	11	
Santa Elena Canyon	29°11′N, 103°45′W	17	76 km
Persimmon Gap	29°37′N, 103°04′W	14	74 km
Tornillo Flat	29°22′N, 103°02′W	24	32 km

Table 1: Locations within Big Bend National Park (Chihuahuan Desert) where gravid females of *Mastigoproctus giganteus* were originally collected. All animals used in these experiments were laboratory-reared descendants of these females.

each experimental condition. Upper and lower lethal temperatures were determined under both xeric (12% RH) and mesic (75% RH) conditions. All subjects were deprived of food for 24 h before testing. For LLT_{50} experiments, the whip scorpions were exposed to low temperatures ranging from -2.0 to $10°C$ at $0.5°C$ intervals for a period of 1 h. Following exposure, the animals were removed from the chamber and returned to normal rearing conditions. The number surviving after a further 24 h was recorded, and lethal temperature values determined using probit analysis (Finney, 1952).

Similar procedures were used for ULT_{50} determinations: whip scorpions were exposed to high temperatures ranging from 37–46°C at 0.5°C intervals under identical RH conditions. A z score was computed using the Mann–Whitney U-test to test for differences between LT values (Sokal & Rohlf, 1995).

CTM_{max} determinations were made according to the procedure described by Seymour & Vinegar (1973). These experiments were conducted on all nymphal stages and adult males. All subjects were acclimated at either 10 or 30°C for one month before testing. Acclimated subjects were placed individually in glass containers that were placed in modified environmental chambers whose front doors contained a one-way window. Tests were initiated at 25°C and temperatures were raised at a rate of 0.5°C/min under xeric (12% RH) and mesic (75% RH) conditions. CTM_{max} was defined as the temperature at which the subjects first exhibited body tremors and vertical movements of one or more legs (Punzo, 1998). When the whip scorpions were removed from testing conditions and returned to their housing cages, body tremors and leg shaking movements ceased within 30 min. Tests were conducted on 20 animals from each nymphal instar as well as on adult males under each test condition. Each subject was tested only once. Data were arc-sine transformed and analysed using a three-factorial design analysis of variance (ANOVA; 3 factors: acclimation temperature, RH, and life cycle stage) (Sokal & Rohlf, 1995). Tukey's tests were used to test for comparisons between treatment means.

Identical procedures were used for CTM_{min} determinations. Whip scorpions acclimated at 10 and 30°C were exposed to an initial test temperature of 10°C and observed as temperatures were lowered at a rate of 0.5°C/min. CTM_{min} was defined as the temperature (reversible) at which the subject first exhibited curling of the legs beneath the body, leading to loss of the righting reflex (Punzo & Thompson, 1990).
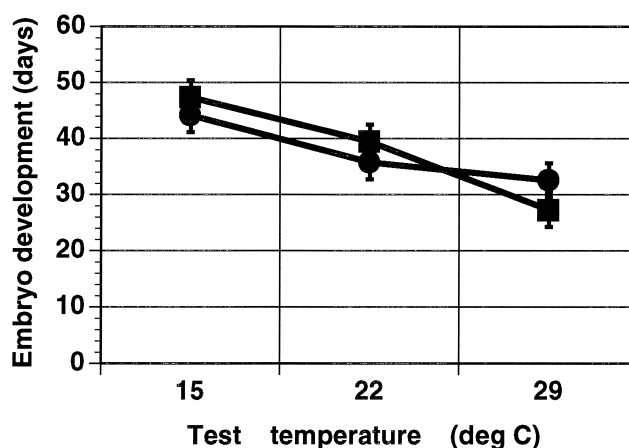

Fig. 1: Combined effect of temperature and relative humidity on duration (in days) of embryonic development in *Mastigoproctus giganteus*. Experiments conducted under a 10L:14D photoperiod regime. $N=20$ embryos per test condition. No embryo completed development at 12% RH, regardless of temperature. Embryonic development was completed in significantly less time at 22 and 29°C compared with 15°C ($p<0.05$), regardless of RH. Squares: RH=75%; circles: RH=40%.

