Intraspecific variation in responses to thermal stress in the tarantula, Dugesiella echina Chamberlin (Orthognatha, Theraphosidae)

Fred Punzo

Dept. of Biology,
Division of Science and Mathematics,
University of Tampa,
Tampa, Florida 33606, USA

Summary

Thermal responses of Dugesiella echina from three altitudinal gradients were investigated. Upper lethal temperature (ULT_{50}) values ranged from 39.76-42.26°C at 12% RH, and from 42.18-44.34° at 72% RH. Lower lethal temperature (LLT_{50}) values were 3.27-4.36 and 3.09-4.37, respectively. Critical thermal minima (CTM_{min}) ranged from 4.91-5.24°C. Critical thermal maxima (CTM_{max}) were 40.8-43.79°, with significantly lower values occurring under xeric conditions. Optimal survival occurred between 15-30°C. The preferred temperature range was 24-27°C. Cuticular water loss was greater under xeric conditions for spiders from higher elevations. There was no significant effect of acclimation on oxygen consumption rates. The rate of increase in oxygen consumption was lower at higher temperatures.

Introduction

It is well established that the distribution and activity of terrestrial arthropods are strongly influenced by ambient temperature (T_a) and moisture regimes (see reviews by Edney, 1977 and May, 1985). Although there have been numerous studies concerning the effects of temperature and relative humidity (RH) on survival (Chew, 1961; Cloudsley-Thompson, 1975; Punzo & Mutchmor, 1980; Punzo & Rosen, 1984; Baehr & Eisenbeis, 1985; Punzo & Huff, 1989), metabolic rate (Anderson, 1970; Anderson & Prestwich, 1985), resistance to cold (Kirchner, 1987; Bromhall, 1988), thermal tolerance (Almquist, 1970; Cloudsley-Thompson & Crawford, 1970; Punzo, 1989c) and behaviour (Cloudsley-Thompson & Crawford, 1970; Humphreys, 1974; Minch, 1978; Casey, 1981; Cloudsley-Thompson, 1983) of arachnids and other terrestrial arthropods, very little information is available on interspecific and intraspecific variation in the thermal responses of spiders (Davies & Edney, 1952; Main, 1982; Cloudsley-Thompson, 1983; Pulz, 1987).

The purpose of the present study has been to analyze intraspecific variations in the thermal responses of the desert theraphosid spider Dugesiella echina Chamberlin from populations at several locations ranging in elevation from 564 to 1646m. The following parameters were investigated: (1) upper (ULT_{50}) and lower (LLT_{50}) lethal temperatures; (2) the combined effects of temperature, relative humidity (RH) and thermal acclimation on critical thermal minima (CTM_{min}) and maxima (CTM_{max}); (3) the effects of temperature and RH on percent survival and transpiratory water loss (TWL); (4) determination of thermal preferenda; (5) the relationship between thermal acclimation and metabolic rate. It is hoped that the investigation of these parameters will contribute significantly to our knowledge of the physiology and ecology of this species.

Methods

Adult male and female Dugesiella echina were collected between May and August, 1984-1988 from the following locations within Big Bend National Park, Brewster Co., Texas, which lies within the Chihuahuan Desert Biome (Ware, 1980): Rio Grande Village (elevation: 564m); Panther Junction (1143m); Chisos Mountains Basin (1646m). A detailed description of the vegetational zones and geology of this area is available in Tinkam (1948) and Maxwell et al. (1967). These locations are characterized by different thermal and moisture regimes, with Rio Grande Village representing one of the lowest (and least variable) elevations within the area, Panther Junc. at an intermediate elevation, and Chisos Mts characterized by a significantly wider range of temperature and experiencing colder temperatures during the winter. The Rio Grande and Panther Junc. locations represent the more arid habitats whereas Chisos Mts is more mesic in nature (Tinkam, 1948; Ware, 1980). Hotter and drier conditions prevail at Rio Grande and Panther Junc., with lower prey availability and more widely spaced burrows, especially at Panther Junc. (personal observation). All spiders were collected at night from burrow entrances or while wandering on the surface, as described by Punzo (1989a, 1989b). They were transported back to the laboratory and housed separately in clear plastic containers. They were maintained at 21-31°C and 70-72% RH, and fed weekly on crickets, cockroaches and grasshoppers. Experiments were conducted over a five-year period depending upon availability of spiders, and whenever possible the tests were conducted within 30 days of capture in order to minimize any effect that prolonged laboratory conditions might have on the thermal responses of these spiders. All temperature experiments were conducted in a Precision Model 816 Incubator (Chicago, Illinois), under conditions of constant darkness. Relative humidity (RH) values were obtained by the use of saturated salt solutions as described by Winston & Bates (1960): LiCl (12%), and NaCl (75%). Salt solutions were placed in plastic trays within the incubator, and RH values checked hourly with hydrion paper (Fisher Scientific, Pennsylvania). Statistical methods used throughout this study follow those described by Sokal & Rohlf (1981).

