The Thermal Biology of *Geolycosa godeffroyi* and Other Burrow Inhabiting Lycosidae (Araneae) in Australia

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Summary. Using both field and laboratory data a detailed examination of behavioural thermoregulation is presented for *Geolycosa godeffroyi* (Koch), a burrow inhabiting Australian wolf spider; comparative data are given for *Schizocosa leuckartii* (Thorell), *Venatrix fuscus* (Hogg), *Lycosa speciosa* Koch, and two undescribed species of *Lycosa*. Egg sac and spider body temperatures were recorded either by implanted thermocouples or biotelemetry. The burrows permitted the spiders access to a wide range of temperature throughout the day but the spiders maintained temperatures above the upper limit of this range except in the middle of the day in summer. In winter the burrows protected the spiders from extreme cold. *G. godeffroyi* thermoregulated throughout the year and could achieve temperatures of 38°C when the global radiation exceeded about 260 mW cm^{-2} d^{-1}. The activity regimes deduced from temperature recording were in accord with those derived using field actographs and photographic recording. The spiders thermoregulated in a manner similar to that used by behaviourally thermoregulating lizards and did so whenever conditions were suitable. They maintained temperatures between 32 and 36°C but the preferred temperature was reduced by lack of food or water, in egg sacs or females carrying egg sacs and in mature males to about 30°C. The data do not support the concept of a refractory zone but suggest two or more set points required for specific physiological or ecological purposes.

Introduction

Thermal preference studies show that lycosids have distinct thermal preferenda which are generally higher than prevailing ambient temperatures (Nørgaard, 1945, 1951; Almquist, 1970; Hallander, 1970), they may shuttle between patches of sun and shade (Nørgaard, 1951) and sun their egg sacs (Nørgaard, 1951;

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Vlijm et al., 1963; Vlijm and Kessler-Geschiere, 1967; Edgar, 1971a); these observations suggest thermoregulatory behaviour; such behaviour has recently been demonstrated for the burrow dwelling wolf spider *Geolycosa godeffroyi* (Koch) in Australia (Humphreys, 1974).

The literature contains some discussion of thermal regimes of spiders in the field; most rely on microclimatic data (Nørgaard, 1945; Hackman, 1957; Pointing, 1965; Moeur and Eriksen, 1972; Seymour and Vinegar, 1973) but Nørgaard (1956) combined these with field experiments to determine the effect of temperature on egg sac moving behaviour of *Theridion saxatile* (now called *Archaearaneae riparia* (Blackwell)). Reichert and Tracy (1975) used energy balance equations to determine the influence of thermal environment on the reproductive success of *Agelenopsis aperta* (Getsch) and Krakauer (1972) made a few direct measurements on *Nephilia claviceps* Linnaeus during a study of thermoregulatory postures.

Very steep gradients of temperature and humidity are found in most environments, especially at interfaces (Burrage, 1971) but they have been most commonly examined in extreme environments (Wellington, 1950; Williams, 1954; Cloudsley-Thompson, 1962; Holm and Edney, 1973) and the significance of burrow dwelling and behavioural thermoregulation in temperate environments has been neglected. In concluding a review of the temperature relations of arthropods Bursell (1964) considered it was necessary to take measurements from the animal itself and that "to assess the conditions to which insects are exposed, one would need to have a rough idea of the proportion of time spent in different types of activity and the places frequented at different times of the day and night, as well as any seasonal variation in these respects". In the same context, 'we have hardly begun to explore the effects of radiant heat ... (and) even were we able to plot ... (this variable) on a most minute scale and in great detail we would remain uncertain as to where the animal's movements actually brought it in relation to such a pattern of variables' (Macfadyen, 1967, p. 395). These problems are overcome by direct continuous monitoring of body temperatures and the burrow dwelling wolf spiders are amenable to such recording.

In any study of behavioural thermoregulation comparison must be made with lizards on which most work of this type has been conducted; even here few studies examine seasonal variation in the field and most rely on spot temperature measurements, which, while they have advantages, lose considerable information about thermal behaviour. The sparcity of information on behavioural thermoregulation in arthropods, especially spiders, warrants a fuller presentation than would be appropriate, for example, to a study on lizards.

Materials and Methods

Synopsis of the Species Studied

Data are presented for six species of lycosids belonging to four genera; the generic grouping follows McKay (1973). These species are listed below with collection localities and representative carapace lengths and weights of mature females.

Geolycosa godeffroyi (Koch, 1865). Kowan Forest, Australian Capital Territory (A.C.T.)' Diamond Creek, Victoria; Clouds Creek State Forest, north-eastern New South Wales. Carapace length 11.7 mm. Weight 1200 mg.

Schizocosa leuckartii (Thorell, 1870). Kowan Forest, A.C.T.; Bundemare Stud, near Trangie, N.S.W. Carapace length 10.4 mm. Weight 900 mg.

Venatrix fuscus (Hogg, 1900). Five Mile Track, Wilson's Promontary, Vic. Carapace length 8.4 mm. Weight 550 mg.

Lycosa speciosa Koch, 1877. Kowan Forest, A.C.T.; Moora Creek Crossing, Victoria Road, Grampians, Victoria. Carapace length 7.6 mm. Weight 370 mg.

Lycosa sp.nov 1. Allied to *Lycosa neboissi* McKay. Kowan Forest, A.C.T. Carapace length 7.9 mm. Weight 800 mg.

Lycosa sp.nov 2. Kowan Forest, A.C.T. Carapace length 6.4 mm. Weight 180 mg.

Material is deposited with the Queensland Museum where Dr. R.J. McKay is revising the Australian Lycosidae.

Female lycosids carry egg sacs on their spinnerettes and when the spiderlings emerge they ride on the back of the female for some time. The spiderlings of *G. godeffroyi* become free living between December and May (summer to autumn) and over-winter twice before breeding; during this period they moult about 15 times and grow from 2.5 to 1500 mg (Humphreys, 1976). The spiders construct burrows which they inhabit for much of their lives and from which they rarely move. Spiders start basking at the burrow entrance in a head-down stance exposing the abdomen to the sun, they later adopt a head-up stance at the burrow entrance and in which position they catch prey. Females with egg sacs feed rarely (Nakamura, 1972; Humphreys, 1975a) and the head-up stance assumes mainly thermoregulatory significance.

Spider Temperatures

Thermocouples were used to measure the body temperature of spiders in the field and laboratory. The method adopted was similar to that used by Hadley (1970) on the hairy scorpion, *Hadrurus arizonensis* and the tenebrionid *Eleodes armata;* it involved the implantation of a thermocouple junction into the cephalothorax. Their habit of burrowing permitted free movement of the spider within and around the burrow when the thermocouple was attached.

