

Intraspecific variation in response to temperature and moisture in *Eremobates palpisetulosus* Fichter (Solpugida, Eremobatidae) along an altitudinal gradient

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Summary

Thermal responses of *Eremobates palpisetulosus* from three altitudinal gradients were investigated. Embryonic development was not successful under xeric conditions (10% RH). Duration of embryonic development ranged from 24.3–31.2 days. Upper lethal temperatures ranged from 39.7–41.2°C at 10% RH, and from 41.4–43.6°C at 70% RH. Lower lethal temperatures ranged from 3.3–4.4 and 3.2–4.5°C respectively. Optimal survival occurred between 20–35°C. Critical thermal minima ranged from 4.8–5.3°C; critical thermal maxima ranged from 38.7–43.6°C. Evaporative water loss was greater under xeric conditions for all animals. The preferred temperature range was 24–27°C for solpugids from lower elevations (900 m), and 21–24°C for those from the highest elevation (1800 m). There was no significant effect of thermal acclimation on oxygen consumption rates. The rate of increase in oxygen consumption was lower at higher test temperatures.

Introduction

The distribution, abundance and activity of terrestrial arthropods are strongly influenced by moisture and ambient temperature (T_a) (see reviews by Cloudsley-Thompson, 1975; Edney, 1977; May, 1985). In arid regions, arthropods exhibit well-defined adaptations to several environmental parameters including extremes of relative humidity (RH) and T_a , relatively sparse vegetation, extended periods of drought and highly fluctuating food resources (Schmoller, 1970; Hadley, 1974; Louw & Seely, 1982). Although numerous studies have determined the effects of T_a and RH on the survival capacity (Cloudsley-Thompson, 1962, 1970; Ahearn, 1970; Seymour & Vinegar, 1973; Punzo, 1991; Punzo & Mutchmor, 1980), thermal tolerance (Almquist, 1970; Bursell, 1974; Punzo, 1989; Punzo & Huff, 1989) and behaviour (Hadley, 1974; Cloudsley-Thompson, 1975; Casey, 1981) of desert arthropods, most of these pertain to insects. Relatively little information is available for spiders (Almquist, 1970; Cloudsley-Thompson, 1983; Punzo & Jellies, 1983; Pulz, 1987) and no comparable data are available for solpugids.

Solpugids represent an important component of the arachnid fauna inhabiting desert regions (Muma, 1951, 1966a,b; Cloudsley-Thompson, 1977) and yet no detailed studies have been conducted on the temperature relationships of species comprising this taxonomic group. The purpose of the present study is to assess the degree of intraspecific variation in the thermal responses of the solpugid, *Eremobates palpisetulosus* Fichter from three populations occurring at different altitudes ranging from 900 to 1800 m. The following parameters were investigated: (1) the combined effects of T_a and RH on

embryonic development; (2) upper (ULT_{50}) and lower (LLT_{50}) lethal temperatures; (3) the effects of T_a , RH and thermal acclimation on critical thermal minima (CTM_{min}) and maxima (CTM_{max}); (4) the effects of T_a and RH on evaporative water loss (EWL); (5) determination of thermal preference; (6) the effect of thermal acclimation on metabolic rate (oxygen consumption).

Methods

Adult males (21–30 mm, total length) and females (22–32 mm) were collected between June and August, 1987–1991, from the following locations within the Chihuahuan Desert region: Presidio (Presidio County, Texas; elevation 900 m), Alpine (Brewster Co., Texas; elevation 1490 m), and 2.4 km north of Shafter (Presidio Co., Texas; elevation 1800 m) on the old Shafter-Marathon Road. A detailed description of the geology and vegetational zones of these locations is given by Tinkam (1948) and Medellin-Leal (1982). Presidio and Brewster Counties are located within the Big Bend Region of Trans Pecos Texas and are characterised by diverse orographic, topographical and floristic features. Shafter is located 88 km southwest of Alpine, and 32 km northeast of Presidio. The higher elevations of Alpine and Shafter are characterised by cooler summer temperatures, higher annual precipitation, and a Mexican Upper Sonoran flora dominated by gramma grasses (*Bouteloua gracilis*, *B. tripoda*), chino grass (*B. breviseta*), shrubs (*Rhus trilobata*, *Lycium pallidum*), snake weed (*Gutierrezia* spp.), catclaw (*Acacia roemeriana*), live oak (*Quercus emoryi*), gray oak (*Q. grisea*) and juniper (*Juniperus monosperma*). Presidio, located in the Lower Sonora Zone (900 m), is characterised by adobe soils and a Rio Grande Valley flora dominated by velvet mesquite (*Prosopis juliflora*), blue thorn (*Condalia lyciodes*), catclaw (*A. gregii*), Mexican jara (*Bacharis glutinosa*), saltbush (*Atriplex cunescens*), creosote (*Larrea divaricata*) and ocotillo (*Fouquieria splendens*).