Survival capacity experiments

These experiments were also conducted in Freas Model 805 environmental chambers (Chicago, Illinois) maintained at various combinations of temperature and RH (5–45°C, at intervals of 5°C, and 12 or 75% RH), and under a 10L:14D photoperiod regime. Owing to the availability of animals at the time of testing, experiments were conducted on 3 test groups: 100 tritonymphs, 100 adult males, and 100 females. We followed procedures similar to those described by Punzo (1980) for survival determinations of the beetle *Tenebrio molitor*. To summarise, whip scorpions were subjected to various conditions of temperature and RH over a 3-h exposure period. Five replicates were run for each test group, each replicate consisting of 20 individuals. Following the 3-h exposure period, subjects were removed from the chamber and isolated in individual holding containers under conditions identical to the rearing conditions described above. Survival capacity was determined by recording the percentage of whip scorpions surviving after 48 h.

Preferred temperature determinations

Experiments to determine the preferred temperature range of various life cycle stages of *M. giganteus* were

Stage	N	Total body length (mm)	Carapace length (mm)	Palpal femur length (mm)	Body weight (g)
Protonymph	743	15.81 (1.3)	5.28 (0.8)	2.34 (0.3)	0.68 (0.1)
Deutonymph	525	21.93 (2.5)	7.63 (1.1)	3.16 (0.5)	2.02 (0.3)
Tritonymph	478	28.56 (3.1)	10.73 (1.5)	4.91 (0.6)	4.45 (0.6)
Tetranymph	334	39.28 (2.9)	14.52 (2.3)	5.99 (0.4)	6.77 (1.2)
Adult male	238	47.82 (4.4)	17.64 (2.4)	9.67 (1.1)	8.02 (1.8)
Adult female	266	53.34 (5.1)	18.15 (3.1)	9.97 (0.9)	8.84 (2.3)

Table 2: Morphometric data on individuals of *Mastigoproctus giganteus* from various life cycle stages, used in these experiments. Data expressed as means; values in parentheses represent ± SE.

RH (%)	Upper lethal temperatures (°C) Life cycle stages (N1–AdM)				
	N1	N2	N3	N4	AdM
12	35.2[a]	35.5[a]	38.1[b]	38.5[b]	40.2[c]
75	38.3[d]	38.7[d]	40.4[e]	41.1[e]	42.6[f]
	Lower lethal temperatures (°C)				
12	4.7[a]	4.9[a]	3.9[b]	3.5[b]	3.3[b]
75	4.5[a]	4.7[a]	3.8[b]	3.3[b]	3.3[b]

Table 3: Upper (ULT_{50}) and lower (LLT_{50}) lethal temperatures for various life cycle stages of *Mastigoproctus giganteus* under xeric (12% RH) and mesic (75%) conditions. N1 (protonymphs), N2 (deutonymphs), N3 (tritonymphs), N4 (tetranymphs). AdM (adult males). $N=35$ for all nymphal stages, 25 for adults. Subjects were exposed (for 1 h) to a temperature range of -2 to 10°C (LLT_{50} determinations), or 37–46°C (ULT_{50}). Values in rows and columns followed by different letters are significantly different ($p<0.05$).

conducted using a temperature-gradient apparatus as described by Punzo (1991) for theraphosid spiders. The apparatus was a wooden trough ($100 \times 7 \times 7$ cm) provided with a copper-plated base (runway) and a transparent glass lid. One end of the copper plate was cooled by contact with a cold-water bath (-2°C), and the opposite end was heated with an electronic thermistor coil (65°C). A temperature gradient (air temperature) of 5–47°C was established in this way and monitored by a series of 15 evenly-spaced overhead thermometers. The steepness of the gradient was 0.5°C ± 0.01 (SE) cm^{-1}. Rising temperature caused a decrease in RH within the runway; the RH gradient ranged from 55–75%. Owing to availability at time of testing, 100 tritonymphs and 100 adult males were tested; each subject was tested once. At the start of each trial, an individual subject was placed in the centre of the apparatus and left undisturbed for 24 h. Following this period, we recorded the position of each subject in the apparatus and the temperature associated with that position. The percentage of subjects choosing a particular temperature gradient interval was recorded and used to determine temperature preference.