Lethal temperatures, critical thermal maxima/minima and survival capacity determinations

Upper (ULT_{50}) and lower (LLT_{50}) lethal temperatures were determined according to the method described by Punzo & Rosen (1984). Experiments were conducted on male and female spiders (weight: 6.1-7.2g). Twenty spiders were placed individually in glass containers for each experimental condition. Lethal temperatures were determined for spiders from each of the three geographical locations under both xeric (12% RH) and mesic (75% RH) conditions. All spiders were deprived of food for two

Location[b]	RH (%)	Lethal temperature (°C)[a]			
		Males		Females	
		ULT_{50}	LLT_{50}	ULT_{50}	50
RGV	12	41.6	4.3	41.5	4.3
	75	44.3	4.3	44.3	4.3
PJ	12	41.1	3.9	41.4	4.2
	75	43.4	3.8	43.7	4.1
CMB	12	39.7	3.2	39.8	3.1
	75	42.1	3.3	42.2	3.2

Table 1: Upper (ULT_{50}) and lower (LLT_{50}) lethal temperature determinations for *Dugesiella echina* from several populations under xeric (12% RH) and mesic (75% RH) conditions ($n = 20$ for each experimental condition).

[a] Experiments were conducted on spiders (weight: 6.1-7.2g) maintained at $22 \pm 1°C$. Period of exposure = 1hr. SD range: ± 0.1-± 0.3.

[b] RGV = Rio Grande Village, elevation 564m; PJ = Panther Junction, 1143m; CMB = Chisos Mountains Basin, 1646m.

days before testing. For LLT_{50} experiments, spiders were exposed to low temperatures ranging from -2.0 to $10°C$ at $0.5°C$ intervals for a period of one hr. Following the exposure period, spiders were removed from the incubator and returned to normal maintenance conditions. The number surviving after a 24hr period was recorded. Identical procedures were used for ULT_{50} determinations; spiders were exposed to high temperatures ranging from 37-46°C at $0.5°C$ intervals under the same RH regimes. These data allowed the determination of lethal temperatures as well as survival capacity (Tables 1 and 4). Since lethal temperature determinations showed no significant differences between males and females (ANOVA, $p > 0.30$), percent survival experiments were conducted on females over a temperature range of 5-45°C under xeric and mesic conditions (Table 4).

CTM_{max} determinations were made according to the procedure previously described by Seymour & Vinegar (1973). These experiments were conducted on females (weight: 6.8-7.2g). Spiders from each geographical location were acclimated at either 10 or 30°C for two weeks before testing. Acclimated animals were placed individually in $450cm^3$ glass containers and were observed closely through a one-way window. Tests were initiated at 25°C and temperatures were raised at a rate of $0.5°C.min^{-1}$ under xeric (12% RH) and mesic (75%) conditions as described above. CTM_{max} was defined as that high temperature at which the animal first exhibited body shaking and vertical movements of one or more of the legs (referred to as "foot tapping" by Seymour & Vinegar, 1973). When spiders were returned to normal temperatures, foot tapping responses ceased and behaviour was normal. Experiments were conducted on 10 spiders for each experimental condition (Table 2).

Identical procedures were used to determine the CTM_{min} (Table 3). Acclimated spiders were exposed to an initial test temperature of 10°C and observed closely as temperatures were lowered at a rate of $0.5°C.min^{-1}$. CTM_{min} was defined as that low temperature (reversible) at which the spider first exhibited a curling of the legs underneath the body (leg-curling).

Temperature preferenda determinations

Temperature preferenda experiments were conducted in a temperature-gradient apparatus using procedures similar to those described by Nørgaard (1951). It consisted of a rectangular wooden trough (100 x 7 x 7cm) provided with a copper-plated base (runway) and a clear plexiglass cover. One end of the copper plate was cooled by contact with a cold-water bath ($-2°C$), while the opposite end was heated with an electrical thermistor coil (65°C). A temperature gradient (air temperature) of 5-46.5°C was established and monitored by a series of 15 overhead thermometers as described by Almquist (1970). The steepness of the gradient was approximately $0.5°C.cm^{-1}$. Rising temperature caused a decrease in RH within the runway; the RH gradient ranged from 55-75%. Experiments were conducted on male and female spiders (weight: 4.8-7.9g). At the start of each test, an individual spider was placed in the centre of the apparatus and left undisturbed for 24hr. Following this period, its position and choice of temperature within the apparatus was recorded. The percentage of spiders choosing a particular temperature gradient interval was determined for 50 spiders from each geographical location (Table 5).

Transpiratory water loss (TWL)

All experiments were conducted in a desiccation apparatus (chamber), as described by Punzo & Jellies (1983). Air was recycled at a flow rate of 3.8 $l.min^{-1}$. TWL experiments were carried out in the incubator described above and identical procedures were used to obtain RH values of 12 and 75%. A test temperature of 35°C and a 24hr exposure period were used throughout these experiments. An air current was bubbled through 1000ml of the salt solution and then passed through cotton traps and polyester fibre filters before entering the desiccation chamber which housed an individual spider. Each spider tested was placed in a glass container provided with small holes for air circulation ($n = 40$ for each treatment and location). Female spiders were weighed individually on a Sartorious M44 electronic balance to the nearest 0.005mg at hourly intervals over a 24hr period. Transpiratory water loss

Location[a]	T_{accl} (°C)[b]	Critical thermal maxima (°C)	
		12% RH	75% RH
RGV	10	43.08 (0.60)	43.16 (0.14)
	30	41.99 (0.54)	43.27 (0.13)
PJ	10	43.21 (0.33)	43.22 (0.80)
	30	41.32 (0.22)	43.15 (0.13)
CMB	10	42.79 (0.30)	42.90 (0.76)
	30	40.80 (0.16)	42.81 (0.44)

Table 2: Combined effects of temperature and relative humidity (RH) on CTM_{max} (°C) in *Dugesiella echina* from several populations (adult females, 6.8-7.4g). Values represent mean temperatures ($n = 10$ for each experimental condition). Numbers in parentheses represent $\pm$ S.D.

