117

The thermal biology of the wolf spider *Lycosa tarentula* (Araneae: Lycosidae) in northern Greece

W. F. Humphreys

Department of Biogeography and Ecology,
Western Australian Museum,
Francis Street, Perth,
Western Australia 6000, Australia

Summary

The thermal biology of *Lycosa tarentula*, a burrow-inhabiting wolf spider, was studied in the field in northern Greece by the use of implanted thermocouples. By behavioural means (sun basking and moving into their burrow) the spiders can to some extent control their body temperature. The frequency distributions of all measures of environmental temperature were normally distributed or positively skewed, but 'that for spider prosoma temperature was negatively skewed. As hypothesised in the literature, the frequency distribution of the temperatures selected by the spiders in the field would result in a frequency distribution of respiration rates and water loss which were normally distributed.

Introduction

Evidence is accumulating that spiders show sophisticated behavioural and physiological ectothermic temperature regulation (Humphreys, 1986, 1987, and unpublished data) which is analogous to that found in small reptiles and ectothermic insects (Humphreys, 1978). Except for wolf spiders (Lycosidae) (Humphreys, 1974, 1978) most of the evidence for temperature regulation has been inferred from the association of specific postural changes with the direction and intensity of incident solar radiation (Pointing, 1965; Krakauer, 1972; Robinson & Robinson, 1974, 1978; Carrel, 1978; Tolbert, 1979; Suter, 1981; review, Humphreys, 1987), or from selection of position by spiders within temperature gradient apparatus (review, Pulz, 1987).

This paper analyses the body temperature of the wolf spider *Lycosa tarentula* (L.) (Lycosidae), and that of its immediate environment, in the field and provides clear evidence of temperature selection.

L. tarentula is a large burrow-dwelling species of southern Europe which inhabits regions of strictly mediterranean climate (winter rainfall) as well as adjacent temperate regions. Mature *L. tarentula* are similar in size, habits and habitat to its ecological homologue *Geolycosa godeffroyi* (L. Koch), which occurs in the southern temperate and mediterranean climates of Australia (Humphreys, 1977, 1983). Peak egg sac production by *G. godeffroyi* occurred in January but a few individuals bred, for the first or second time, in April (Humphreys, 1976). In western Jugoslavia and northern Greece most *L. tarentula* had egg sacs in mid-August to mid-September (Humphreys, 1983) which suggests that is the main breeding period. Both species, therefore, have major breeding periods shortly after the appropriate summer solstice and the females normally die by late winter (Humphreys, 1976, 1983). They differ in the timing of spiderling dispersal: while all spiderlings of *G. godeffroyi* disperse from the

mother at the same time, those of *L. tarentula* from Jugoslavia had a mixed dispersal strategy with some individuals remaining on the female over winter and dispersing in spring (Humphreys, 1983).

Methods

The field site was situated on a limestone ridge 1 km north of Arnissa in northern Greece. The surface was strewn with small limestone rocks and the area was covered by regularly spaced, shallow diggings, the unused preparations for tree planting. *Lycosa tarentula* was studied between 1 and 23 August 1979 in and around an exposure of talc which had been quarried on a small scale. The talc digging was unvegetated while the surrounding area was sparsely covered by tussock grass.

Spider burrows were located and the occupant was captured, measured using a Lupe (×7; Peak), weighed on a torsion balance and prepared for thermocouple implantation. Burrow dimensions were measured from polyurethane casts made of the burrows at the end of the field work.
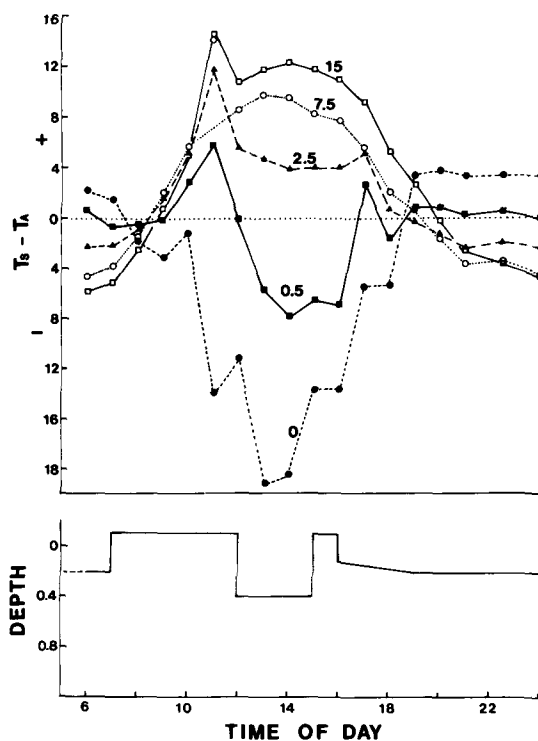