Results

Duration of embyronic development

None of the embryos exposed to 12% RH completed embryonic development. The effects of various combinations of ambient temperature and higher RH values (40 and 75%) on duration of embryonic development are shown in Fig. 1. An ANOVA showed an overall significant effect of temperature ($F=24.88$, $p<0.01$) and RH ($F=11.93$, $p<0.05$) on developmental rate ($F=24.88$, $p<0.01$). Additionally, development was most rapid at 75% RH and 29°C. At 15 and 22°C, however, development was faster at 40% RH than at 75% (Tukey's test, $p<0.05$).

Lethal temperatures and critical thermal minimum and maximum

Lethal temperatures for the various life cycle stages of *M. giganteus* are shown in Table 3. RH had no effect on resistance to low temperature stress ($z=0.09$, $p>0.60$). However, RH had a pronounced effect on upper lethal temperatures. Whip scorpions from all life cycle stages were able to withstand significantly higher temperatures under mesic conditions compared with animals exposed to xeric conditions ($z=2.43$, $p<0.05$).

The combined effects of acclimation temperature and RH on CTMmin and CTMmax values are shown in Table 4. The results showed an overall significant effect of acclimation temperature ($F=14.32$, $p<0.05$), RH ($F=11.67$, $p<0.01$) and life cycle stage ($F=9.03$, $p<0.05$) on CTMmin and CTMmax values.

CTMmin values were significantly lower for subjects from all life cycle stages acclimated at 10°C compared with those acclimated at 30°C (Tukey's tests, $p<0.05$). In addition, tetranymphs and adult males were able to withstand significantly lower temperatures than earlier nymphal stages at both acclimation temperatures ($p<0.06$). There were no significant differences in

Taccl	RH (%)	Critical thermal minimum (°C)				
		N1	N2	N3	N4	AdM
10	12	6.18 (0.21)[a]	5.99 (0.17)[a]	5.84 (0.14)[a]	4.91 (0.29)[b]	4.72 (0.32)[b]
	75	6.22 (0.22)[a]	6.02 (0.11)[a]	5.98 (0.13)[a]	5.04 (0.18)[b]	4.93 (0.26)[b]
30	12	7.54 (0.27)[c]	7.51 (0.18)[c]	6.83 (0.12)[c]	5.75 (0.18)[d]	5.69 (0.24)[d]
	75	7.51 (0.18)[c]	7.46 (0.13)[c]	6.84 (0.12)[c]	5.59 (0.21)[d]	5.71 (0.19)[d]
		Critical thermal maximum (°C)				
10	12	37.3 (1.2)[a]	37.6 (1.4)[a]	40.2 (1.9)[b]	40.4 (2.1)[b]	40.8 (1.8)[b]
	75	37.6 (2.1)[a]	37.9 (2.2)[a]	40.5 (0.8)[b]	40.7 (2.4)[b]	41.2 (2.3)[b]
30	12	37.5 (0.8)[a]	37.7 (1.6)[a]	40.4 (0.7)[b]	40.6 (1.8)[b]	40.7 (0.9)[b]
	75	38.7 (0.6)[c]	39.2 (0.8)[c]	41.5 (0.5)[d]	41.8 (1.3)[d]	41.9 (1.6)[d]

Table 4: Effects of temperature and relative humidity (RH) on critical thermal minimum and maximum temperatures for life cycle stages of *Mastigoproctus giganteus*. Data expressed as means; values in parentheses represent $\pm$ SE. Taccl=acclimation temperature (animals maintained at this temperature [°C] for one month before testing). Twenty subjects were tested for each condition of life cycle stage and RH. N1 (protonymphs), N2 (deutonymphs), N3 (tritonymphs), N4 (tetranymphs), AdM (adult males). Values followed by different letters are statistically significant ($p<0.05$).