To prevent excessive fluid loss the spider was relaxed with carbon dioxide anaesthesia and a thermocouple inserted above the third leg through the carapace 2 mm into the dorsoventral muscles of the cephalothorax. The hole was immediately sealed with medical tissue adhesive (Isobutyl-2-cyanoacrylate monomer; COAPT, Ethicon, Hamburg). A drop of rapidly polymerising epoxy resin provided a secure anchorage for the thermocouple lead to the carapace and spiders normally retained the thermocouple until the next moult. The thermocouple lead contained 48 gauge (0.041 mm dia.) copper and constantan wires embedded in medical grade P.V.C. (Dural Plastics, Dural, N.S.W.) 0.45 mm in diameter. The prepared junctions were stripped of the coating for 2 mm and only the wires inserted through the carapace. The lead weighed 2.3 mg cm^{-1} and an adult spider would have to lift a maximum of 35 mg if the lead was freely suspended in the burrow; females may carry egg sacs of 1.9 g. The spiders appeared to behave normally and two females successfully constructed egg sacs, oviposited, incubated and hatched eggs with the thermocouples implanted, one in the field and one in the laboratory. Occasionally the spiders would attach the lead to the burrow wall with silk; such records were discarded as the spider was not free to traverse the full thermal environment normally available.

In the field, temperature was measured with an electric thermometer (Comark) using an external reference of melting fresh water ice and recorded on a chart recorder (Rustrak, Gulton Industries, Manchester, New Hampshire) with 6 cm chart width at 7.6 cm h^{-1}. The Kowan recordings were made using manual switching through 10°C ranges but at Clouds Creek the range was expanded to 40°C and a multiplexor gave four channel capacity.

Most laboratory recording was made with a 12 channel potentiometric thermocouple recorder with 16.5 cm chart width (50°C range) at 5.1 cm h^{-1} (Speedomax H, Leeds and Northrup Co.). In the laboratory spiders were provided with a burrow of appropriate size in large containers of soil held at laboratory temperature (about 20°C) or in a constant temperature room at 10°C.
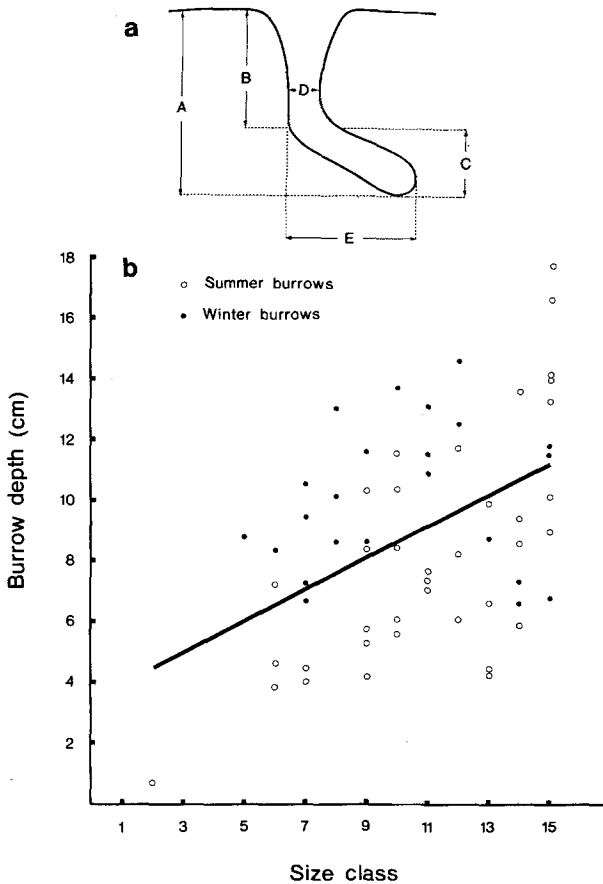
Fig. 1
a Schematic diagram showing
the measurements made on the
casts of *Geolycosa godeffroyi*
burrows. It represents the
burrow of a mature female;
other burrows have a neck more
nearly parallel.
b The relationship between
burrow depth and size class
of the spider occupant. The line
represents the regression
through all the data. Size classes
are closely equivalent to instars;
carapace width of size class
$1 = 1.04$ mm and of size class
$15 = 8.52$ mm (Humphreys, 1976)

An incandescent bulb or an infra-red bulb was suspended above the container to provide a photother-
mal gradient with a 12 h photoperiod. Ambient, soil and deep burrow temperatures were recorded
and the thermal environment available was similar to the range found in the field in summer;
it will be seen that these burrows gave data similar to those derived from field recording.

Egg Sac Temperatures

Temperature transmitters were used to record egg sac temperatures in the field. The transmitters
were implanted in the egg sac after removal of about 70% of eggs and after light suturing were
returned to the spider to complete repair (cf. Whitcomb and Eason, 1964). Females were kept
receptive to the egg sacs during removal by provision of a surrogate egg sac, either real or a
plaster block. The output was recorded via a domestic radio on to magnetic tape with appropriate
time marks and controls. Implanted thermocouples were later used to record egg sac temperature
both in the field and the laboratory.

Thermal Microenvironment

At Kowan the thermal microenvironment available to *G. godeffroyi* was examined in detail
throughout 1972. The environment available was related to the spiders' behaviour and the characteris-
tics of their burrows, particularly their depth (see 'Burrows').

Thermocouples were placed at various depths ($+1$, surface, -2, -5, -8, -11.5 and -16 cm). in fine horizontal borings from a hole dug in the field site. Soil was packed over the probes and well watered and they were left permanently in place. Small thermistors were placed in a spider burrow at 2 and 10 cm depth to relate soil temperature profiles to burrow temperature. Temperatures were measured every hour when I was present on the field site (dates in Humphreys, 1973) save for about 6 h at night. Originally these temperature profiles were to be used in conjunction with a field actograph to relate the spider's position to temperature. When I found that the spiders thermoregulated the thermocouple implantation technique was developed to measure actual spider temperatures and the former technique used to verify that the spiders' behaviour was consistent with the interpretation of data using the latter method which involved no tethering or implantation.

The field actograph (Humphreys, 1973) had sensors at six depths in an artificial burrow of a size appropriate to the spider being monitored. Movement of the spiders through the burrow broke a beam of red light (lycosid eyes have a weak response to red light, DeVoe et al., 1969) at the appropriate depth and the data recorded on a six channel event recorder. The position of the spider was related to the soil isotherms.

Spider temperatures were recorded at Kowan (35° 16'S, 149° 15'E) on 27 full days between February and November 1972; these data have been used elsewhere (Humphreys, 1973, 1974, 1975c, 1977b) but not interpreted. The characteristics of the field site at Kowan and the climatic and synoptic data have been given elsewhere (Humphreys, 1975c, 1976). Field recordings were also made at Clouds Creek (30° 05'S, 152° 37'E) for 35 days during 1974 and 1975; climatic data for this area have been given in How (1972) and the area described (Barnett et al., 1976). Laboratory recording was mainly in Melbourne and field recording from egg sacs at Kowan and Clouds Creek.

Burrows

Casts of *G. godeffroyi* burrows were made at Kowan using either high melting point wax or liquid polyurethane which foamed, expanded and hardened in the burrow. The burrows were of similar form and allowed a series of linear measurements to be made and related to the size class (closely equivalent to instars, Humphreys, 1976) of the occupant. The data are not random as some burrows associated with rocks or roots could not be excavated.

Movement in and around Burrows

This was examined using continuous photographic recording of individual burrows at Kowan. A 'beta-light' (a tritium filled glass bead coated internally with a phospor and emits a weak light; Hawker Siddeley) was cemented to the carapace of the spider and an automatic camera fixed 1 m above the burrow to expose each frame for 0.5 h at night. The resulting negative showed any movement of the spider within and around the burrow. A second 'beta-light' was placed in the camera's field of view as a control.