Fig. 1: Temperature differentials (spider – soil temperature; °K) between the prosoma of *L. tarentula* and the soil temperature at various depths during one day (20-21 August 1979). The points represent the mean of 5 to 9 spiders. The standard deviations, which are not shown, vary between 0.8 and 3.6. Line 0 is the soil surface temperature; other numbers indicate the depth (cm) in the soil at which the temperature was measured. Spider (Ts) and soil (Ta) temperatures are equal on the horizontal dotted line. The lower plot denotes the average position of the spider (log depth in cm down burrow), as inferred from the soil temperature profiles and the various measures of ambient temperature which are not shown in the above plot; when the line is above the ground surface the spider is fully exposed to the sun.

Temperature measurement

Copper-constantan thermocouples were read using an electric thermometer (Comark) with a 10-channel switch box; one channel was recorded on a strip chart (Rustrac) and the remainder manually recorded at intervals during the day, usually on the hour, for the 23 days. The electric thermometer was connected to an external reference temperature and the calibration verified before each reading.

Soil temperature

The thermal characteristics of the soil were measured in the talc and in the soil surrounding the talc outcrop. A hole was dug and thermocouples inserted 20 cm into the walls of the hole at depths of 0.5, 2.5, 7.5 and 15 cm. The hole was refilled, compacted and left for three weeks to re-equilibrate thermally. In addition, at each site, a bare thermocouple was laid in contact with the soil surface.

Ambient temperature and humidity

Screened daily maximum and minimum temperatures were recorded at a height of 5 cm, and wet and dry bulb temperatures taken with a whirling hygrometer at a height of 10 to 20 cm. An unshielded mercury in glass thermometer was laid on top of closely cropped grass turf and is throughout referred to as the exposed ground level temperature (EGLT). A 24-gauge thermocouple was inserted into the centre of a ball of modelling clay (diam. 10 mm) and the ball positioned 5 mm above bare earth; this is similar in position and substrate to a spider sunning itself at the burrow entrance and is referred to as the model temperature. These measures of ambient temperature were recorded at the same time as spider temperatures.

Spider temperatures
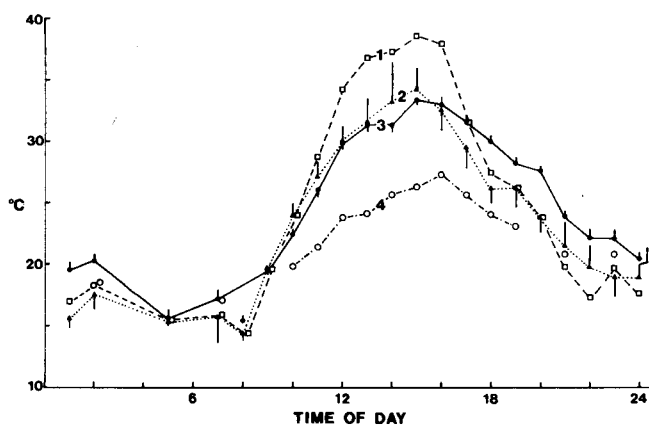
Copper-constantan thermocouples (46 or 48 gauge:

Fig. 2: Daily course of the mean spider and ambient temperatures (°C) in August at Arnissa. 1 = model temperature (n = 155); 2 = EGLT (n = 157); 3 = spider temperature (n = 1651); 4 = dry bulb temperature (n = 192). Standard error bars are shown on one side of the mean for spider and EGLT temperatures. Some points are offset by 10 minutes to permit plotting. Line 4 is shown only where it is clearly separated from the other lines.
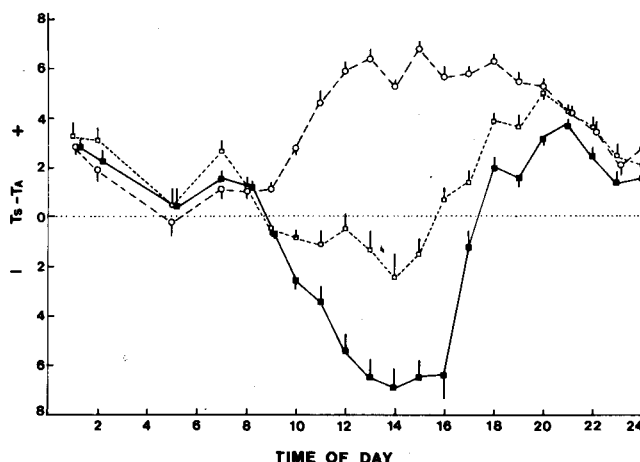

Fig. 3: Temperature differentials (Ts – Ta °K) during the day between the prosomal temperature of *L. tarentula* (Ts) and three measures of ambient temperature (Ta). The means and their standard errors are shown for nine spiders measured between 1 and 23 August 1979. The ambient temperatures considered are: open circles = dry bulb (n = 1450); open squares = exposed ground level thermometer (n = 1158); closed squares = 10 mm clay model (n = 1248). Spider and ambient temperatures are equal on the horizontal dotted line. Some points are offset by 10 minutes to permit plotting.

Dural Plastics, Dural, New South Wales) were implanted in the prosoma of spiders anaesthetised by carbon dioxide, bleeding prevented by cyanoacrylate glue (Superglue) and the thermocouple leads secured to the prosoma with rapid setting epoxy resin (5-minute Araldite). Spiders were returned to their burrows where, with the lead attached, they could traverse the space used in their normal daily excursions. This technique has been shown, using temperature transmitters and in laboratory experiments, not to affect the temperature selected by large burrowing lycosids; with the thermocouples attached the spiders can feed, produce and rear their egg sacs (Humphreys, 1978).

The temperatures of usually 9 (minimum 5) spiders were recorded on each sampling occasion. When a thermocouple malfunctioned another spider, sometimes one used previously, was substituted; the data recorded over the 23 days encompass 15 individuals; no spiders died.

Water loss

To determine the relative effect of thermal behaviour on expected water loss the environmental data from Arnissa were fed into the multiple regression model derived for *G. godeffroyi*, a species similar in size, habitat and habits to *L. tarentula*; the equation predicts water loss from spider size, body temperature and saturation deficit and accounted for 92% of the variance in the data (Humphreys, 1975). Water loss was predicted under different assumptions: (a) that spiders were at dry bulb air temperature and ambient saturation deficit; (b) that spiders were at spider temperature and ambient saturation deficit; (c) by applying an evaporation drive model (Humphreys, 1975) to account for the effect of elevated body

temperature on the evaporating power of the air. Although resistance to water loss in *L. tarentula* may differ from that of *G. godeffroyi*, the same physical laws will apply, hence the calculations will determine the relative, rather than the absolute, cost of thermoregulation, in terms of water loss.

Statistical procedures

Statistics of the frequency distributions and analysis of variance on the slopes and intercepts of regression lines and the GT2 a posteriori multiple comparison test followed the algorithms in Sokal & Rohlf (1981).

Results

Spider and egg sac sizes

The egg sac weight is directly related to spider weight with a slope not different from 1.0 ($t_7 = 0.272$, $p = 0.79$); within the size range of spiders considered (0.71 – 1.73 g after laying the egg sac) they produced egg sacs between 42 and 43% of the combined weight of the egg sac and the spider; hence spiders of different size invest a constant proportion of body weight in the eggs and their sac.

Soil temperature

Temperature at the soil surface varied by 41°K, but by only 8°K at the burrow base (150 mm) due to the thermal lag in the soil. The deep burrow temperature varied during the day between 20 and 28°C, and this is the minimum temperature available to the spiders during the heat of the day within the range of their normal excursions.