Test temp. (°C)	Percent survival (%)					
	12% RH			75% RH		
	N3	AdM	AdF	N3	AdM	AdF
5	1	4	2	4	7	9
10	5	9	8	9	15	13
15	24	37	32	34	51	59
20	38	67	61	54	71	74
25	88	94	93	91	94	100
30	85	90	89	85	93	91
35	43	65	68	61	75	72
40	5	12	15	9	31	36
45	0	0	0	0	0	0

Table 5: Percent survival of tritonymphs and adult males and females of *Mastigoproctus giganteus* when exposed for a 3-h period to various combinations of temperature and relative humidity (RH). $N = 100$ subjects for each test condition. N3 (tritonymphs), AdM (adult males), AdF (adult females).

CTM$_{min}$ values between tetranymphs and adults ($p > 0.50$).

Under mesic conditions (75% RH), CTM$_{max}$ values were significantly higher for all life cycle stages acclimated at 30°C compared with subjects acclimated at 10°C ($p < 0.05$). There was no significant difference between warm and cold-acclimated groups under xeric conditions ($p > 0.60$). Tritonymphs, tetranymphs and adults exhibited significantly higher CTM$_{max}$ values than younger nymphal stages regardless of T$_{accl}$ (Tukey's tests, $p < 0.05$).

Survival capacity

Results showing the combined effect of temperature and RH on survival capacity are shown in Table 5. There was an overall significant effect of temperature (ANOVA: $F = 27.44$, $p < 0.01$) and RH ($F = 19.75$, $p < 0.01$) on survival. In addition, under both xeric and mesic conditions and for both nymphs and adults, survival was greatest (85–100%) between test temperatures of 25 and 30°, but less than 10% at 5°C, and no animals survived at 45°C (Tukey's tests, $p < 0.05$). Under xeric conditions, survival was low at an ambient temperature of 40°C (5% for nymphs, 12–15% for adult males and females); under mesic conditions: 9% (nymphs), 31–36% (adult males and females). There were significant increases in survival, under both mesic and xeric conditions, when test temperatures were raised from 10 to 15°C and from 20–25° (Tukey's tests, $p < 0.05$), and significant decreases between 35 and 40°C.

Preferred temperature range

Results of preferred temperature determinations are shown in Table 6. No significant differences were found between the responses of tritonymphs versus adults ($z = 0.57$, $p > 0.60$). The majority of whip scorpions chose a temperature range of 23–25.9°C, followed by a range of 26–28.9°C. With only a few exceptions, temperatures below 17°C (2 adults) and above 31.9°C (one adult) were avoided.

Discussion

This study presents for the first time a detailed analysis of the combined effects of ambient temperature and RH on duration of embryonic development, lethal temperatures, critical thermal minimum and maximum, survival capacity, and preferred temperature range of *M. giganteus*.

Over a temperature range of 15–29°C, no embryos completed development when exposed to markedly dry air (12% RH). This is in general agreement with previous studies on embryonic development in terrestrial arthropods (Edney, 1977; Punzo, 2000a). It is well known that the eggs of many arthropod species absorb water during embryonic development (Nation, 2002), and will cease to develop if conditions become too dry (Punzo, 1980; Punzo & Jellies, 1983). Under both xeric and mesic conditions, embryonic development was most rapid at 29°C, a temperature that has been observed within burrows occupied by *M. giganteus* at lower elevations in the Chihuahuan and Sonoran deserts (Punzo, unpubl. data). As a result, these individuals should reach the protonymph stage and begin to disperse earlier in the spring when densities of other arthropods, such as theraphosid and lycosid spiders, scorpions, centipedes, and solifugids, that feed on juvenile whip scorpions, are lower (Punzo, 2000a).

These results also show that the resistance of *M. giganteus* to high temperature stress is reduced under xeric conditions, suggesting that the epicuticle of *M. giganteus* is not an efficient barrier to EWL. Ahearn (1970) reported a relatively high water loss rate of 2.06%/hr at 40°C, compared with much lower rates (1.14%/hr) for some desert scorpions (Edney, 1977; Hadley, 1990). Desert scorpions and millipedes possess a thicker epicuticular layer with higher concentrations of the hydrocarbons which function as an efficient water-proofing material (Hadley, 1984; Cloudsley-Thompson, 1991). In contrast, many spiders and solifugids inhabiting xeric habitats are similar to *M. giganteus* in having a thinner epicuticle and exhibit higher rates of EWL (Edney, 1977; Punzo, 1998, 2000a). Like many other