Data Analysis

Individual records were analysed by taking the spider's temperature at each 0.5 or 1.0 h during the thermoregulatory period or throughout the day as appropriate; all times are Australian Eastern Standard Time. The standard error for the individual was calculated and the standard error for pooled data derived by:

$$\text{S.E.} = \sqrt{\frac{\sum (\text{variance} \times n)}{\sum n}} \times \frac{1}{\sqrt{N}}$$

where n = number of data in individual means and N = number of individuals. Further details of data analysis are given where appropriate.
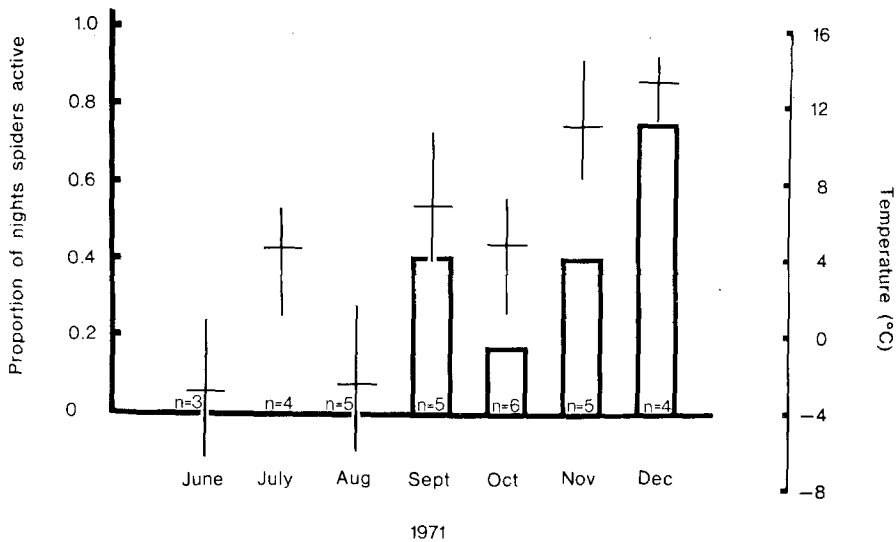
Fig. 2. Results of photographic recording of spider movement at night. N is the number of nights per month for which records were available. The *left band axis* and the *histograms* represent the proportion of nights during which the spiders were active at the top of the burrow any time between sunset and sunrise. The *horizontal bars* show the mean minimum temperatures for the nights on which recording was made and the *vertical lines* the range of minimum temperatures

Results and Discussion

The Burrow of Geolycosa godeffroyi

The measurements made on burrows and their generalised mean shape are shown in Figure 1 a. Only the depth ('A' in Fig. 1 a) is considered here as it is the most significant factor influencing the thermal environment of the spiders. The relationship between burrow depth and size class of the occupant (Fig. 1 b) shows that winter burrows (May–August) were deeper than summer burrows (rest of the year; $\chi^2 = 11.92, P = <0.005$). During the severe winter of 1971 at Kowan a number of burrows were deepened by the addition of a second vertical section (Humphreys, 1973). Although the burrows may be important for the spiders to gain access to soil water, water was least scarce in winter (Humphreys, 1975c) and it seems probable that the deepening was related to the thermal environment.

The orientation of the burrows (taken as the direction of the entrance from the blind end) was significantly different from a uniform circular distribution ($P < 0.001$, $n = 98$; Kolmogorov-Smirnov test) and 70% of the burrows were orientated north of the line of latitude with a mean direction of 333°. This bearing is similar to that of 337° found for the funnels of an agelenid spider in the northern hemisphere and which there gave minimum exposure to the sun (Reichert and Tracy, 1975).
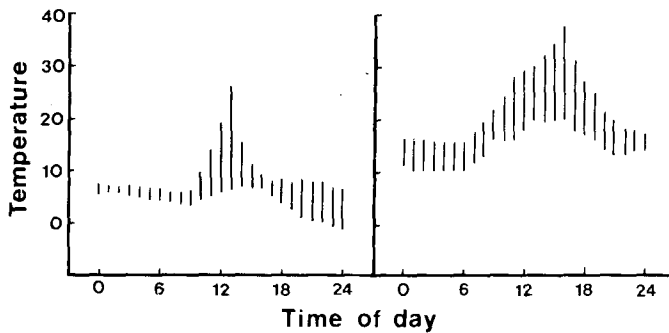
Fig. 3. The available thermal environment of *G. godeffroyi* for a day in winter and summer. The range represents the maximum and minimum temperature (°C) available at each hour between +1 cm and a soil depth of 12 cm

Microenvironment

The thermal microenvironment available to *G. godeffroyi* depends on the energy balance of its habitat at ground level, the thermal flux through the soil to the maximum burrow depth and the excursions of the spiders through this thermal range.

Using continuous photographic recording at night the proportion of nights that the spiders were active at the top of their burrows could be related to the mean minimum temperature (Fig. 2). There is correlation between mean minimum temperature and the proportion of nights (after angular transformation) the spiders were active in any month ($r=0.896$, $P<0.001$). None of the photographic negatives showed the spiders moving more than 3 cm from the burrow at night and that infrequently.

This evidence suggests that the thermal environment between +1 cm and the depth of the burrow need be considered. The temperature was measured at hourly intervals throughout the day at eight levels from +1 cm to −16 cm. The available thermal environment is then the difference between the maximum and minimum temperature on these eight probes at any time. These data are shown for a mild day in both winter and summer on the Kowan site in Figure 3. In both summer and winter the spiders could select from a wide range of thermal conditions but could potentially maintain roughly constant temperatures throughout the day. The available soil-water environment was similarly modified by the spiders' burrowing behaviour (Humphreys, 1975c).