The temperature difference between the spiders and the soil at various depths is shown in Fig. 1, together with the inferred position of the spiders within their burrows deduced by comparing the soil and spider temperatures.

Spider temperature

In Fig. 2 the mean daily course of the prosomal temperature of the spiders and several measures of ambient temperature are plotted at hourly intervals. The spider temperature rises synchronously with the ambient temperatures in the morning but is offset to the right during the fall in temperature in the afternoon.

In Fig. 3 the data are expressed as the difference between the spider and the several measures of ambient temperature throughout the day; positive and negative values indicate that the spider temperature is respectively greater than or less than the ambient temperature measurement. The spider temperature is greater than the dry bulb temperature throughout the day but, between early morning and late afternoon, is below the temperature of the model and of the exposed surface thermometer (EGLT). At night the spiders withdraw into the burrows and remain warmer than any measurement of ambient temperature due to the thermal lag in the soil (see Fig. 1).

Spider temperatures for the entire study are plotted against the various, simultaneously recorded, measures

of ambient temperature in Fig. 4. Note that, with the exception of the dry bulb temperature, the relationships are strongly curved and that the spider temperature is always less than the ambient temperature when the ambient temperature exceeds 40°C.

Frequency distributions of the spider and ambient temperatures are shown in Fig. 5 and the statistics of the distributions in Table 1. Only the data for the model temperatures show significant kurtosis, whereas the data for spider temperatures and EGLT temperatures show significant skewness; note, however, that the spider data are skewed to the left while the ambient data are skewed to the right.

Temperature trends

Throughout the study both ambient and spider temperatures declined and the temperature range increased due to the onset of wet weather and colder nights. All spider temperatures and ambient temperatures showed significant decline through the period of the study ($p < 0.0001$). To examine the trend
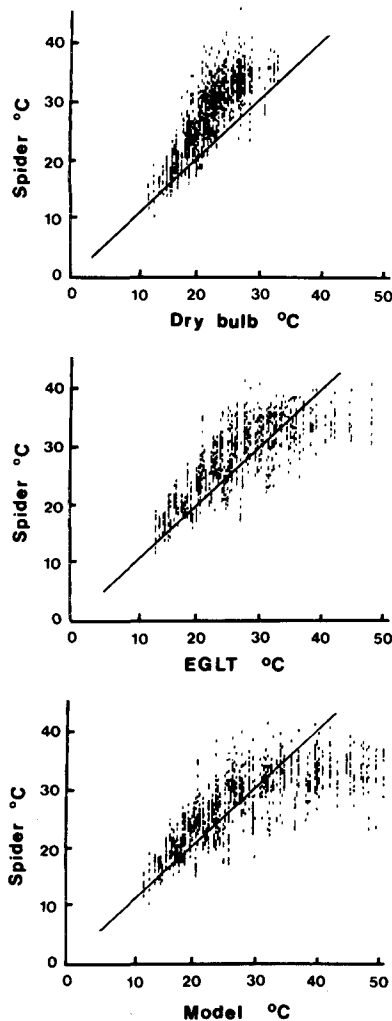

Fig. 4: Prosomal temperatures of *L. tarentula* measured throughout the day between 1 and 23 August 1979 and plotted against several measures of ambient temperature measured at the same time. The ambient temperatures considered are: (a) dry bulb ($n = 1459$); (b) exposed ground level thermometer ($n = 1167$); (c) 10 mm clay model ($n = 1257$). Along the diagonal line spider and ambient temperatures are equal.

in spider temperature during periods when it was sufficiently warm for basking, all the spider temperature data were extracted, for times when the model temperature exceeded 30°C and when it exceeded 40°C; the subset was separated into the maximum temperature (peak values) and the minimum temperature (trough values), and the regression lines compared. The difference between the two is an indication of the temperature range within which the spiders tried to remain. Both analyses gave comparable results and only that for model temperatures exceeding 30°C are given. There was no significant regression of either minimum (t_{87} = 0.409, p = 0.68) or maximum (t_{179} = 0.231, p = 0.82) temperature against sequence of recording. Hence on days suitable for basking the spiders showed no trend in the temperature they maintained during the course of the study despite the general decline in ambient temperatures. The mean minimum (30.7°C) and maximum (33.6°C) temperatures differed significantly ($F_{1,134}$ = 50.45, $p < 0.0001$) and give a range of only 2.98°K.