Solpugids were collected at night while they were wandering on the ground. All experiments were conducted on adult females (weight 1.9–2.4 g) since these represented the majority of specimens collected. Solpugids were transported back to the laboratory and maintained individually in clear plastic containers at 21–23°C and 70–72% RH. They were fed twice per week on a diet of crickets, mealworm larvae, spiders and grasshoppers. Experiments were conducted over a four-year period, and whenever possible tests were conducted within 30 days of capture. All experiments were conducted in a Percival Model I-35VL Environmental Chamber (Boone, Iowa) which allowed for precise temperature and RH control. Statistical methods used throughout this study follow those described by Sokal & Rohlf (1981). Arcsine transformations were conducted on all data used for ANOVA analyses.

Embryonic development

Gravid females were allowed to oviposit and the eggs were collected after 30 h, placed in petri dishes ($n = 20$

eggs/dish) and then allowed to develop at various combinations of T_a and RH. Fertilised eggs were white, translucent, subspherical in shape, possessed truncate papillae on the chorion and had a mean diameter of 1.59 mm. Unfertilised eggs were yellow and shrunk noticeably within 24 h of oviposition. Each condition of T_a and RH was assessed for 20 eggs from each of 20 females. Eggs were placed on a piece of filter paper (Whatman No. 3) lining the bottom of a glass petri dish. Developing embryos were exposed to ambient test temperatures of either 15, 27 or 35°C at 10 or 70% RH. The duration of embryonic development was recorded as the mean number of days from time of oviposition to hatching (Table 1). The percentage of eggs successfully completing embryonic development at each test condition was also recorded (Table 1).

Survival capacity, lethal temperatures and critical thermal minima / maxima

Upper and lower temperatures were determined according to the procedure of Punzo & Rosen (1984). Twenty adult females from each geographical location were placed individually in glass vials for exposure to experimental conditions. All solpugids were deprived of food for 48 h before testing. For ULT_{50} determinations (Table 2), different groups of 20 animals were exposed to temperatures ranging from 35–46°C at 0.5°C intervals for 1 h under mesic (70% RH) and xeric (10% RH) conditions. Following the exposure period, solpugids were removed from the environmental chamber and returned to normal holding conditions. The number surviving after a 24 h period was recorded. Animals were considered dead if they did not respond to successive tactile stimulations with a plastic probe. Identical procedures were used for LLT_{50} determinations (Table 2). Solpugids were exposed to temperatures ranging from -2.0 to 10°C at 0.5°C intervals. Lethal temperatures were obtained using probit analysis (Finney, 1952). Percent survival (Table 3) was determined over a temperature range of 5–45°C under mesic and xeric conditions as described by Punzo (1991).

CTM_{min} determinations (Table 4) were conducted according to the method reported by Seymour & Vinegar (1973). Ten solpugids from each location were acclimated at either 10 or 30°C for 14 days before testing. Acclimated animals were placed individually in 500 cm³ glass containers and observed through a one-way mirror. Experiments were initiated at 20°C and temperatures were lowered at 0.5°C min⁻¹ under mesic and xeric conditions as described above. The CTM_{min} was defined as that reversible low temperature at which the animal first exhibited a curling of the legs beneath the body. Identical procedures were employed for CTM_{max} determinations (Table 4). Acclimated animals were exposed to an initial test temperature of 15°C and observed closely as temperatures were elevated at a rate of 0.5°C min⁻¹. The reversible high temperature at which solpugids first exhibited body tremors and leg-curling was taken as the CTM_{max} .