[a] RGV = Rio Grande Village, elevation 564m; PJ = Panther Junction, 1143m; CMB = Chisos Mountains Basin, 1646m.

[b] Animals were maintained at acclimation temperature for two weeks before testing.

(cuticular permeability) was expressed as a percentage of initial body weight (Table 6). Spiders were deprived of food for 72hr before testing with defecation being minimal or absent. The surface area of each spider was determined using the relationship, $S = kW^{2/3}$ as described by Edney (1977), where S represents surface area (cm^2), W the body weight, and k a constant. The value of k was determined by using spiders of known weight and clearing them in a KOH solution. The exoskeletons were spread over a grid paper provided with 0.25mm squares and measured with a Unitron H60 dissecting microscope.

Effects on oxygen consumption

Each of 10 spiders acclimated at 10 or 30°C was placed in a glass container ($470 \ cm^3$) sealed with a rubber stopper and provided with a three-way stopcock. Individual spiders from each acclimation group were exposed to test temperatures ranging from 10-40°C (Table 7) for a period of two hrs. Air samples were removed from the containers with a 50 cm^3 syringe and injected into a Beckman E3 oxygen analyzer through a plastic tube containing silica gel to absorb CO_2 and water vapour. The analyzer was recalibrated with atmospheric air following each test. Oxygen consumption rates were calculated according to the method of Depocas & Hart (1957) and expressed in $\mu l.g\text{-}hr^{-1}$.

Results

Lethal temperatures

The ULT_{50} and LLT_{50} values for male and female D. echina are shown in Table 1. No significant differences were found between males and females within each geographical location. RH had no effect on resistance to low temperature stress. However, ULT_{50} temperatures were reduced by 1-2°C under xeric conditions (12% RH) as compared to those values obtained under mesic conditions, for both sexes. This indicates that under xeric conditions, resistance to high temperature stress is reduced in this species. A Wilcoxon Signed Rank Test (Sokal & Rohlf, 1981) showed these differences to be significant ($Z = 2.91$, $p < 0.01$). The results also indicate that spiders from

Location[a]	T_{accl} (°C)[b]	Critical thermal minima (°C) 12% RH	75% RH
RGV	10	5.23 (0.31)	5.21 (0.56)
	30	5.14 (0.21)	5.16 (0.38)
PJ	10	4.93 (0.18)	4.92 (0.43)
	30	5.02 (0.24)	4.95 (0.67)
CMB	10	4.91 (0.41)	4.93 (0.81)
	30	5.22 (0.52)	5.24 (0.30)

Table 3: Combined effects of temperature and relative humidity (RH) on CTM_{min} (°C) in Dugesiella echina from several populations (adult females, 6.8-7.2g). Values represent mean temperatures ($n = 10$ for each experimental condition). Numbers in parentheses represent ± S.D.

[a] RGV = Rio Grande Village, elevation 564m; PJ = Panther Junction, 1143m; CMB = Chisos Mountains Basin, 1646m.

[b] Animals were maintained at acclimation temperature for two weeks before testing.

higher elevations (Chisos Mts) exhibited lower LLT_{50} values (3.1-3.3°C) than those from lower elevations (3.8-4.3°), regardless of RH, indicating a greater resistance to cold temperature stress. The effect of geographical location on lower lethal temperatures was found to be significant (ANOVA: $F_{2,44} = 7.52$, $p < 0.05$). Conversely, spiders from lower elevations (Rio Grande, Panther Junc.) exhibited higher ULT_{50} values than those from Chisos Mts, indicating greater tolerance of higher temperatures. This is in general agreement with results reported for other desert arachnids (Ahearn, 1970; Almquist, 1970; Cloudsley-Thompson & Crawford, 1970; Cloudsley-Thompson, 1983) as well as terrestrial insects (Edney, 1977; Punzo & Mutchmor, 1980; Punzo & Rosen, 1984; May, 1985; Punzo & Huff, 1989).

Critical thermal maxima/minima

The combined effects of temperature and RH on CTM_{max} and CTM_{min} for female spiders are shown in Tables 2 and 3, respectively. Acclimation, RH and geographical location had no significant effect on CTM_{min} ($Z = 0.45, p > 0.40$). Critical thermal minima ranged from 4.91-5.24°C. However, with respect to CTM_{max} (Table 2), the overall effect of geographical location was found to be significant at 12% RH (ANOVA: $F_{2,44} = 9.02$, $p < 0.01$). Critical thermal maxima ranged from 40.80-43.21°C under xeric conditions, and from 42.81-43.27°C under mesic conditions. Seymour & Vinegar (1973) reported a mean CTM_{max} of 43.25 and 43.07°C for another theraphosid, Aphonopelma sp. B, from Portal, Arizona (elevation: 1460m), acclimated at 10 and 30°C, respectively.