The characteristics of heat movement through soil have been well documented elsewhere (Sinclair, 1922; Williams, 1954), suffice here to say that temperature fluctuates less with increasing depth and that the times of maximum and minimum temperatures lag more with increasing depth. These effects are shown in Figure 4 in which the position of the spiders, determined from field burrow actographs, is related to the changing thermal conditions with depth and through time for two days in winter. The protection from temperature extremes afforded by the burrow and the relative thermal stability with depth are appar-
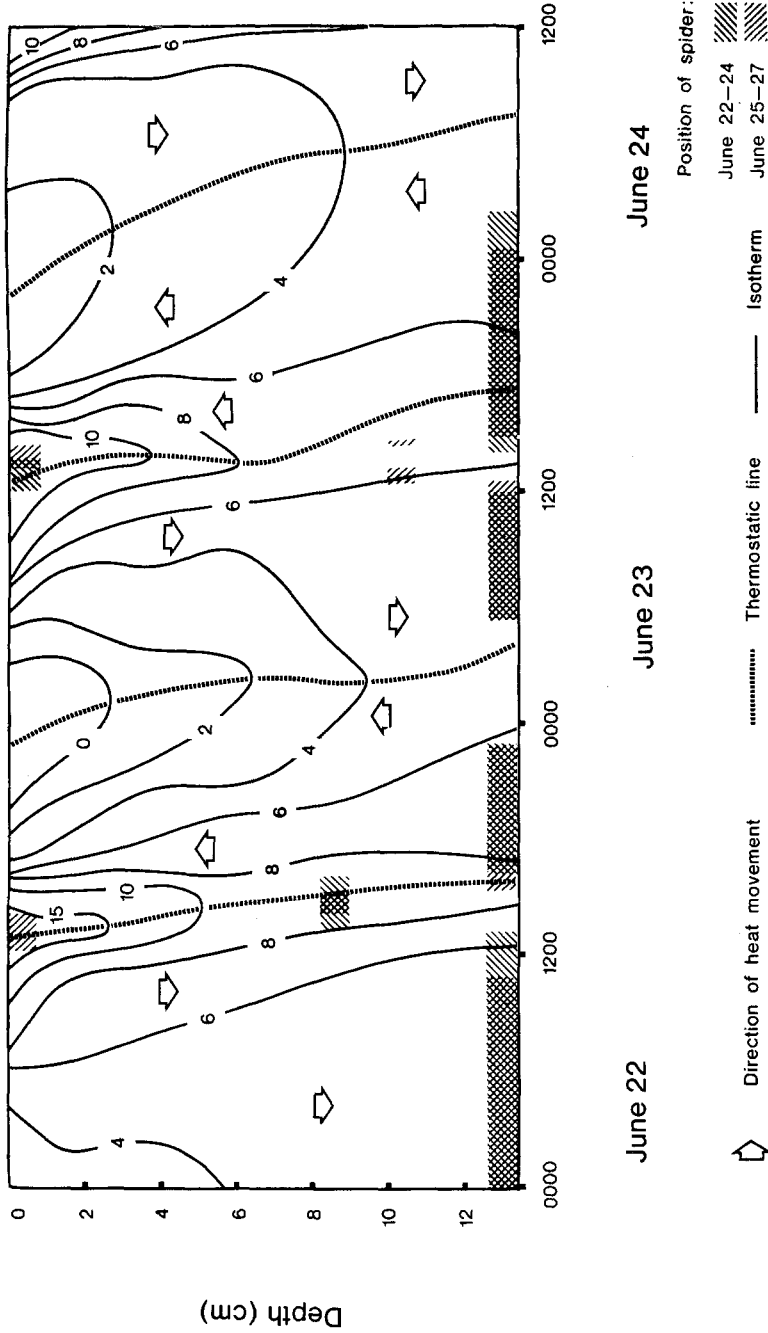
Soil isotherms June 22 - 24 1971

Fig. 4. Soil isotherms and the position of spiders in an artificial burrow fitted with a field actograph from June 22 to 24, 1971. Thermostatic lines indicate a reversal in the direction of temperature change (Williams, 1954) and the numbers on isotherms represent °C. The position of a mature female is shown on the days represented by the isotherms and the position of a penultimate instar male during the subsequent 3 days is superimposed to illustrate the consistency of the activity period. Minimum screen temperatures for the period June 22–26 were respectively 0.9, −3.7, −0.4, −6.5 and 1.8°C and maximum screen temperatures for the period June 22–25 were 15.2, 9.7, 11.0 and 11.7°C
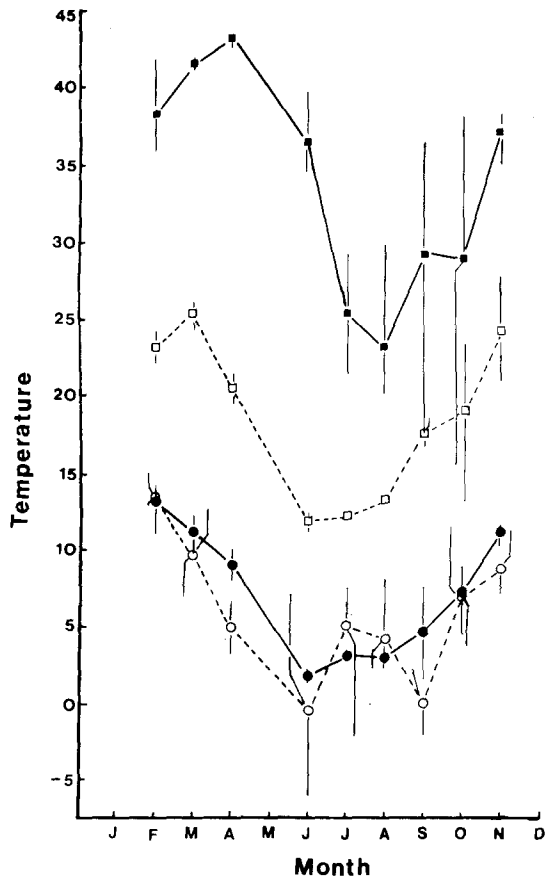
Fig. 5. Maximum and minimum spider *(solid symbols)* and screen *(open symbols)* temperatures (°C) throughout 1972 at Kowan. The *vertical lines* show the range of maximum and minimum temperatures

ent; the latter applies also to soil water but on a longer time base (Humphreys, 1975c). It will be seen later that this activity pattern for free spiders conforms with the interpretation of spider temperatures in winter obtained using implanted thermocouples.

The Temperature of G. godeffroyi in the Field

Definitions: T_S = body temperature of spider
T_{A10} = air temperature in screen 10 cm above ground
T_{A1} = screened air temperature 1 cm above ground
T_G = temperature of ground surface
T_B = soil temperature at a depth of 12.5 cm

I published a short note on the thermoregulation of *G. godeffroyi* in 1974 and some of the data not discussed there will be considered here. That paper gave examples of the daily course of T_A and T_S from individual spiders. In addition it showed that at Kowan the mean daily temperature of *G. godeffroyi* on clear days in 1972 was 4.6°C greater than the mean T_{A1} throughout the year; this constant relationship throughout the year was due to the summation of the effects of the temperature differential between T_{A1} and T_S and the time
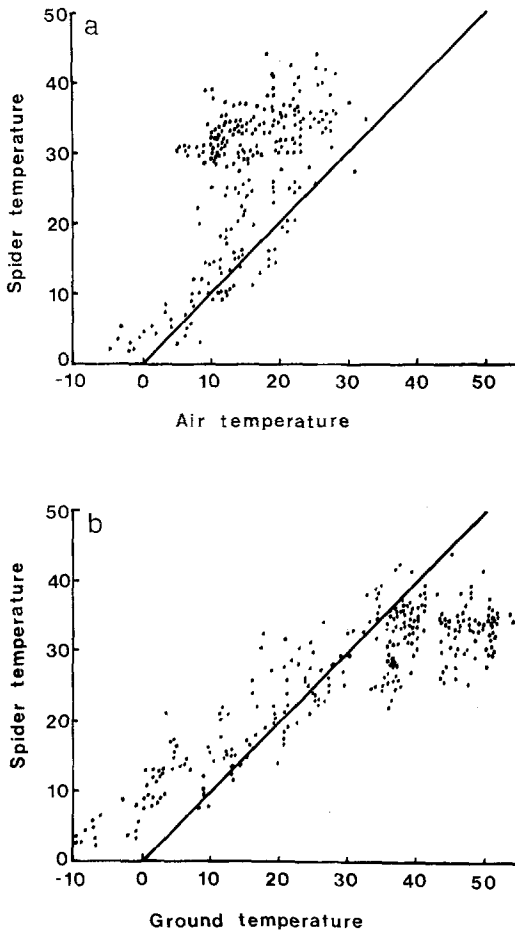
Air temperature