Temperature interval (°C)	Percent choosing interval (%)	
	Tritonymphs	Adult males
5–7.9	0	0
8–10.9	0	0
11–13.9	0	0
14–16.9	0	2
17–19.9	5	4
20–22.9	9	8
23–25.9	45	52
26–28.9	31	29
29–31.9	10	4
32–34.9	0	1
35–37.9	0	0
38–40.9	0	0
41–43.9	0	0
44–47	0	0

Table 6: Preferred temperature range for tritonymphs ($n = 100$), and adult males ($n = 100$) of *Mastigoproctus giganteus*. Tests were conducted in a linear temperature gradient apparatus.

desert arthropods, *M. giganteus* reduces desiccation by being active at night and seeking refuge within burrows, rock crevices or under plant debris during the heat and low RH of the day (Crawford & Cloudsley-Thompson, 1971; Cloudsley-Thompson, 1975; Punzo, 2000a, b). Fossoriality as a behavioural mechanism of thermoregulation is common in animals inhabiting hot-dry environments (Cloudsley-Thompson, 1975; Punzo, 2000a).

It is well-known that EWL can be significantly higher when animals are exposed to dry air (Edney, 1977; Baehr & Eisenbeis, 1985; Huey & Kingsolver, 1993) and can have a significant effect on an animal's ability to withstand high and low temperature stress (Johnston & Bennett, 1996). Results on upper and lower lethal temperatures for *M. giganteus* are similar to those reported for some species of spiders (Pulz, 1987; Punzo, 1991), solifugids (Punzo, 1998), and centipedes (Cloudsley-Thompson, 1991) inhabiting desert regions. In contrast, some species of desert insects, scorpions and millipedes can withstand a wider range of temperature extremes under xeric conditions (May, 1985; Hadley, 1990; Cloudsley-Thompson, 2001).

Studies on critical thermal minima and maxima (CTMs) for arachnids are few, with spiders receiving most of the attention (Pulz, 1987; Cloudsley-Thompson, 1991). For example, threshold activity temperatures ranged from 10–12.6°C for the lycosids *Pardosa pullata* (Clerck) and *P. chelata* (Müller) (Hallander, 1970), and from 41–44°C for several species of sand dune spiders (Almquist, 1970). Under mesic conditions (75% RH), CTM_{min} and CTM_{max} values were 5.16°C and 43.27°C, respectively, for adults of the theraphosid spider *Dugesiella* (=*Aphonopelma*) *echina* Chamberlin acclimated at 30°C, and 5.14 and 41.99°C, respectively, under xeric (12% RH) conditions (Punzo, 1991). Seymour & Vinegar (1973) reported mean CTM_{max} values of 43.25 and 43.07°C for another theraphosid (*Aphonopelma* sp. B, from the Sonoran Desert), acclimated at 10 and 30°C, respectively.

The CTM_{min} and CTM_{max} values reported for *M. giganteus* in this study ranged from 4.72–7.54°C and 37.3–41.9°C, respectively, depending on RH and life cycle stage. Because CTMs result in immobility, animals would be unable to find the required resources or escape from predators, and therefore should seek shelter sites as ambient temperatures approach CTM values.

These data also show that an 85–100% survival rate occurred for all life cycle stages of *M. giganteus* at temperatures of 25 and 30°C under both xeric and mesic conditions, and survival ranged from 61–75% at 35°C under mesic conditions, decreasing to 43–68% under xeric conditions. Additionally, adults exhibited greater resistance to cold and high temperature stress than tritonymphs. It should be pointed out that lethal temperatures are a function of the length of time that an animal is exposed to stressful conditions. Furthermore, lethal temperatures (LTs) as well as CTM_{min} and CTM_{max} (CTMs), that are determined under conditions where temperature is steadily increased or decreased, are not comparable to LTs or CTMs observed over extended periods of exposure (Hadley, 1990). Nonetheless, the results from the present study are comparable to data on survival under temperature and moisture stress for desert-inhabiting solifugids (Punzo, 1998) and spiders (Pulz, 1987; Punzo & Chapla, 2002). In contrast, some species of desert scorpions and millipedes are capable of withstanding temperatures in excess of 42°C under xeric conditions (Hadley, 1990; Cloudsley-Thompson, 1991).