Survival capacity

The combined effects of temperature and RH on the percent survival (survival capacity) of D. echina females from different geographical locations under xeric and mesic conditions are shown in Table 4. The results showed that the overall effects of temperature (ANOVA: $F_{8,44} = 31.23, p < 0.01$), RH ($F_{1,44} = 14.72$, $p < 0.01$) and location ($F_{2,44} = 11.33$, $p < 0.01$) on survivorship were significant. The results also indicate that spiders from higher elevations (Chisos Mts) can withstand significantly colder temperatures than those from lower elevations (Scheffe $F = 6.98$, $p < 0.01$). The percent survival of mountain spiders exposed to 5°C is 50 and 70% under mesic and xeric conditions, respectively, as compared with only 10-30% in Rio Grande and Panther Junc. spiders. A temperature range of 15-30° appears to be optimal for this species. At 75% RH, Rio Grande spiders exhibit 60% survival at high stressful temperature (40°C) compared with 0% in mountain spiders. Under xeric conditions (12% RH), 40% of the Rio Grande animals survived at 40°C. None of the mountain spiders survived these conditions.

Temperature preferenda

The results of temperature preferendum experiments are shown in Table 5. No significant

differences were found between the sexes. The majority of spiders (51-61%) chose a temperature range of 24-27°C; 12-39% chose a range of 27-30°C. This represents a relatively wider thermal preferendum range than has been reported for other spiders (Nørgaard, 1951; Almquist, 1970; Pulz, 1987). It is interesting to note that 7-9% of the Chisos Mts spiders (higher elevation) were found in the 15-18°C section of the apparatus, and 6-7% of the Rio Grande animals (lowest elevation) chose the 30-33°C range. These results are consistent with the results described above for survival capacity, lethal temperatures and critical thermal minima and maxima.

Transpiratory water loss

The relationship between RH and TWL in animals exposed to high temperature stress (35°C) over a 24hr period is shown in Table 6. Water loss rates were significantly higher under xeric conditions in spiders from all locations. In addition, Chisos Mts spiders exhibited significantly higher TWL in dry air (27.4% of initial body weight) than spiders from other locations (16.8-19.3%), suggesting that spiders from lower elevations are characterized by a greater resistance to water loss than conspecifics from higher elevations. This is consistent with the observation that Rio Grande and Panther Junc. spiders are associated with microhabitats that are characterized by higher ambient temperatures and more arid conditions, especially during the summer months. Seymour & Vinegar (1973) reported a 15-23% water loss in the tarantula, *Aphonopelma* at 30°C. Although these Arizona spiders were collected from an elevation comparable to the Chisos Mts spiders in the present study, they are characterized by a greater resistance to TWL.

Effects on oxygen consumption

The effects of temperature on mean oxygen consumption rates in various populations of *D. echina* females acclimated at 10 and 30°C are shown in Table 7. Oxygen consumption increased with

| Temperature interval (°C) | Percentage choosing interval[a] | | | | | |
| | Males | | | Females | | |
	RGV	PJ	CMB	RGV	PJ	CMB
10 – 12	0	0	0	0	0	0
12 – 15	0	0	0	0	0	0
15 – 18	0	1	9	0	0	7
18 – 21	1	4	23	2	7	18
24 – 27	52	61	54	57	57	51
27 – 30	39	31	12	35	30	24
30 – 33	7	3	2	6	6	0
33 – 36	1	0	0	0	0	0
36 – 39	0	0	0	0	0	0
39 – 42	0	0	0	0	0	0

Table 5: Temperature preferences of *Dugesiella echina* from several locations. Values represent the percentage of spiders choosing a particular temperature gradient interval ($n = 50$ for each location).

[a] All spiders were maintained at 22 ± 1°C and 70-72% RH and tested within 30 days after capture. Weight of spiders: males 4.8-6.2g, females 6.4-7.9g. RGV = Rio Grande Village, elevation 564m; PJ = Panther Junction, 1143m; CMB = Chisos Mountains Basin, 1646m.

increasing temperature for all experimental groups. However, the rate of increase, as reflected by Q_{10} values, was lower at higher temperatures: $Q_{10} = 1.52$ between 30-40°C; 2.9 (20-30°C); 3.01 (10-20°C). This is in general agreement with the results for rate of increase reported for other arachnids (Anderson, 1970; Seymour & Vinegar, 1973; Anderson & Prestwich, 1985). No significant differences were found in spiders from different locations in either acclimation group. There was also no effect of acclimation on oxygen consumption. The regression equation showing the relationship between test temperature and oxygen consumption rates for spiders acclimated at 10° is: $y = 4.704x-52.48$ ($r^2 = 0.93$); for 30° acclimated spiders: $y = 4.736x-52.62$ ($r^2 = 0.925$).