Ground temperature

Fig. 6
a The relationship between the temperature (°C) of *G. godeffroyi* and air temperature at Kowan and Clouds Creek.
b The relationship between the temperature of *G. godeffroyi* and surface temperature at Kowan and Clouds Creek. Some data for ground temperatures $> 40°$ C are from the laboratory.
In both figures the diagonal line represents $T_S = T_{environment}$

available for thermoregulation at various times of the year: the temperature differential was greatest in winter but the time available for thermoregulation was short, the reverse was true in summer. This constant relationship has important properties when attempting to derive the rate of physiological processes in the field; it results in the proportional error introduced by using the mean T_{A1}, being greater when the ambient temperature is low than when it is high — the error being 98% and 30% at 5 and 20°C mean T_A respectively. Assuming a constant Q_{10} these errors would be reflected on the same basis in physiological rate estimates. Similar arguments apply to the rate of water loss (Humphreys, 1975c). The actual temperatures obtained by the spiders have a greater effect than that indicated by the mean temperatures due to the rate-temperature relationships of the variables considered (water loss — Humphreys, 1975c; respiration — Humphreys, 1975b, 1977b).

Seasonal changes in the maximum and minimum T_S and T_{A10} from field recordings at Kowan throughout 1972 are shown in Figure 5 for *G. godeffroyi*.
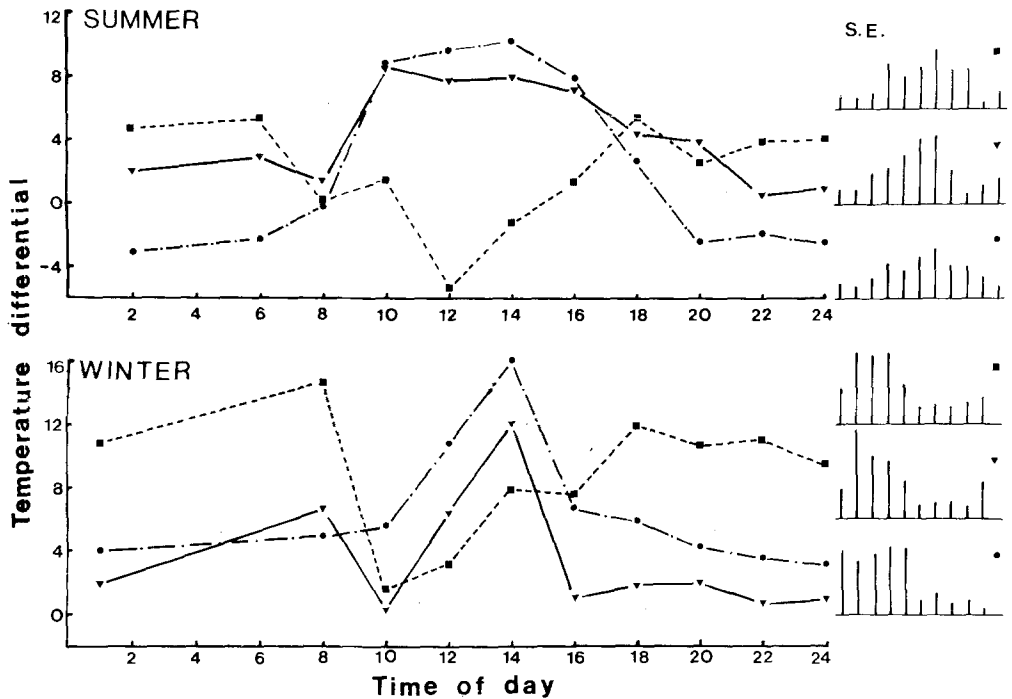
Fig. 7. Daily course of differences in temperature (°C) between *Geolycosa godeffroyi* and the air temperature (T_A *triangles*), ground temperature (T_G *squares*) and burrow temperature (T_B *circles*) in both summer and winter. The *vertical bars* to the right of the graph represent one standard error for each data point in sequence from left to right across the graph

While maximum T_S were considerably greater than T_{A10} throughout the year, the minimum T_S and T_{A10} were quite close although the differential increased when the latter was very cold. It will be seen later that unscreened ground temperatures were considerably colder and the differential consequently greater. Several months during the winter show that maximum T_S were lower than during the remainder of the year; while this suggests that the preferred temperature may vary during the year it will be seen later that this probably reflects the weather conditions at Kowan.

The relationships between T_S and both T_{A1} and T_G are shown in Figure 6a and 6b respectively using data from Clouds Creek, Kowan and some laboratory data for $T_G > 40°C$; the data sets are not identical due to limited recording facilities. T_S was normally greater than T_{A1} and rarely fell below it. T_S had a different relationship to T_G; in the mid temperature range T_S followed T_G more closely but departed strongly from it at both high and low temperatures clearly showing the spiders' thermoregulatory behaviour relative to T_G. When ground temperature was high $T_G > T_S$ and vice versa at low T_G.

The above presentation hides diurnal and seasonal changes in spider temperature relative to its environment. These changes are considered in Figure 7 using
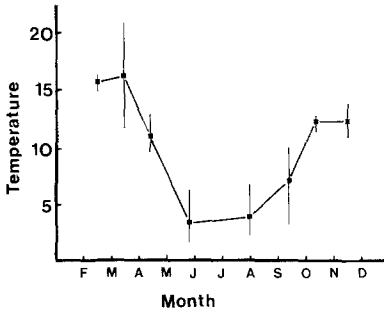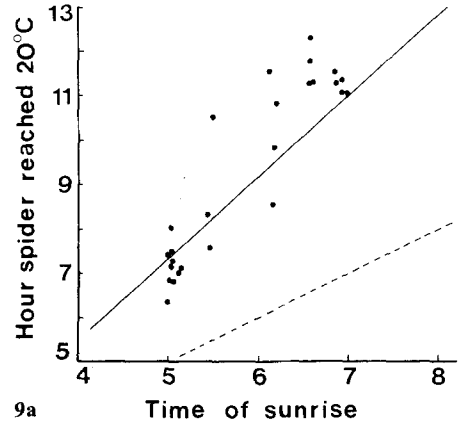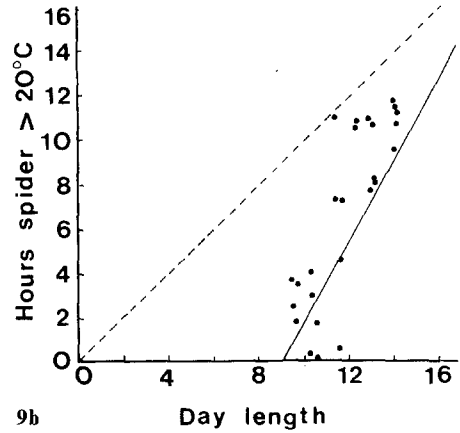
Fig. 8. Mean temperature (°C) at which *G. godeffroyi* commenced thermoregulating at Kowan throughout 1972. The *vertical bars* represent the range

Fig. 9. a The relationship between the time of sunrise and the time *G. godeffroyi* started to thermoregulate as indicated by an increase in temperature above 20°C. The *null (broken)* assumes the times are equal and the continuous line represents the time the sun reached the 30° almacantar. **b** The relationship between the duration of the thermoregulatory period of *G. godeffroyi* (duration greater than 20°C). The *null line (broken)* assumes the times are equal and the continuous line represents the time the sun was above the 30° almacantar

1972 field data from Kowan. Several points deserve comment. The winter thermoregulatory period is shorter than that in summer; T_S, T_G and T_A approximate each other on emergence of the spider both in winter and summer; the trend in the relationships is similar in both winter and summer but the lines are shifted up the vertical axis in winter. In winter T_G never rises above T_S but it does in summer during the middle of the day. Similar relationships between these variables have been described for the desert living lizard, *Amphibolurus inermis,* near Alice Springs (Heatwole, 1970).