One of the behavioural mechanisms of thermoregulation used by ectotherms involves orienting their bodies with respect to the position of the sun or by moving to locations characterised by favourable microclimatic conditions. One experimental approach to studying such orientation movements involves the determination of temperature preferences within some type of linear temperature gradient apparatus (Cokendolpher & Francke, 1985). Forty-five and 52% of tritonymphs and adult males of *M. giganteus*, respectively, chose a temperature range of 23–25.9°C in a temperature gradient. Seventy-six percent of tritonymphs and 81% of adults were found between 23 and 28.9°C. These thermal preferenda are not surprising in view of the fact that the highest survival rates of *M. giganteus* occurred between 25 and 30°C. Wider thermal preferences ranging from 20–36°C have been reported for some desert scorpions (Hadley, 1990), insects (Cloudsley-Thompson, 2001), and dune-inhabiting spiders (Chew, 1961; Almquist, 1970) under xeric conditions. It should be mentioned that thermal preference can change as a function of body water content and typically decreases when terrestrial arthropods lose between 60–70% of their hydrated body weight (May, 1985; Johnston & Bennett, 1996).

In conclusion, the upper and lower lethal temperatures, critical thermal minimum and maximum, thermal preference, and survival capacity under thermal stress for *M. giganteus* are not as pronounced as in many other species of desert-inhabiting arthropods. Its cuticle is not a particularly efficient barrier to EWL, as is the case with some species of scorpions and millipedes. This whip scorpion is able to survive in desert regions by avoiding harsh conditions associated with high ambient temperatures and low relative humidity. It achieves this primarily through nocturnal activity patterns and fossoriality.

Acknowledgements

References

AHEARN, G. A. 1970: Water balance in the whipscorpion, *Mastigoproctus giganteus* (Lucas) (Arachnida, Uropygi). *Comp. Biochem. Physiol.* **35**: 339–353.

ALMQUIST, S. 1970: Thermal tolerances and preferences of some dune-living spiders. *Oikos* **21**: 230–235.

ANDERSON, J. F. 1970: Metabolic rates of spiders. *Comp. Biochem. Physiol.* **33**: 51–72.

BAEHR, B. & EISENBEIS, G. 1985: Comparative investigations on resistance to desiccation in Lycosidae, Hahniidae, Linyphiidae and Micryphantidae (Arachnida, Araneae). *Zool. Jb.* (Syst.) **112**: 225–234.

CHEW, R. M. 1961: Ecology of the spiders of a desert community. *Jl N. Y. ent. Soc.* **69**: 5–41.

CLOUDSLEY-THOMPSON, J. L. 1975: Adaptations of Arthropoda to arid environments. *A. Rev. Ent.* **20**: 261–283.

CLOUDSLEY-THOMPSON, J. L. 1991: *Ecophysiology of desert arthropods and reptiles.* Springer, Heidelberg.

CLOUDSLEY-THOMPSON, J. L. 2001: Thermal and water relations of desert beetles. *Naturwissenschaften* **88**: 447–460.

COKENDOLPHER, J. C. & FRANCKE, O. F. 1985: Temperature preferences of four species of fire ants (Hymenoptera: Formicidae: *Solenopsis*). *Psyche, Camb.* **92**: 91–101.

CRAWFORD, C. S. & CLOUDSLEY-THOMPSON, J. L. 1971: Water relations and desiccation-avoiding behaviour in the vinegaroon *Mastigoproctus giganteus* (Arachnida, Uropygi). *Entomologia exp. appl.* **14**: 99–106.

EDNEY, E. B. 1977: *Water balance in land arthropods.* 1–287. Springer, Heidelberg.

FINNEY, D. J. 1952: *Probit analysis* (2nd ed.). Cambridge University Press, Cambridge.

HADLEY, N. F. 1984: Cuticle: ecological significance. *In* J. Bereiter-Hahn, A. G. Matolsky & K. S. Richards (eds.), *Biology of the integument. Vol. 1. Invertebrates*: 685–694. Springer, Berlin.