Water loss

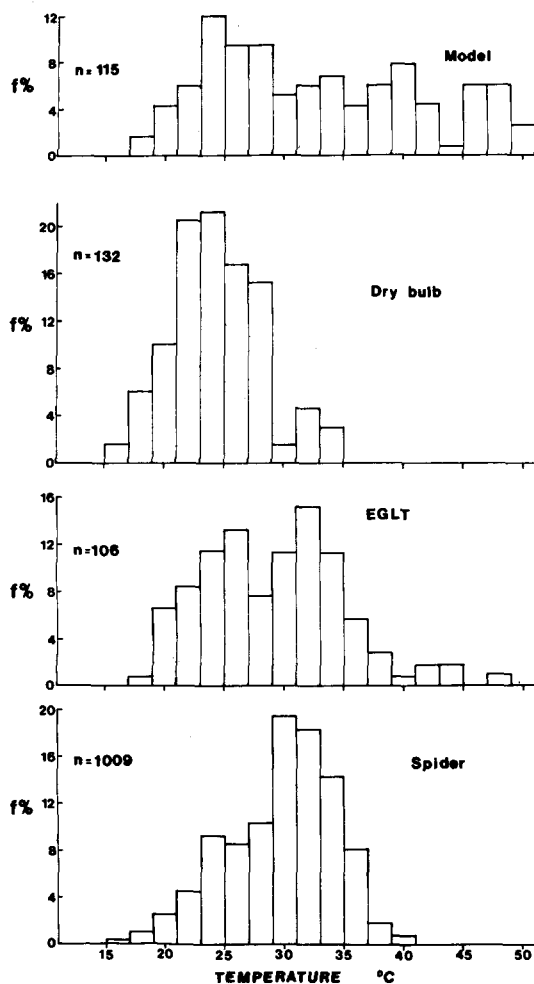Table 2 shows the expected water loss from the

Fig. 5:   Prosomal temperatures of *L. tarentula* and several ambient temperatures measured at the same time throughout the day between 1 and 23 August 1979 and plotted as frequency distributions (two degree intervals). The statistics of these distributions, based on one degree classes, are given in Table 1.

spiders under different assumptions. Condition 1 represents water loss if the spider is at ambient temperature and saturation deficit, while conditions 2 and 3 are the limits for the range of water loss to be expected due to the elevation of the body temperature above that of the air. The lower end of the range (condition 2) is the water loss expected from the elevation of spider temperature from the dry bulb temperature to the spider temperature at the ambient saturation deficit. The upper end of the range (condition 3) is derived using the spider temperature and the expected effective evaporation deficit (evaporation drive; Humphreys, 1975) resulting from the increase in surface temperature of the spider.

Discussion

The form of the burrow of *L. tarentula* is similar to that of *G. godeffroyi* as described by Humphreys (1978), with a vertical shaft turning about 45° into a sloping terminal chamber (L. Dufour cited in Fabre, 1912). The burrow provides a refuge from both low and high ambient temperatures (Humphreys, 1978) and under given conditions of solar radiation the diurnal temperature range within the burrow is determined by the depth of the burrow and the thermal properties of the soil.

The combination of the temperature profile of the soil, various measures of ambient temperature and of the spider temperature can be used to infer the location of the spider in relation to the burrow (Fig. 1). These data indicate that the spider basks in the sun until about midday, when it withdraws about 2.5 cm into the burrow. In the late afternoon it basks again, and then withdraws into the burrow and remains just within the burrow mouth (c. 0.5 cm) for the remainder of the night. This means that the spider is in a position suitable for prey capture for all but about three hours of the day and night. This differs from *G. godeffroyi* in winter, when the spider remained at the base of the burrow for most of the day and where it avoided extreme cold; in summer, however, the spiders became progressively more active at night as the minimum temperature rose (Humphreys, 1978).