Factors Controlling the Thermoregulatory Regime

Much of the work on behavioural thermoregulation in ectotherms arises from studies on lizards but few are extensive in time and most rely on spot recordings of cloacal temperature. Nevertheless several workers have recorded temperature independent emergence in lizards (Heath, 1962; Stebbins and Barwick, 1968) and it has been suggested that emergence of *Amphibolurus inermis* was related to a photic or biological rhythm (Heatwole, 1970). Potential cues for emergence of *G. godeffroyi* was examined from both laboratory and field data.

The temperature at which the spiders emerged in the morning was determined by examining the relationship between T_S and the environmental temperature in the continuous recordings from individuals (e.g. Humphreys, 1974). A temperature cue is improbable owing to the variability in T_S and T_A at which spiders emerged in different seasons at Kowan (Fig. 8). This does not preclude a thermal cue as the threshold temperature for emergence could vary with season or the state of thermal acclimation; a thermal cue for emergence is *a priori* unlikely in a burrowing species due to the thermal lag in the soil.

The field site at Kowan had a line of hills to the east of the site running north to south and from the site the crest subtended an angle to the horizontal of between 28° and 34°, being higher in the north. The time of sunrise at Kowan is plotted against the time of emergence of *G. godeffroyi* during 1972 in Figure 9a. The null line equating the time of emergence with sunrise diverges from the data. The line representing the time at which the sun reached the 30° almacantar (calculated from List 1968) approximates the data and the departure in winter probably being due to the greater height of the hills to the north-east. Similar divergence is found between day length and the duration of the thermoregulatory period and again there is reasonable agreement with the line representing the duration of the sun above the 30° almacantar (Fig. 9b); the field site was shaded by high trees to the west (see plates in Humphreys, 1976). These field data suggest that the spiders thermogulate whenever conditions are suitable and for as long as possible. In the laboratory spiders thermoregulated continuously over many days if a heat source was available (unpublished data). Changes in field temperatures (Cogger, 1974) and relatively delayed emergence in winter (Pianka, 1969) which have been reported for lizards may also be attributable to the relatively prolonged shading by vegetation in winter.

The mean monthly maximum temperatures obtained by *G. godeffroyi* varied over the year (Fig. 5) at Kowan. This could be due to 1) a change in preferred temperature of the spiders through the year, 2) the thermal properties of the spiders permitting a constant maximum temperature excess (Digby, 1955), or 3) insufficient solar radiation to achieve greater temperatures. The first is not causal as winter collected spiders maintained similar temperatures to summer collected spiders in the laboratory and spiders at Clouds Creek also thermoregulated at these high temperatures in winter (unpublished data). Under given environmental conditions the main parameter affecting the temperature excess of arhropods is size (Parry, 1951; Digby, 1955); the smallest spiders used in this study (94 mg) were able to achieve a large temperature excess. The third possibility was examined using the field records from Kowan.
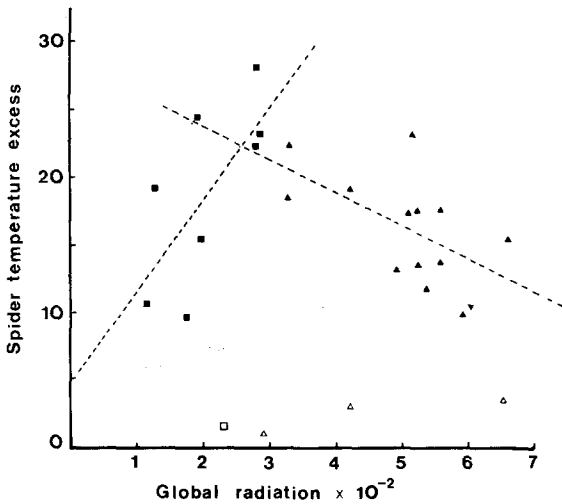
Fig. 10. Relationship between the global radiation ($mW\,cm^{-2}\,d^{-1}$) at Uriarra and the maximum temperature excess (maximum differential between the spider and air temperatures, °C) of *G. godeffroyi*. Regressions are drawn through the winter data *(squares)* and summer data *(triangles)* separately; four points *(open symbols)* from continuously overcast days were excluded from the analysis. The relationship is discussed in the text

No solar radiation records were available for Kowan but daily global radiation figures were available from Uriarra 28 km to the west. An examination of data for the relevant days shows that the relationship between global radiation and sun hours was quite different in winter and summer. The relationships are respectively $Y=29.8X+243$ and $Y=19.7X+129$, where Y=global radiation ($mW\,cm^{-2}\,d^{-1}$) and X=h of sunshine. Using this relationship as support for the division of spider data into summer and winter periods the maximum temperature excess of the spiders at Kowan in 1972 is plotted in Figure 10 against the global radiation. The data fall into two distinct relationships; the temperature excess of spiders in summer is inversely related to global radiation as at high radiation levels, T_A approaches the thermoregulatory temperature of the spiders. In winter the temperature excess was directly related to global radiation probably as at low radiant energy the spiders were unable to maintain their preferred temperature. It is suggested that the intercept of these two relationships at $254\,mW\,cm^{-2}\,d^{-1}$ represents the threshold radiation level below which the spiders were unable to maintain their preferred temperature. The absolute maximum temperature obtained by the spiders also increased with global radiation and reached a plateau temperature at $38.0 \pm 0.37°C$ when global radiation exceeded $266\,mW\,cm^{-2}\,d^{-1}$, a value supporting the previous finding. Over much of the geographical range of *G. godeffroyi,* mean global radiation is below $260\,mW\,cm^{-2}\,d^{-1}$ for between one and 4 months per year.