Evaporative water loss

These experiments were conducted in a desiccation apparatus previously described by Punzo & Jellies (1983). Air was recycled at a flow rate of 3.4 l min⁻¹. EWL determinations were carried out at RH values of 10 and 70%. RH values were obtained by using saturated salt solutions as described by Winston & Bates (1960) and Punzo (1991): LiCl + silica gel (10%), and NaCl + urea (70%). A test temperature of 35°C over a 24 h exposure period was used throughout these experiments. An air current was bubbled through 1000 ml of the saturated salt solution and then passed through cotton traps and polyester fibre filters before entering the desiccation chamber which housed an individual solpugid. Each animal to be tested was placed in a glass container provided with holes for air circulation. Twenty female solpugids from each location were tested at 10 and 70% RH. Solpugids were weighed individually on a Metler electronic analytical balance to the nearest 0.005 mg at hourly intervals over a 24 h period. EWL (across both integument and respiratory surfaces) was expressed as a percentage of initial body weight (Table 5). All animals were deprived of food for 72 h before testing (defecation was minimal or absent).

Temperature preferenda determinations

Temperature preferenda determinations were conducted in a temperature gradient apparatus (Punzo, 1991) using procedures similar to those described by Nørgaard (1951). The apparatus consisted of a rectangular wooden trough (100 × 7 × 7 cm) fitted with a copper-plated base (runway) and a clear plexiglass cover. One end of the copper plate was heated with an electrical thermistor coil (65 ± 1°C). The opposite end was cooled by contact with a cold water bath (-2°C). This resulted in the establishment of a temperature gradient which ranged from 5–46°C; this gradient was monitored by a series of 15 overhead thermometers as described by Almquist (1970). The steepness of the gradient was approximately 0.5°C cm⁻¹. Increasing

Location	Temp. (°C)	Mean time (days)		Hatching success (%)	
		10%RH	70% RH	10% RH	70% RH
Presidio (900 m)	15	D	D	0	0
	27	D	31.2 (3.7)	0	77
	35	D	25.4 (2.1)	0	58
Alpine (1490 m)	15	D	D	0	0
	27	D	30.6 (2.7)	0	75
	35	D	26.3 (2.4)	0	42
Shafter (1800 m)	15	D	D	0	0
	27	D	29.8 (1.9)	0	73
	35	D	24.3 (3.1)	0	38

Table 1: Combined effects of temperature and relative humidity (RH) on the duration of embryonic development (in days) and percent hatching success in *Eremobates palpisetulosus*. Values for duration represent mean number of days from time of oviposition to hatching ($n = 400$ fertilised eggs for each experimental condition). Numbers in parentheses represent ± S.D. D = death (embryos did not complete development).

Location	RH (%)	Lethal temperatures (°C)	
		LLT ₅₀	ULT ₅₀
Presidio (900 m)	10	4.4 (0.2)	41.2 (0.4)
	70	4.5 (0.1)	43.6 (0.3)
Alpine (1490 m)	10	3.9 (0.1)	40.2 (0.3)
	70	3.7 (0.2)	41.8 (0.4)
Shafter (1800 m)	10	3.3 (0.1)	39.7 (0.3)
	70	3.2 (0.2)	41.4 (0.4)

Table 2: Upper (ULT₅₀) and lower (LLT₅₀) lethal temperatures for *Eremobates palpisetulosus* under mesic (70% RH) and xeric (10% RH) conditions ($n = 20$ animals for each experimental condition). Numbers in parentheses represent \pm S.D. Period of exposure = 1 h.

temperature resulted in a decrease in RH within the runway; the RH gradient ranged from 53–72%. For each experiment, a solpugid was placed individually at the centre of the apparatus and left undisturbed for 24 h. Its position and choice of temperature interval within the apparatus was then recorded. The percentage of animals choosing a particular temperature gradient interval was determined for 100 solpugids from each location (Table 6).

Oxygen consumption determinations

Solpugids were acclimated at 10 or 30°C for 7 days before testing. Each solpugid was placed in a glass container (500 cm³) sealed with a rubber stopper and provided with a three-way stopcock. Individual animals from each acclimation group were exposed to ambient test temperatures ranging from 10–40°C (Table 7) for a period of 2 h. Air samples were removed from the holding containers using a 50 cm³ syringe and injected into a Beckman E3 oxygen analyser through a plastic tube containing silica gel to absorb CO₂ and water vapour. The analyser was recalibrated with atmospheric air following each test. Oxygen consumption rates were calculated using the method described by Depocas & Hart (1957) and expressed in $\mu\text{l g-h}^{-1}$.