Spider temperature

Spider temperature is markedly off-set from all measures of ambient temperature after 1600 h (Fig. 2). In the morning, spider temperature closely follows one measure of ambient temperature, namely EGLT, and during this period EGLT is a good model for the rise in spider temperature. After 1600 h, however, the spider temperature is elevated above all measures of ambient temperature, presumably due to the spider withdrawing into the burrow and taking advantage of the lag in soil temperature, as has been described for other lycosids (Humphreys, 1978).

Differentials between ambient and spider temperatures

The bimodal form of the curve for the temperature difference between the spiders and the model (Fig. 3) is similar to that found on hot days in summer for an

Location	g1	t	p	g2	t	p
Spider prosoma	−0.25*	3.33	<0.001	−0.20	−1.31	0.190
Exposed ground level air	0.51*	2.15	0.032	0.11	0.24	0.814
Clay model at 5 mm	0.35	1.58	0.118	−0.97*	−2.18	0.029
Dry bulb	0.38	1.80	0.074	−0.08	0.20	0.841
Wet bulb	−0.09	−0.40	0.686	−0.69	−1.63	0.102

Table 1: Statistics describing the distributions of prosomal temperatures of *L. tarentula* and of several measures of ambient temperature at Arnissa; g1 and g2 are statistics of skewness and kurtosis respectively. Significant statistics are denoted by *.

agelenid, *Agelenopsis aperta* Gertsch, by Riechert & Tracy (1975), for *G. godeffroyi* by Humphreys (1978), and for an agamid lizard, *Amphibolurus inermis*, in an Australian desert (Heatwole, 1970). Winter curves for the latter two species were also similar to each other but, unlike the summer curves, the surface temperature differentials were unimodal and greater than zero throughout the day. All are in accord with the model of invertebrate activity described by Williams (1966). In all cases the animal varies its thermal relationship with particular measures of ambient temperature to maintain its body temperature as close as possible to its preferred temperature. Although this is suggestive of optimisation, the process being optimised is unknown, however, as discussed below in relation to the skewness of the temperature frequency distributions, the data being consistent with the normalisation of at least two physiological processes.

Skewness of spider temperature data

As the recordings were made at the same time, it is valid to compare the frequency distribution of the spider temperatures with those of the various measures of ambient temperature. The spider temperature data are negatively skewed, whereas all measures of ambient temperature are either not skewed or are positively skewed, i.e., there is a wider range of selected temperature below the median than above it. This finding is in accord with the analysis of the frequency distributions of the temperatures of a wide range of ectothermic animals that are free to select any temperature throughout a wide temperature range (DeWitt & Friedman, 1979). DeWitt & Friedman (ibid.) hypothesised that the negatively skewed

temperature distributions have as their basis, not the regulation of temperature *per se* but rather of a physiological rate process whose rate is an exponential function of temperature, i.e., they serve to normalise the frequency distribution of physiological rates.

Unlike the data discussed in DeWitt & Friedman (ibid.), in which the animals were permitted a choice from a wide range of temperatures in thermal gradient apparatus, *L. tarentula* was constrained in its choice by the available ambient temperatures. The ambient temperature with which the spiders were most in accord (EGLT) showed strong positive skewness, while the distribution of spider temperature was negatively skewed; hence the spiders' behaviour results in the selection of a subset of the ambient temperatures such that the form of their temperature distribution differs significantly from any measure of the environmental temperature. This provides the clearest evidence available for thermoregulation in spiders.

Multiple regression models have been published for lycosids which predict respiration rate from body weight and body temperature (Humphreys, 1977), and water loss from body weight, temperature and saturation deficit (Humphreys, 1975). Applying these equations (spider weight = 1000 mg, saturation deficit calculated for 75% relative humidity), to the frequency distribution of the body temperature of *L. tarentula* permits calculation of the frequency distribution of respiration and water loss. The equations can be applied in this manner because the power functions are in close agreement with other data (Humphreys, 1977: table 1; Humphreys, 1975: 307) and it is the power function rather than the magnitude of the calculation which determines the resulting frequency distribution. While the frequency distribution of body temperature was negatively skewed, the resulting frequency distributions of both respiration ($g1 = 0.076$, $t = 0.985$, $p = 0.325$) and water loss ($g1 = 0.074$, $t = 0.947$, $p = 0.344$) have normal distributions. Hence the frequency distribution of temperatures determined for *L. tarentula* in the field when applied to rate-temperature curves of physiological processes of lycosids are in agreement with the prediction of the hypothesis of DeWitt & Friedman (1979).