Discussion

The theraphosid tarantula spiders represent one of the most conspicuous elements of the arachnid fauna associated with the deserts of the southwestern United States (Gertsch, 1949; Punzo, 1989a). They are characterized by a sedentary, fossorial mode of life, especially the females which may inhabit the same burrow for many years (Baerg, 1958; Minch, 1977). The males appear to spend more time wandering on the surface during the reproductive season in search of females. These mygalomorph spiders excavate relatively deep burrows (Gertsch, 1949) which provide them with shelter from adverse climatic conditions as well as a location from which to ambush prey (Main, 1982; Punzo, 1989a). Deserts are characterized by high levels of solar radiation, irregular rainfall patterns, convective winds and extremes of moisture and temperature resulting in a high saturation deficiency in the surrounding air (Cloudsley-Thompson, 1983) which increases transpiratory, respiratory and evaporative water loss (Edney, 1977; Main, 1982; Pulz, 1987). In order to maintain homeostasis as well as normal behavioural patterns, desert spiders must keep fluctuations in water loss and body temperature (T_b)

| Test temp. (°C) | Percent survival[a] | | | | | |
| | 12% RH | | | 75% RH | | |
	RGV[b]	PJ	CMB	RGV	PJ	CMB
5	10	30	70	10	20	50
10	60	90	100	100	100	90
15	90	100	100	100	100	100
20	100	90	100	90	100	100
25	100	100	90	90	100	100
30	100	100	100	100	100	100
35	100	90	60	100	80	70
40	40	10	0	60	40	0
45	0	0	0	0	0	0

Table 4: Effects of temperature and relative humidity (RH) on percent survival in *Dugesiella echina* from various locations.

[a] $n = 10$ female spiders (6.5-7.5g) for each experimental condition; period of exposure was 3hr.

[b] RGV = Rio Grande Village, elevation 564m; PJ = Panther Junction, 1143m; CMB = Chisos Mts Basin, 1646m. RGV – CMB also represents a gradient from lower to higher humidity.

within tolerable limits. In spiders, as well as other arachnids, T_b is determined by a number of factors including evaporative heat loss (H_w), metabolic heat production (H_m), and heat exchange via radiation (H_r), convection and conduction (H_c). Thus, total heat loss or gain (H_t) can be expressed by the following relationship: $H_t = H_m - H_w \pm H_c \pm H_r$. Solar radiation can affect the rate of heat absorption (Q_{abs}) of an organism as follows: $Q_{abs} = EA_sS$, where E represents the emissivity of the body surface, A_s the surface area across which radiant heat exchange occurs, and S, the solar flux (Cloudsley-Thompson, 1983). The rate of heat exchange (dH/dt) can also be related to conduction as follows: $dH/dt = kA_c (T_s-T_g)$, where k represents the conductivity of the substrate, A_c the area across which conduction occurs, T_s and T_g the body surface and substrate temperatures, respectively (May, 1985). With respect to convection, heat transfer is expressed as: $dH/dt = hA_h (T_s-T_{air})$, where h is the coefficient of convection. For a detailed discussion of the mathematical relationships governing avenues of heat and water exchange, the reader is referred to Prosser (1973) and Bursell (1974). In desert spiders and other xeric-adapted arthropods, T_b and T_s can be regulated via behavioural mechanisms (Casey, 1981; Cloudsley-Thompson, 1983), physiological compensation (May, 1985; Pulz, 1987), evaporative cooling over short periods (Davies & Edney, 1952; Chew, 1961; Ahearn, 1970; Punzo & 'Mutchmor, 1980; Punzo & Jellies, 1983; Pulz, 1987; Punzo, 1989c; Punzo & Huff, 1989), and changes in body coloration which can affect the reflectance properties of the body surface or cuticle (Cloudsley-Thompson, 1983; Pulz, 1987). These animals can alter the effects of conduction or radiation via behavioural mechanisms such as microhabitat selection and/or varying body posture or orientation thereby affecting A_c. It is well known that fossorial spiders such as theraphosids (Baerg, 1958; Seymour & Vinegar, 1973; Minch, 1977) and burrowing wolf spiders (Humphreys, 1974) can effectively regulate their T_b by changing their positions within the burrow. When surface temperatures become extreme, they move deeper within their retreats and will come closer to the surface only when temperatures are more favourable or at night when they are feeding (Minch, 1978; Punzo, 1989a). The effects of convection can be

influenced by a number of factors including changes in body position which alter wind velocity gradients (May, 1985), as well as insulative structures. Theraphosid spiders such as *D. echina* possess numerous insulative hairs/setae which can alter convective heat loss.