Results

Embryonic development

The duration of embryonic development ranged from 24.3 to 31.2 days depending on temperature and RH (Table 1). All embryos died when exposed to xeric conditions (10% RH) regardless of the test temperature (Table 1). Even under mesic conditions (70% RH), all embryos died when exposed to a temperature of 15°C. In general, developmental rates increased when exposure temperatures were raised from 27 to 35°C. Optimal hatching success (73–77%) for embryos from all locations was observed at 27°C under mesic conditions. Although developmental rates were accelerated at higher temperatures (35°C), hatching success decreased significantly (ANOVA: $F = 12.1$, $p < 0.01$, arcsine transformation) from 73–77% to 38–58% (Table 1). The only other comparable data available are those reported by Muma (1966b,c) for *E. durangonus* from the San Simone

Valley of southeastern Arizona and southwestern New Mexico. In this species, the mean number of days required for embryonic development was 25 (range 18–33 days) at 27°C.

Lethal temperatures, survival capacity and critical thermal minima / maxima

The ULT₅₀ and LLT₅₀ values for adult female *E. palpisetulosus* are shown in Table 2. Although RH had no effect on resistance to low temperature stress, ULT₅₀ temperatures decreased by 1.6–2.4°C under xeric conditions compared with those values obtained under mesic conditions. A Wilcoxon Signed Rank Test (Sokal & Rohlf, 1981) showed these differences to be significant ($Z = 3.03$, $p < 0.01$). These results show that resistance to high temperature stress is reduced due to desiccation when these solpugids are exposed to dry air. In addition, animals from lower elevations (Presidio) exhibit a greater resistance to high temperature stress than those from Alpine and Shafter ($Z = 2.88$, $p < 0.01$). Conversely, solpugids from higher elevations exhibited lower LLT₅₀ values compared with those from lower elevations ($Z = 2.92$, $p < 0.01$). This is in general agreement with results reported for the tarantula *Dugesia echina* Chamberlin from a similar altitudinal gradient in Trans Pecos Texas (Punzo, 1991).

The combined effects of temperature and RH on the survival capacity of *E. palpisetulosus* are shown in Table 3. The overall effects of temperature (ANOVA: $F_{8, 56} = 23.4$, $p < 0.01$), RH ($F_{1, 56} = 12.7$, $p < 0.01$), and location ($F_{2, 56} = 13.4$, $p < 0.01$) on survival capacity were significant. Solpugids from higher elevations (Shafter) can tolerate markedly cooler temperatures than those from lower elevations (Presidio) under both mesic and xeric conditions (Scheffe $F = 7.71$, $p < 0.01$). Conversely, solpugids from lower elevations characterised by higher temperatures and drier climatic conditions, exhibited a greater tolerance of high test temperatures and xeric conditions. When exposed to 40°C and 70% RH, 60% of the solpugids from the Presidio population survived whereas only 45% of the Shafter animals survived under these conditions

Test temp. (°C)	Percent survival					
	10% RH			70% RH		
	Presidio	Alpine	Shafter	Presidio	Alpine	Shafter
5	5 *	25	40	10	20	45
10	40	60	80	35	60	75
15	85	95	95	90	100	100
20	100	100	90	95	100	95
25	100	100	95	100	95	100
30	100	95	100	100	100	100
35	90	90	85	90	85	95
40	40	25	20	60	50	45
45	0	0	0	0	0	0

Table 3: Effects of temperature and relative humidity (RH) on percent survival for adult females of *Eremobates palpisetulosus* under mesic (70% RH) and xeric (10% RH) conditions ($n = 20$ solpugids for each experimental condition). Period of exposure = 1 h. Presidio, 900 m; Alpine, 1490 m; Shafter, 1800 m.