Condition	Time of day (2 h intervals)												Daily
	1	3	5	7	9	11	13	15	17	19	21	23	total
1	1.9	1.9	1.7	1.7	2.1	2.6	3.1	3.6	3.1	2.7	2.3	2.0	28.75
2	2.1	2.0	1.6	1.8	2.2	3.3	4.1	4.7	4.0	3.3	2.6	2.2	34.03
3	2.2	2.1	1.7	1.8	2.4	4.1	5.4	5.5	5.1	4.0	2.8	2.4	39.52
2/1%	109	105	99	102	108	125	132	132	129	123	112	111	118
3/1%	115	109	99	104	115	155	175	153	168	148	122	119	137

Table 2: The expected water loss (mg) in two-hour intervals and the total daily water loss from *Lycosa tarentula* during August. The assumptions used in the calculations are: condition 1, spider at dry bulb temperature and ambient saturation deficit; condition 2, spider at spider prosoma temperature and ambient saturation deficit; condition 3, spider at spider prosoma temperature and the saturation deficit adjusted to take account of the temperature difference between the spider and the air (saturation drive model; Humphreys, 1975). Conditions 2 and 3 encompass the range of estimated water loss in the field and their differences from condition 1 are measures of the cost, in terms of water loss, of the spider's thermoregulatory behaviour.

Water loss

Of the total water loss from *L. tarentula, c.* 27% is a direct result of thermoregulatory behaviour. If *L. tarentula* has the same resistance to water loss as *G. godeffroyi,* a mature female would lose about 4% of its body water a day. The local environment at Arnissa was less water-stressful than that of *G. godeffroyi* for the equivalent season in the Australian Capital Territory (Humphreys, 1975).

Range of preferred temperature

Using shuttleboxes (Hammel *et al.,* 1967; Berk & Heath, 1975; Barber & Crawford, 1979) the lower (TL) and upper (TU) limits of voluntary thermal tolerance can be well defined. For a range of ectothermic animals there is an inverse relationship between the temperature range for activity (TU-TL) and body weight (W g) such that (TU-TL) = 11.8 – 2.64 log W (r = 0.88, n = 9; Dreisig, 1985); This gives a predicted range of 11.3°K at a body mass of 1500 mg, about the size of mature *L. tarentula.* The mean value of TU-TL for *L. tarentula* was only 2.98°K (between 30.7 and 33.6°C; cf. *G. godeffroyi* range = 5.0 to 6.4°K; Humphreys, 1978) when defined as the difference between the mean temperatures at which the body temperature troughs or peaks when conditions were suitable for thermoregulation, *i.e., when the* temperature was voluntarily selected. However, *L. tarentula* voluntarily accepts temperatures well outside this range; analysis of the distribution of these data (n = 268) showed that frequencies in excess of 5% occupied a temperature range of 8°K (30 to 37°C) and were more in accord with the value predicted from shuttlebox studies. This suggests that in the field, under suitable conditions, the spiders maintain their body temperature within a much narrower range than that defined by their voluntary thermal tolerance; this is in accord with the model of thermoregulation proposed by Dreisig (1985).

Acknowledgements

References

BARBER, B. J. & CRAWFORD, E. G. 1979: Dual threshold control of peripheral temperature in the lizard *Dipsosaurus dorsalis. Physiol.Zool.* **52**: 250-263.

BERK, M. L. & HEATH, J. E. 1975: An analysis of behavioural thermoregulation in the lizard *Dipsosaurus dorsalis. J.Thermal Biol.* **1**: 15-22.

CARREL, J. E. 1978: Behavioural thermoregulation during winter in an orb-weaving spider. *Symp.zool.Soc.Lond.* **42**: 41-50.

DEWITT, C. B. & FRIEDMAN, R. M. 1979: Significance of skewness in ectotherm thermoregulation. *Am.Zool.* **19**: 195-209.