The results from the present study indicate that under xeric conditions, resistance to high temperature stress is reduced (Tables 1 and 4) and TWL is significantly greater (Table 6). This suggests that *D. echina* does not possess a particularly effective epicuticular barrier to water loss, which is characteristic of many desert scorpions and insects (Cloudsley-Thompson, 1983; Hadley, 1984). These spiders avoid particularly unfavourable environmental conditions primarily through nocturnal activity patterns (Minch, 1978; Punzo, 1989a) and fossoriality (Gertsch, 1949; Main, 1982). Minch (1977) reported that the tarantula, *Aphonopelma chalcodes* Chamberlin (Arizona) frequently seals the burrow entrance during the day in the warmest months. Humphreys (1974) has shown that the burrowing wolf spider, *Geolycosa godeffroyi* (L. Koch), maintains its T_b between 32-36°C regardless of T_a extremes by changing its location within the burrow. Similar observations have also been reported for other burrowing arthropods (Cloudsley-Thompson, 1983; Pulz, 1987). The results also showed that spiders collected from higher elevations had lower LLT_{50} values than those from lower sites. This is not surprising in view of the fact that temperatures in the Chisos Mountains during the winter, late autumn and early spring can be markedly colder compared with those found at lower elevations. The ULT_{50} values for *D. echina* are similar to the value reported for *Pardosa pullata* (Clerck) (43°C) by Nørgaard (1951), but slightly lower than those (45-50°C) reported for numerous other spiders (see Cloudsley-Thompson, 1970).

The data on lethal temperatures (Table 1) and percent survival (Table 4) are also consistent with the results found for CTM_{max} (Table 2) and CTM_{min} (Table 3). Although studies on $CTM_{max/min}$ for spiders are few, there have been reports on other parameters which are related to CTM, and for the most part, these studies have shown a great deal of variation in thermal responses. For example, threshold activity temperatures can range from 10°-12.6°C for the lycosids, *Pardosa pullata* and *P. chelata* (Müller) (Hallander, 1970), and from 41-44°C for several species of dune spiders (Almquist, 1970). It is also known that locomotor activity can be stimulated by decreasing temperatures in some spiders. Movement in the wolf spider, *Lycosa ceraticola* Gertsch & Wallace, is stimulated by cooler soil temperatures (Pulz, 1987). Similar observations were reported for the tarantula, *A. chalcodes* (Minch, 1978) and are most likely responsible for the nocturnal activity patterns characteristic of desert theraphosids, including *D. echina*. In addition, it has also been shown that theraphosids become spontaneously active as T_a decreases but become rapidly ataxic if temperatures are suddenly increased. This suggests that some neural mechanism(s) may be responsible for modulating the diel activity patterns of nocturnal spiders (Pulz, 1987).

Weight loss (%)

Location[a]		12% RH	75% RH	p^b
RGV		16.8	9.4	0.01
	NS			
PJ		19.3	10.4	0.01
	0.01			
CMB		27.4	11.1	0.01

Table 6: Relationship between relative humidity (RH) and transpiratory water loss (expressed as percentage of initial body weight) in *Dugesiella echina* females (initial body weight: 6.4 ± 0.3g) exposed to 35°C over a 24hr period ($n = 40$ for each experimental condition).

[a] RGV = Rio Grande Village, elevation 564m; PJ = Panther Junction, 1143m; CMB = Chisos Mountains Basin, 1646m.

[b] Level of significance computed using a Chi Square analysis (Sokal & Rohlf, 1981). NS = not significant.

Similar results have been reported for some insects and slugs (Cloudsley-Thompson, 1970; May, 1985; Pulz, 1987). Temperature can also affect rates of development (Prosser, 1973; Pulz, 1987), metabolic efficiency (Anderson & Prestwich, 1985; May, 1985), courtship displays (Cloudsley-Thompson, 1970), moulting periodicity (Minch, 1977; Cloudsley-Thompson, 1983) and foraging activities (Chew, 1961; Punzo, 1989a).

Dugesiella echina shows a relatively wide temperature preference range (Table 5) in comparison with data previously reported for other spiders (Nørgaard, 1951; Almquist, 1970); 51-61% of males and females chose a temperature range of 24-27°C, and 12-39% were found at 27-30°C. Although no significant differences were found between sexes, it should be pointed out that no experiments were conducted on females with fertile egg sacs (none was collected). Studies on the wolf spider, *Pirata piraticus* (Clerck) (Nørgaard, 1951) showed that the optimal temperature zone of males and females without egg sacs ranged from 18-24°C, whereas females with egg sacs chose a markedly higher range (26-32°). The females of some lycosid species are known to carry their egg sacs to the surface and expose them to solar radiation (Gertsch, 1949; Nørgaard, 1951). However, results from the same study on *Pardosa pullata* indicated no difference in the temperature preferences of females with or without egg sacs. Further studies on theraphosids as well as other species are needed in order to determine the incidence of occurrence for such differences between females of different reproductive status. Such differences, where they do exist, are most likely associated with temperature changes required for optimal embryonic development. It has been widely accepted that interspecific differences in the temperature preferenda of terrestrial arthropods correspond to the thermal regimes associated with particular microhabitats (Nørgaard, 1951; Chew, 1961; Almquist, 1970; Cloudsley-Thompson, 1970; Cloudsley-Thompson & Crawford, 1970; Humphreys, 1974; Kirchner, 1987; Punzo, 1989c) which, in turn, define the thermal niche. However, very little information is available concerning intraspecific variation in thermal responses. In the present study, spiders collected from higher (7-9% of mountain spiders chose a range of 15-18°C) and lower (6-7%, Rio Grande, 30-33°C) elevations exhibited some degree of variation in temperature preference.