Location	T _{acc} (°C)	Critical thermal minima (°C)		Critical thermal maxima (°C)	
		10% RH	70% RH	10% RH	70% RH
Presidio (900 m)	10	5.2 (0.2)	5.1 (0.3)	40.8 (0.4)	43.1 (0.2)
	30	5.3 (0.4)	5.3 (0.2)	41.2 (0.1)	43.6 (0.2)
Alpine (1490 m)	10	5.1 (0.1)	4.9 (0.2)	39.1 (0.4)	42.2 (0.2)
	30	5.3 (0.3)	4.8 (0.1)	39.7 (0.3)	42.4 (0.1)
Shafter (1800 m)	10	4.9 (0.1)	4.8 (0.1)	38.7 (0.1)	41.4 (0.3)
	30	5.1 (0.3)	4.9 (0.2)	39.4 (0.2)	41.2 (0.1)

Table 4: Effects of temperature and relative humidity (RH) on CTM_{min} (°C) and CTM_{max} (°C) for *Eremobates palpisetulosus* under mesic (70% RH) and xeric (10% RH) conditions. Values represent mean temperature ($n = 10$ for each experimental condition). Numbers in parentheses represent \pm S.D. Animals maintained at acclimation temperature (T_{acc}) for 7 days before testing.

($Z = 2.84, p < 0.01$). Survival of Presidio animals decreased from 60% under mesic conditions to only 40% under xeric conditions. The data also suggest that a temperature range of 20–30°C appears to be optimal for adult survivorship in this species.

The effects of temperature and RH on CTM_{min} and CTM_{max} are shown in Table 4. Geographical location, thermal acclimation and RH had no significant effect on CTM_{min} ($Z = 0.31, p > 0.50$). Critical thermal minima ranged from 4.8–5.3°C (Table 4). However, with respect to critical thermal maxima values (Table 4), the overall effect of geographical location (ANOVA: $F_{2, 56} = 10.8, p < 0.01$) was found to be significant under xeric conditions. CTM_{max} values ranged from 38.7–41.2°C at 10% RH, and from 41.2–43.6°C at 70% RH.

Evaporative water loss

The relationship between EWL (as reflected by percent body weight loss) and RH for animals exposed to 35°C over a 24 h period is shown in Table 5. Weight loss was significantly higher under xeric conditions for solpugids from all locations (ANOVA: $F_{2, 56} = 11.4, p < 0.01$). Solpugids from the Shafter population exhibited significantly higher weight loss (22.6%) than those from the Presidio population (11.4%) ($\chi^2 = 3.81, p < 0.01$). This indicates that solpugids from higher elevations exhibit less resistance to EWL than conspecifics from lower altitudes. This is consistent with the observation that Presidio contains microhabitats characterised by hotter and drier climatic conditions (especially in summer months) than those found in the mountainous regions of Alpine and Shafter (Tinkam, 1948).

Location	Weight loss (%)		p
	10% RH	70% RH	
Presidio (900 m)	11.4	5.7	0.01
Alpine (1490 m)	15.3	7.1	0.01
Shafter (1800 m)	22.6	8.7	0.01

Table 5: Effect of relative humidity (RH) on evaporative water loss (EWL) (expressed as a percentage of initial body weight) in adult females of *Eremobates palpisetulosus* exposed to 35°C over a 24 h period ($n = 20$ for each experimental condition). Level of significance computed using a Chi Square contingency analysis and ANOVA on actual weights (Sokal & Rohlf, 1981).

Temperature preferenda determinations

The temperature preferenda for adult females of *E. palpisetulosus* from various locations are shown in Table 6. The majority (60%) of solpugids from the Presidio population chose a temperature gradient interval of 24–27°C, with an additional 31% of this population choosing an interval of 27–30°C. The largest number of the Alpine and Shafter animals chose a cooler temperature interval of 21–24°C (44 and 53%, respectively). Only 4% of the Presidio solpugids chose the interval of 21–24°C, and none of these solpugids chose the 18–21°C interval compared with 14 and 21% respectively of the Alpine and Shafter animals. Whereas 31% of the Presidio solpugids chose an interval of 27–30°C, only 7% of the Alpine and none of the Shafter animals chose this interval. These results indicate that solpugids from lower elevations exhibit a higher temperature preferendum (Scheffe $F = 14.3, p < 0.01$) than those from higher elevations.