DREISIG, H. 1985: A time budget model of thermoregulation in shuttling ectotherms. *J.Arid Environ.* **8**: 191-205.

FABRE, J. H. 1912: The works of J. H. Fabre — *The life of the spider.* Transl. A. T. de Mattos. Hodder and Stoughton, London.

HAMMEL, H. T., CALDWELL, F. T. & ABRAMS, R. M. 1967: Regulation of body temperature in the blue-tongued lizard. *Science, N.Y.* **156**: 1260-1262.

HEATWOLE, H. 1970: The thermal ecology of the Desert Dragon *Amphibolurus inermis. Ecol.Monogr.* **40**: 425-457.

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

HUMPHREYS, W. F. 1975: The influence of burrowing and thermoregulatory behaviour on the water relations of *Geolycosa godeffroyi* (Araneae: Lycosidae), an Australian wolf spider. *Oecologia, Berl.* **21**: 291-311.

HUMPHREYS, W. F. 1976: The population dynamics of an Australian wolf spider, *Geolycosa godeffroyi* (L. Koch, 1965) (Araneae: Lycosidae). *J.Anim.Ecol.* **45**: 59-80.

HUMPHREYS, W. F. 1977: Respiration studies on *Geolycosa godeffroyi* (Araneae: Lycosidae) and their relationship to field estimates of metabolic heat loss. *Comp.Biochem.Physiol.* **57A**: 225-263.

HUMPHREYS, W. F. 1978: The thermal biology of *Geolycosa godeffroyi* and other burrow inhabiting Lycosidae (Araneae) in Australia. *Oecologia, Berl.* **31**: 319-347.

HUMPHREYS, W. F. 1983: Temporally diphasic dispersal in siblings of a wolf spider: a game of Russian roulette? *Bull.Br. arachnol.Soc.* **6**: 124-126.

HUMPHREYS, W. F. 1986: Heat shunting in spiders. *In* J. A. Barrientos (ed.), *Actas X Congreso Internacional de Aracnologia* **1**: 41-46. Jaca.

HUMPHREYS, W. F. 1987: Behavioural temperature regulation. *In* W. Nentwig (ed.), *Ecophysiology of spiders:* 56-65. Springer Verlag, Berlin.

KRAKAUER, T. 1972: Thermal responses of the orb-weaving spider *Nephila clavipes* (Araneae: Argiopidae). *Am.Midl.Nat.* **88**: 245-250.

POINTING, P. J. 1965: Some factors influencing the orientation of the spider *Frontinella communis* (Hentz) in its webs (Araneae: Linyphiidae). *Can.Ent.* **97**: 69-78.

PULZ, R. 1987: Temperature relations. *In* W. Nentwig (ed.), *Ecophysiology of spiders:* 26-55. Springer Verlag, Berlin.

RIECHERT, S. E. & TRACY, C. R. 1975: Thermal balance and prey availability: bases for a model relating web site characteristics to spider reproductive success. *Ecology* **56**: 265-284.

ROBINSON, M. H. & ROBINSON, B. C. 1974: Adaptive complexity: the thermoregulatory postures of the golden-web spider *Nephila clavipes* at low altitudes. *Am.Midl.Nat.* **92**: 386-396.

ROBINSON, M. H. & ROBINSON, B. C. 1978: Thermoregulation in orb-web spiders: new descriptions of thermoregulatory postures and experiments on the effects of posture and coloration. *Zool.J.Linn.Soc.* **64**: 87-102.

SOKAL, R. R. & ROHLF, F. J. 1981: *Biometry: The principles and practice of statistics in biological research.* W. H. Freeman and Company, San Francisco.

SUTER, R. B. 1981: Behavioural thermoregulation: solar orientation in *Frontinella communis* (Linyphiidae), a 6-mg spider. *Behav.Ecol.Sociobiol.* **8**: 77-78.

TOLBERT, W. W. 1979: Thermal stress of the orb weaving spider *Argiope trifasciata* (Araneae). *Oikos* **32**: 386-392.

WILLIAMS, G. C. 1966: *Adaptation and natural selection.* Princeton University Press, Princeton, New Jersey.