Extremes of temperature and RH can also affect the water relations of terrestrial arthropods (see reviews by Cloudsley-Thompson, 1970; Edney, 1977; Pulz, 1987). Water serves as a major component of spider haemolymph (Punzo, 1989b) and is essential in maintaining the volume of body fluids necessary to sustain life. Body fluids also play an important role in the generation of hydrostatic pressures essential for normal locomotion (Anderson & Prestwich, 1985). At high temperature stress, percent water loss (TWL) in *D. echina* from all locations was significantly higher under xeric conditions (Table 6). In addition, Chisos Mts spiders showed significantly higher TWL than those from lower altitudes. Further studies are needed to determine if these differences between individuals from various populations are associated with differences in the chemical composition and structural integrity of the cuticle which have been implicated in interspecific variations among other terrestrial arthropods (Hadley, 1984). Values reported by previous investigators for lethal water loss in spiders, expressed as percentage of initial body weight (see Davies & Edney, 1952; Pulz, 1987), range from 16-23%. In the present study, TWL ranged from 16.8-27.4% at 12% RH, and 9.4-11.1% at 75% RH, with 92% survival. Theraphosids such as *D. china* and *A. chalcodes* require drinking water at regular intervals in order to survive (personal observation). In fact, Baerg (1958) reported that *D. entzi* was able to survive far longer periods without food than water. Tarantulas have been reported to exhibit higher rates of TWL immediately after moulting (Stewart & Martin, 1982) and will drink copiously if water is available (Baerg, 1958; personal observation). Also, under high temperature stress, many spiders release various water-containing secretions from gnathocoxal and rostral glands and the mouth. At 35-40°C, for example, the theraphosid *Brachypelma smithi* (F.O.P.-Cambridge), exhibited significant liquid water loss (LWL) which must be differentiated from TWL (Pulz, 1987). TWL can also be effective as a mechanism for evaporative cooling in spiders, but only for short periods of time (Cloudsley-Thompson, 1970; Punzo & Jellies, 1983; Pulz, 1987) owing to limited water stores and concomitant osmotic problems associated with water loss (Anderson & Prestwich, 1985).

The relationship between T_a, acclimation temperature and oxygen consumption rates in *D. echina* (Table 7)

Mean oxygen consumption rate (μl.g-hr^{-1})
Acclimation temperature (°C)

Test temp. (°C)		10°C			30°C	
	Location[a]: RGV	PJ	CMB	RGV	PJ	CMB
10	11.1 (0.7)	10.9 (0.9)	11.6 (0.8)	11.2 (1.1)	11.4 (1.3)	11.3 (0.9)
15	16.2 (1.8)	16.1 (0.9)	15.9 (1.5)	16.3 (2.1)	16.4 (1.4)	15.8 (0.8)
20	33.4 (3.4)	31.2 (2.5)	32.2 (1.9)	34.1 (4.1)	32.9 (3.1)	34.1 (2.2)
25	61.3 (4.1)	60.2 (2.9)	62.4 (4.1)	60.9 (3.4)	61.9 (5.1)	60.5 (2.8)
30	97.6 (8.9)	94.9 (7.9)	96.5 (8.8)	101.2 (11.1)	99.6 (7.6)	100.2 (9.9)
35	107.8 (9.1)	109.1 (11.1)	108.3 (9.2)	106.9 (10.4)	107.1 (6.1)	108.7 (8.7)
40	148.2 (8.4)	151 (14.1)	153.3 (12.1)	149.6 (13.1)	149.9 (9.9)	152.7 (7)

Table 7: Effects of temperature and mean oxygen consumption rates (μl.g-hr^{-1}) in *Dugesiella echina* females (6.7-7.3g) from several locations acclimated at 10 and 30°C. Numbers in parentheses represent ± S.D. ($n = 10$ for each location and experimental condition).

[a] RGV = Rio Grande Village, elevation 564m; PJ = Panther Junction, 1143m; CMB = Chisos Mountains Basin, 1646m.

indicates no significant acclimatory effect. This is in contrast with the results reported for insects (see reviews by Cloudsley-Thompson, 1970; Bursell, 1974; May, 1985). Oxygen consumption rates at 15-30°C are comparable to rates reported by Anderson (1970) for other theraphosids. Spiders are, as a group, characterized by relatively low oxygen consumption (Anderson, 1970; Seymour & Vinegar, 1973; Anderson & Prestwich, 1985) which represents an adaptive response to environments characterized by xeric conditions and/ or widely fluctuating prey densities. Both of these conditions are prevalent in desert habitats.

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.

ANDERSON, J. F. & PRESTWICH, K. N. 1985: The physiology of exercise at and above maximal aerobic capacity in a theraphosid (tarantula) spider, *Brachypelma smithi* (F. O. Pickard-Cambridge). *J. comp. Physiol.* (B) **155**: 529-539.

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

BAERG, W. J. 1958: *The tarantula.* 1-88. Univ. Kansas Press, Lawrence, Kansas.

BROMHALL, C. 1988: *Argyroneta aquatica* (Clerck), overwintering behaviour and super-cooling point. *Bull. Br. arachnol. Soc.* **7**: 225-228.