Effects on metabolic rate

The effects of T_a, acclimation temperature and RH on oxygen consumption rates for adult females of *E. palpisetulosus* are shown in Table 7. Oxygen consumption rates increased with increasing ambient temperatures for all experimental groups. However, the rate of increase

Temperature interval (°C)	Percentage choosing interval		
	Presidio (900 m)	Alpine (1490 m)	Shafter (1800 m)
9–12	0	0	0
12–15	0	0	0
15–18	0	4	7
18–21	0	14	21
21–24	4	44	53
24–27	60	31	19
27–30	31	7	0
30–33	5	0	0
33–36	0	0	0
36–39	0	0	0

Table 6: Temperature preferences of *Eremobates palpisetulosus*. Values represent the percentage of adult female solpugids choosing a particular temperature gradient interval ($n = 100$ for each experimental condition). All animals maintained at $22 \pm 1^\circ\text{C}$ and 70–72% RH before testing.

T_a	Mean oxygen consumption rate ($\mu\text{l g-hr}^{-1}$)					
	Acclimation temperature ($^{\circ}\text{C}$)					
	10 $^{\circ}\text{C}$			30 $^{\circ}\text{C}$		
	Presidio	Alpine	Shafter	Presidio	Alpine	Shafter
10	8.9 (0.2)	9.1 (0.1)	9.3 (0.1)	9.0 (0.2)	8.7 (0.3)	8.8 (0.1)
15	10.2 (1.1)	9.8 (0.3)	10.1 (0.7)	10.3 (0.4)	9.9 (0.2)	9.7 (0.3)
20	21.4 (3.1)	22.1 (1.7)	20.8 (2.3)	22.3 (3.1)	20.7 (1.9)	21.6 (0.8)
25	40.7 (3.9)	39.6 (3.1)	42.1 (2.8)	41.8 (3.1)	41.3 (0.9)	39.8 (2.2)
30	71.6 (6.5)	70.3 (5.7)	67.4 (4.7)	74.6 (7.1)	69.8 (4.6)	71.2 (3.7)
35	84.3 (8.7)	82.1 (6.9)	80.3 (7.2)	86.1 (4.9)	83.9 (5.7)	84.6 (6.2)
40	99.4 (9.1)	94.6 (6.8)	91.3 (8.2)	98.2 (7.7)	96.8 (8.8)	101.2 (6.8)

Table 7: Effects of ambient temperature (T_a , $^{\circ}\text{C}$) on mean oxygen consumption rates ($\mu\text{l g-hr}^{-1}$) in *Eremobates palpisetulosus* females acclimated at 10 and 30 $^{\circ}\text{C}$. Numbers in parentheses represent \pm S.D. ($n = 10$ for each experimental condition). Presidio, 900 m; Alpine, 1490 m; Shafter, 1800 m.

as reflected by Q_{10} values was lower at higher temperatures ($Q_{10} = 1.43$ between 30–40 $^{\circ}\text{C}$; 3.17 (20–30 $^{\circ}\text{C}$); 2.14 (10–20 $^{\circ}\text{C}$). This is in general agreement with values reported for other arachnid species (Anderson, 1970). No significant effect of acclimation temperature on oxygen consumption was found for solpugids from any of the populations analysed. The regression equation showing the relationship between T_a and oxygen consumption rates for solpugids acclimated at 30 $^{\circ}\text{C}$ is: $y = 3.92x - 46.41$ ($r^2 = 0.931$); for solpugids acclimated at 10 $^{\circ}\text{C}$: $y = 3.46x - 41.83$ ($r^2 = 0.928$).

Discussion

Although numerous studies have been conducted concerning the temperature and water relations of desert-inhabiting spiders (see review by Cloudsley-Thompson, 1983) and scorpions (see review by Hadley, 1974), little information is available on the thermal biology and behaviour of solpugids (Junqua, 1958; Cloudsley-Thompson, 1961, 1977; Muma, 1967). Solpugids are common inhabitants of most desert regions worldwide with the exception of Madagascar and Australia (Cloudsley-Thompson, 1977). They are usually associated with xeric desert scrub habitats although some species are found at higher altitudes characterised by more mesic conditions (Fichter, 1940; Muma, 1966a). Many species are fossorial while others are commonly found within rock crevices or beneath stones and decaying vegetation (Cloudsley-Thompson, 1961; Muma, 1966a,b, 1967). Although most species avoid the severe day-time temperatures seasonally associated with desert regions via nocturnal activity patterns, some species are diurnal or crepuscular (Cloudsley-Thompson, 1977). Desert regions are associated with irregular rainfall patterns, high levels of solar radiation and extremes of moisture and temperature resulting in a high saturation deficiency in the surrounding air which increases evaporative and transpiratory water loss (Bursell, 1974; Edney, 1977; Punzo, 1989). In order to regulate homeostasis so that normal behavioural patterns can continue, desert arthropods must minimise fluctuations in water loss and maintain body temperature within tolerable limits. This can be accomplished via behavioural mechanisms of thermoregulation such as fossoriality, noctur-