HADLEY, N. F. 1990: Environmental physiology. *In* G. Polis (ed.), *The biology of scorpions*: 321–340. Stanford University Press, Stanford, California.

HALLANDER, H. 1970: Environments of wolf spiders *Pardosa chelata* (O. F. Müller) and *P. pullata* (Clerck). *Ekol. pol.* **18A**: 1–72.

HUEY, R. B. & KINGSOLVER, J. G. 1993: Evolution of resistance to high temperature in ectotherms. *Am. Nat.* **142**: S21–S46.

JOHNSTON, I. A. & BENNETT, A. F. 1996: *Animals and temperature: phenotypic and evolutionary adaptation.* Cambridge University Press, Cambridge.

KIRCHNER, W. 1987: Behavioural and physiological adaptations to cold. *In* W. Nentwig (ed.), *Ecophysiology of spiders*: 66–77. Springer, Berlin.

MAY, M. L. 1985: Thermoregulation. *In* G. A. Kerkut & L. Gilbert (eds.), *Comprehensive insect physiology, biochemistry and pharmacology* **4**: 507–552. Pergamon Press, New York.

NATION, J. L. 2002: *Insect physiology and biochemistry.* CRC Press, Boca Raton, Florida.

PULZ, R. 1987: Thermal and water relations. *In* W. Nentwig (ed.), *Ecophysiology of spiders*: 26–55. Springer, Berlin.

PUNZO, F. 1980: Effects of temperature, relative humidity and period of exposure on the survival capacity of *Tenebrio molitor* (Coleoptera: Tenebrionidae). *J. Kans. ent. Soc.* **53**: 260–270.

PUNZO, F. 1991: Intraspecific variation in response to thermal stress in the tarantula, *Dugesiella echina* Chamberlin (Orthognatha, Theraphosidae). *Bull. Br. arachnol. Soc.* **8**: 277–283.

PUNZO, F. 1998: *The biology of camel-spiders (Arachnida, Solifugae).* 1–301. Kluwer Acad. Publs., Norwell, Massachusetts.

PUNZO, F. 2000a: *Desert arthropods: life history variations.* 1–230. Springer, Heidelberg.

PUNZO, F. 2000b: Diel activity patterns and diet of the giant whipscorpion *Mastigoproctus giganteus* (Lucas) (Arachnida, Uropygi) in Big Bend National Park (Chihuahuan Desert). *Bull. Br. arachnol. Soc.* **11**: 385–387.

PUNZO, F. 2001: Substrate preferences, and the relationship between soil characteristics and the distribution of the giant whip-scorpion, *Mastigoproctus giganteus* (Lucas) (Arachnida, Uropygi). *Bull. Br. arachnol. Soc.* **12**: 35–41.

PUNZO, F. & CHAPLA, M. 2002: The effects of incubation temperature on locomotor activity in juvenile *Hogna carolinensis* (Araneae: Lycosidae). *Tex. J. Sci.* **54**: 261–268.

PUNZO, F. & JELLIES, J. 1983: Comparative water relations of araneid and lycosid spiderlings. *Comp. Biochem. Physiol.* **74A**: 981–988.

PUNZO, F. & ROSEN, L. 1984: Comparative temperature and water relations of *Tenebrio obscura* larvae (Coleoptera: Tenebrionidae). *Comp. Biochem. Physiol.* **77A**: 779–785.

PUNZO, F. & THOMPSON, D. 1990: Effects of temperature and acid stress on hatching, survival capacity, and postural reflexes in caenid mayflies (Ephemeroptera). *Comp. Biochem. Physiol.* **95A**: 69–72.

SEYMOUR, R. S. & VINEGAR, A. 1973: Thermal relations, water loss and oxygen consumption of a native American tarantula. *Comp. Biochem. Physiol.* **44A**: 83–96.

SOKAL, R. R. & ROHLF, B. J. 1995: *Biometry* (3rd ed.). W. H. Freeman, New York.

WEYGOLDT, P. 1971: Notes on the life history and reproductive biology of the giant whipscorpion, *Mastigoproctus giganteus* (Uropygi, Thelyphonidae) from Florida. *J. Zool., Lond.* **164**: 137–147.