Effect of Water on Preferred Temperature

Under the standard laboratory conditions the mean temperature of *G. godeffroyi* increased from 29.6 to 33.1°C following drinking by water deprived spiders. The mean temperature difference of $3.9 \pm 0.61°C$ was greater than the difference in spider temperature between the morning and afternoon ($0.6 \pm 0.31°C$;
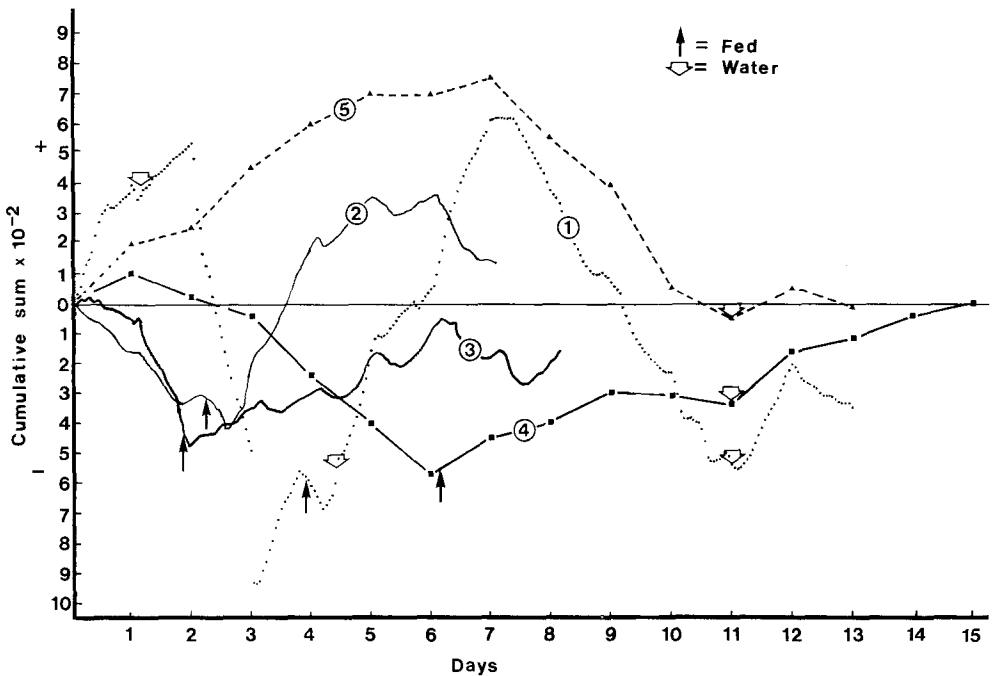
Fig. 11. Representative cumulative sum plots to show the effect of food and water on the preferred temperatures of various spiders. The data were cumulated during the thermoregulatory period on successive days: data for spiders 1-3 were cumulated every 0.5 h and those for spiders 4 and 5 based on daily means; the latter gives plots of the same form but with less resolution and the cumulative sum is $\times 10^\circ$. The addition of water alone resulted in elevated temperatures (shown by a positive change in slope) for about one day; feeding gave elevated temperatures for about 4 days (spiders 1-4). The main changes in slope are significant ($P < 0.001$, span test; Woodward and Goldsmith, 1964). $1 = G. godeffroyi$ (juvenile, base of cumulative sum $= 35.0^\circ$C), from day 4 onward read day $+1$ for this spider; $2 = G. godeffroyi$ (♀ mature, base $= 28.8^\circ$C; $3 = Lycosa speciosa$ (♀ m, base $= 34.4^\circ$C); $4 = G. godeffroyi$ (♂ penultimate instar, base $= 31.0^\circ$C); $5 = G. godeffroyi$ (♀ m, base $= 32.0^\circ$C)

$P < 0.001, n = 13$). The latter comparison was required as the spiders had higher preferred temperatures if water was added later in the day ($Y = 1.01X - 8.37$, $r = 0.80$, $n = 7$; where Y is the time water provided and $X =$ temperature differential in °C). Water was added between 0900 and 1400 h at which times the temperature differentials are predicted to be 0.7 and 5.8°C respectively. Lycosids can drink from the soil against high soil-water tension (Parry, 1954) but *G. godeffroyi* could not obtain soil-water during extreme drought (Humphreys, 1975c).

Water loss from *G. godeffroyi* was very rapid and was directly related, among other factors, to temperature. A reduction in temperature excess of the spider reduced water loss disproportionately owing to the effect on the evaporation drive (Humphreys, 1975c). A change in T_S from 35 to 30°C at a T_A of 20°C would reduce the evaporation drive 81% more than if the spider passively followed a similar change in air temperature. It has been suggested that two species of lizard which showed abnormal inverse relationships between ambient

and body temperature in the field may do so to reduce water loss (see discussion in Huey and Slatkin, 1976) but I am unaware of work relating hydration state to preferred body temperature in lizards.

Effect of Feeding on Preferred Temperature

The relationship between preferred temperature and feeding status was analysed by sequential analysis of data from infrequently fed individual spiders using the cumulative sum technique (Woodward and Goldsmith, 1964) to eliminate the differing preferred temperature of individuals. Individuals of *G. godeffroyi, Lycosa* sp. nov. 2, *L. speciosa,* and *Venatrix fuscus* maintained significantly higher temperatures after feeding with a mean difference of $2.71 \pm 0.67°C$ $(n=7)$ compared with a mean difference of $3.9°C$ associated with drinking.

It is difficult to separate the effects of feeding from that of fluid intake during feeding save that the effect of water intake was of short duration (about 1 day) while the elevated temperature preference following feeding continued for about four days (Fig. 11) but apparently spontaneous changes in preferred temperature took place in some individuals during periods of food deprivation (e.g. spider 5 in Fig. 11). Similar changes have been shown in some lizards (Cogger, 1974). The persistence of elevated temperature following feeding is noteworthy as under constant temperature conditions lycosid respiration increased after feeding (Miyashita, 1969; Hagstrum, 1970; Nakamura, 1972; Humphreys, 1977b) but was reduced to a plateau level (Nakamura, 1972) or close to the fasting level (Hagstrum, 1970) after 4 days; similarly the food passed through the gut of *Pardosa laura* Karsch in 4 days at $25°C$ (Nakamura, 1972). These data suggest that the elevated temperature after feeding was associated with digestion and that the spiders may select lower temperatures to reduce maintenance costs during periods of food shortage; such behaviour has also been reported for ectothermic vertebrates (Brett, 1971; Lillywhite et al., 1973).

Temperatures of Breeding Females and Egg Sacs

The measurement of mean temperatures in the field is compounded by shading due to vegetation and clouds. The field data for the mean temperature during thermoregulation has to be selected from periods during which the spiders were obviously thermoregulating. To impose greater objectivity individual temperature traces were examined and all peak and through temperatures greater than $20°C$ were taken and the mean calculated. It will be seen that this method gives similar values to data derived by integration from more controlled laboratory conditions.