nal patterns of activity, stiling and body orientation (Casey, 1981), and physiological mechanisms such as haemolymph osmoregulation and evaporative cooling (May, 1985; Punzo, 1989, 1991).

The results from the present study indicate that under xeric conditions, embryonic development is significantly impaired (Table 1), resistance to high temperature stress is reduced (Tables 2–4) and EWL is significantly increased (Table 5) in *E. palpisetulosus* from all geographical locations (elevations). These data suggest that this species does not possess a particularly effective epicuticular barrier to EWL which is characteristic of many desert scorpions (Hadley, 1974), insects (Cloudsley-Thompson, 1975) and at least one solpugid species, *Galeodes granti* (24 h exposure), from the Sudan (Cloudsley-Thompson, 1977). The most important adaptation exhibited by *E. palpisetulosus* to its xeric environment appears to be its nocturnal behaviour pattern (personal observation). Similar nocturnal circadian rhythms have been reported for other North American solpugids (Muma, 1966a) as well as theraphosid (Punzo, 1991) and lycosid (Cloudsley-Thompson, 1983) spiders, uropygids (Ahearn, 1970), scorpions (Hadley, 1974) and insects (Cloudsley-Thompson, 1975; Punzo, 1989).

Embryonic mortality is 100% in *E. palpisetulosus* when fertilised eggs are exposed to xeric conditions, regardless of T_a . Under more favourable conditions (70% RH), embryonic development is completed within 24–32 days depending on the T_a and geographical location. The mean number of days for successful development at 27 $^{\circ}\text{C}$ and 70% RH ranged from 29.8 days for eggs obtained from Shafter females, to 31.2 days (eggs from Presidio females). Muma (1966c) reported a developmental period of 18–33 days (mean 25 days) for *E. durangonus* under the same conditions of temperature and RH. This contrasts sharply with the eggs of *G. granti* which hatch within 48 h following oviposition (Cloudsley-Thompson, 1967). Future studies are needed on many more species so that a better understanding of the variation in developmental rates for these arachnids can be obtained and correlated with microhabitat preferences.

It is also apparent that under xeric conditions, resistance to high temperature stress is significantly reduced

(Tables 2, 3), and EWL is markedly higher (Table 5). The degree of EWL observed for *E. palpisetulosus* in this study is greater than that reported after 24 h exposure for *G. granti* (Cloudsley-Thompson, 1977) from the Sudan. In addition, the ability of *E. palpisetulosus* females to maintain normal body posture and movements is impaired to a greater extent when exposed to high temperature stress under xeric conditions (Table 4). The data on lethal temperatures (Table 2) and percent survival (Table 3) are also consistent with the results obtained for CTM_{min} and CTM_{max} (Table 4). At 10% RH, the ULT₅₀ for *E. palpisetulosus* ranged from 39.7–41.2°C. Previous work on several arthropods from the Sudan (Cloudsley-Thompson, 1970) reported ULT₅₀ values of 38°C for the orthopteran insect *Gryllus bimaculatus*, 37°C for *Periplaneta americana*, and 48°C for the scorpion *Leiurus quinquestriatus*, when exposed for 24 h to RH values of 10%. The only solpugid assessed under these conditions exhibited a ULT₅₀ of 50°C, significantly higher than that found for *E. palpisetulosus* in the present study. Some representative studies on North American desert arthropods exposed to xeric conditions have reported ULT₅₀ values of 39.8–41.5°C for the theraphosid spider *Dugesia echina* along an altitudinal gradient (Punzo, 1991), 40°C for the tenebrionid beetle *Eleodes* sp. (Cloudsley-Thompson, 1970), and 41°C for the scorpion *Vejois* sp. (Cloudsley-Thompson, 1977). These data suggest that lethal temperatures can vary widely among desert arthropods and that these animals exhibit a wide array of adaptations to desert conditions.