BURSELL, E. 1974: Environmental aspects: temperature. *In* M. Rockstein (ed.), *The physiology of the Insecta* **2**: 1-77. Academic Press, New York.

CASEY, T. M. 1981: Behavioral mechanisms of thermoregulation. *In* B. Heinrich (ed.), *Insect thermoregulation:* 80-114. John Wiley, New York.

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

CLOUDSLEY-THOMPSON, J. L. 1970: Terrestrial invertebrates. *In* G. G. Whittow (ed.), *Comparative physiology of thermoregulation* **1**: 15-77. Academic Press, New York.

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

CLOUDSLEY-THOMPSON, J. L. 1983: Desert adaptations in spiders. *J. arid Envir.* **6**: 307-317.

CLOUDSLEY-THOMPSON, J. L. & CRAWFORD, C. S. 1970: Lethal temperatures of some arthropods of the southwestern United States. *Entomologist's mon. Mag.* **106**: 26-29.

DAVIES, M. E. & EDNEY, E. B. 1952: The evaporation of water from spiders. *J. exp. Biol.* **29**: 571-582.

DEPOCAS, F. & HART, J. S. 1957: Use of the Pauling oxygen analyzer for measurement of oxygen consumption of animals in open circuit systems and in short-lag, closed circuit apparatus. *J. appl. Physiol.* **10**: 388-392.

EDNEY, E. B. 1977: *Water balance in land arthropods.* 1-287. Springer-Verlag, New York.

GERTSCH, W. J. 1949: *American spiders.* Van Nostrand, New York.

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-Verlag, Berlin.

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

HUMPHREYS, W. F. 1974: Behavioural thermoregulation in a wolf spider. *Nature. Lond.* **251**: 502-503.

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

MAIN, B. Y. 1982: Adaptations to arid habitats by mygalomorph spiders. *In* W. R. Barker & P. J. M. Greenslade (eds.), *Evolution of the flora and fauna of arid Australia:* 273-283. Peacock Publs., Frewville, Australia.

MAXWELL, R. A., LONSDALE, J. T., HAZZARD, R. T. & WILSON, J. A. 1967: Geology of Big Bend National Park, Brewster County, Texas. *Univ. Tex. Publs* **6711**: 1-320.

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.

MINCH, E. W. 1977: *The behavioral biology of the tarantula, Aphonopelma chalcodes.* 1-86. Ph.D. dissertation, Arizona State University, Tempe.

MINCH, E. W. 1978: Daily activity patterns in the tarantula *Aphonopelma chalcodes* Chamberlin. *Bull. Br. arachnol. Soc.* **4**: 231-237.

NØRGAARD, E. 1951: On the ecology of two lycosid spiders (*Pirata piraticus* and *Lycosa pullata*) from a Danish sphagnum bog. *Oikos* **3**(1): 1-21.

PROSSER, C. L. 1973: *Comparative animal physiology,* 3rd ed. 1-966. Saunders, Philadelphia.

PULZ, R. 1987: Thermal and water relations. *In* W. Nentwig (ed.), *Ecophysiology of spiders:* 26-55. Springer-Verlag, New York.

PUNZO, F. 1989a: Effects of hunger on prey capture and ingestion in *Dugesiella echina* Chamberlin (Orthognatha, Theraphosidae). *Bull. Br. arachnol. Soc.* **8**(3): 72-79.

PUNZO, F. 1989b: Composition of the hemolymph of mygalomorph spiders. *Comp. Biochem. Physiol.* **91B**: 87-93.

PUNZO, F. 1989c: Comparative temperature and water relations and hemolymph osmoregulation in the desert insects, *Taeniopoda eques* and *Schistocerca vaga* (Orthoptera, Acrididae). *Comp. Biochem. Physiol.* **93A**(4): 751-755.

PUNZO, F. & HUFF, G. 1989: Comparative temperature and water relations and the effects of thermal acclimation on *Tenebrio molitor* and *Tenebrio obscurus* (Coleoptera: Tenebrionidae). *Comp. Biochem. Physiol.* **93A**: 527-533.

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

PUNZO, F. & MUTCHMOR, J. A. 1980: Effects of temperature, relative humidity and period of exposure on the survival capacity of *Tenebrio molitor* (Coleoptera: Tenebrionidae). *J. Kans. ent. Soc.* **53**(2): 260-270.

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

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

SOKAL, R. R. & ROHLF, F. J. 1981: *Biometry,* 2nd ed. W. H. Freeman & Co., New York.

STEWART, D. M. & MARTIN, A. W. 1982: Moulting in the tarantula, *Dugesiella hentzi. J. comp. Physiol.* (B) **149**: 121-136.

TINKAM, E. R. 1948: Faunistic and ecological studies on the Orthoptera of the Big Bend Region of Trans-Pecos Texas. *Am. Midl. Nat.* **40**: 521-663.

WARE, R. H. 1980: *Naturalist's Big Bend.* 1-149. Texas A & M Univ. Press, College Station, Texas.

WINSTON, P. W. & BATES, D. H. 1960: Saturated salt solutions for the control of relative humidity in biology research. *Ecology* **41**: 232-237.