Adult females of *E. palpisetulosus* exhibit a relatively wide temperature preference range. Similar results were reported for the tarantula *D. echina* (Punzo, 1991). No comparable data are available for other solpugid species. However, previous studies have reported a narrower range for most spiders (Nørgaard, 1951; Almquist, 1970; Pulz, 1987) and many insects (Bursell, 1974; Cloudsley-Thompson, 1975; May, 1985; Punzo & Huff, 1989). Ninety-one percent of females from lower elevations chose a temperature range of 24–30°C (Table 6); 72–75% from higher elevations chose a temperature range of 21–27°C. Although such experiments were not conducted in the present study, it would be interesting to assess the differences, if any, in temperature preference between males and females, as well as any seasonal shifts that may occur. Differences in temperature preference associated with sex have been reported in some spiders (Nørgaard, 1951; Cloudsley-Thompson, 1983). It has been widely accepted that interspecific differences in the temperature preference of terrestrial arthropods correspond to the thermal regimes associated with specific microhabitats (Almquist, 1970; Louw & Seely, 1982; Punzo & Rosen, 1984), which in turn define the thermal niche of a species.

No significant effect of thermal acclimation on oxygen consumption rates was found for *E. palpisetulosus* (Table 7). This is in agreement with results reported by Punzo (1991) for a theraphosid spider. However, acclimatory effects have been reported for the solpugid, *G. granti* (Carlisle & Cloudsley-Thompson, 1968) as well as for insects (see reviews by Bursell, 1974; May, 1985).

Acknowledgements

I wish to thank J. Bottrell and T. Punzo who assisted in the collection of solpugids, Drs B. Garman and K. Dove for consultation on statistical procedures, and Drs W. Price and G. Sich for useful comments on earlier drafts of the manuscript. I would also like to thank the University of Tampa for a Faculty Development Grant which made much of this work possible.

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Bull. Br. arachnol. Soc. (1994) **9** (8), 262–266

On the spider genus *Zimiromus* (Araneae: Gnaphosidae) in Central Amazonia

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Summary

We describe for the first time the male of *Zimiromus boistus* Platnick & Höfer, 1990 and the female of *Zimiromus beni* Platnick & Shadab, 1981, from a whitewater inundation forest near Manaus. A female from Bolivia, originally described as *Zimiromus beni*, is redescribed as *Zimiromus platnicki*, new species.

Introduction

The genus *Zimiromus* Banks, 1914 contains about forty neotropical species (Platnick & Shadab, 1976; 1979; 1981; Platnick & Höfer, 1990; Buckup & Brescovit, 1993). Platnick & Höfer (1990) described three *Zimiromus* species: *Z. atrifus*, *Z. boistus* (♀ only) and *Z. cristus*, from a blackwater inundation forest near Manaus. During further evaluation of material collected during the same ecological study (Höfer, 1990), we found males and females of two very similar, but different, species. The females of one species proved to be *Z.*

boistus Platnick & Höfer, 1990 and the males of the other species were *Z. beni* Platnick & Shadab, 1981. The male holotype of *Z. beni* was described from a specimen collected in the Beni department (Río Baures, Río Iténez), Bolivia. The original description included a female paratype collected near this locality (Pampa de Meio, Río Iténez). However, this female is not conspecific with either species from Manaus.

The whitewater inundation forest near Manaus was studied by an intensive ecological sampling programme, using various types of traps during a complete non-inundated period (Höfer, 1990). In spite of that we are unable to match males and females of the two species, because all males and females occurred in the same stratum (ground surface and tree trunks) within the same period (October to January). Therefore we propose the most parsimonious procedure and put the undescribed female together with the described male of *Z. beni* and the undescribed male together with the described female of *Z. boistus*. Both species belong to the same species group within the genus, characterised by a single short retrolateral tibial apophysis on the male palp and a distinct, but unstriated epigynal scape. The female originally described as *Z. beni* belongs to another species group, characterised by a striated epigynal scape, and is now redescribed as *Zimiromus platnicki*, new species.

Study area, methods and material

Spiders were collected in an area of approximately 2 ha of a whitewater-inundation forest (várzea) on the first island upstream from Manaus in the Rio Solimões. This island "Ilha da Marchantaria" is a traditional study area of the Max-Planck working group "Tropical