The mean temperature of egg sacs measured biotelemetrically at Kowan was $29.9 \pm 0.92°C$ $(n=4)$. Measurements made in the laboratory gave a mean egg sac temperature of $29.1°C$ (range 28.3–29.9). Using implanted thermocouples the mean field temperature of egg sacs at Clouds Creek was $30.1 \pm 0.47°C$ $(n=3)$ giving a mean for all data of $29.7 \pm 0.29°C$ $(n=9)$.
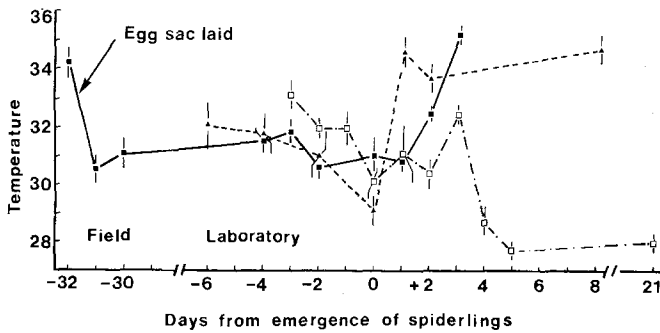
Fig. 12. Mean daily temperature (°C ± standard error) of three *Geolycosa godeffroyi* before and after the emergence of spiderlings from the egg sacs. The spider which produced an egg sac in the field at Clouds Creek was thereafter recorded in laboratory photothermal gradients where the other individuals were recorded

Two data sets have been excluded from this analysis as the temperature traces showed distinct qualitative differences in spider behaviour from other records. They will be treated separately later as they may give some insight into the methods used by the spiders to control temperature.

The egg sac temperatures are lower than the preferred temperatures of female spiders not carrying egg sacs. Spiders with egg sacs had a mean temperature of $30.3 \pm 0.58°C$ ($n=9$) but the mean temperature hides much of the variability in the data. For three spiders with egg sacs data are available over a period of time. All three show mean temperatures greater than the mean value just given. In one the spider was being recorded in the field when it produced the egg sac and data are available for this individual at intervals until after the spiderlings emerged. The other two individuals were recorded in the laboratory over the period in which the spiderlings emerged (Fig. 12). The temperature dropped after production of the egg sac from the preferred temperature of spiders without egg sacs. All three showed a drop in temperature when the spiderlings emerged; this was mainly due to the spiders spending less time at the top of the burrow at this time, falling from about 12 to 5 h a day. Following spiderling emergence two spiders assumed temperatures characteristic of females without egg sacs while the other assumed an abnormally low temperature. The former gained weight, a characteristic of females which would produce another egg sac in the field, while the latter lost weight and died like mature *G. godeffroyi* which became 'senile' in the field (Humphreys, 1973). Spiders which carried egg sacs in the field fed seldom (Humphreys, 1975a) and resumed feeding after spiderling emergence only if they were to produce a second egg sac.

Laboratory studies on other lycosids indicate that a change in preferred temperature may often be associated with egg sacs, at least in standard laboratory temperature gradients. *Pirata piraticus* Clerck normally had a preferred temperature of 21 °C which increased to 29 °C when carrying egg sacs (Nørgaard, 1951). *Lycosa pullata* Clerck and *Pardosa amentata* (Clerck) which had a normal thermal preference of about 30°C showed no change in temperature preference when carrying egg sacs (Nørgaard, 1951; Vlijm et al., 1963). Nørgaard *(op. cit.)*

thought that a temperature of 30°C could be optimal for the development of lycosid eggs. The results for *G. godeffroyi* support his hypothesis as do the data from *Venatrix fuscus* presented later in this paper.

Sex

Mature male *G. godeffroyi* maintained consistently lower temperatures (29.1 ± 0.80°C, $n=4$) than mature females without egg sacs while penultimate instar males of this species and *Schizocosa leuckartii* maintained temperatures similar to that of females without egg sacs (Table 2). Mature males ate seldom so it is not possible to determine whether this change in preferred temperature is innate or caused by lack of food.

Refractory Zone

A species showing behavioural thermoregulation may have an upper and lower temperature threshold to cue behavioural changes in response to temperature. The difference between these two temperatures is the refractory zone within . which the animal will not be stimulated to alter its response to thermal conditions. If this range is too narrow the animal will continually be changing its behaviour to seek shade or sun (Heath, 1970) and have insufficient time to perform the other tasks for which the higher temperature affords some advantage (but see Huey and Slatkin, 1976). In ectotherms this zone may be as narrow as 2.7°C in an iguanid or as wide as 6.8°C in a cicada (Heath, 1970); it may be added that the refractory zone may be expected to be wider in smaller than in larger species due to the lower thermal capacity and hence more rapid temperature change in small bodies.

Table 1. Analysis of peak and trough temperatures from continuous recordings of *G. godeffroyi* in the laboratory and on clear days (for $T_S > 20°C$) in the field

Source of data	Number of indi- viduals	Temperature (°C)				
		Mean maximum	Mean minimum	Differ- ence	$\dfrac{\text{Max.} + \text{Min.}}{2}$	Mean field
Field:						
Kowan	18	35.9 ± 0.87	29.5 ± 1.11	6.4	32.7	32.7
Clouds Ck.	4	35.5 ± 1.11	30.9 ± 1.03	4.6	33.2	33.9
Laboratory:						
Normal	6	36.4 ± 1.35	31.4 ± 0.85	5.0	33.9	
'Square wave'[a]	1	36.5 ± 0.37	30.1 ± 0.23	6.4	33.3	
Weighted mean		36.0 ± 1.69	30.1 ± 1.95	5.9	33.0	33.4

[a]   Individual discussed in text and Figure 13

The width of a possible refractory zone in *G. godeffroyi* was estimated by taking the mean temperature of both troughs and peaks from continuous temperature recordings both in the field and laboratory. The latter analysis was conducted on all the data while in the former only temperatures on clear days greater than 20°C were considered to maintain objective criteria whilst eliminating data when the spider was not thermoregulating. This analysis gave similar results for field and laboratory data (Table 1) and indicates a refractory zone of about 5.9°C between 30.1 and 36.9°C. This is supported by the similarity between the mean daily preferred temperature and the mid-point of the refractory zone (Table 1).

The concept of a refractory zone has been applied particularly to lizards which often have specific sunning perches and move some distance to shaded areas (Heath, 1970; Heatwole, 1970). The concept is perhaps inapplicable to the spiders as they perform their prey catching at the burrow mouth and can select a position of appropriate temperature for much of the day and catch prey; they often have only their forelegs outside the burrow. That they do this, rather than shuttle, is indicated by the long periods both in the laboratory and field during which the spiders could maintain virtually constant temperatures; at Kowan these plateau temperatures averaged 35.3 ± 0.68 ($n = 10$) (Table 2) which is close to the upper level of the refractory zone as defined here.

Of particular interest here is the record from two individuals which adopted abnormal temperature regulation while carrying egg sacs; the records are unusual in that the spiders regularly alternated their temperature between well defined maximum and minimum temperatures with prolonged plateau temperatures presenting a square wave appearance (Fig. 13) between 30.1 and 36.5°C (Table 1). The interest lies in the equivalence of these temperatures to those measured under different conditions; they are similar to the limits of the refractory zone as determined here (Table 1), the lower temperature is similar to that of unwatered spiders (29.6°C), mature males (29.1°C), egg sacs (29.7°C) and females carrying egg sacs (30.3°C). The upper level is similar to the upper temperature adopted by non-breeding spiders both in the field and the laboratory (Table 2). Again the prolonged plateau temperatures do not indicate a temperature cue for the change of behaviour unless the temperature change required was very small (< 0.1°C) or of short duration (< 5 s) and so beyond the resolution of the equipment; the change from one temperature preference to the other appears spontaneous. No records were made of the egg sac temperature of that individual but the possibility that the behavioural changes were mediated by changes in egg sac temperature must be examined. A simultaneous record of egg sac and spider temperatures is shown in Figure 14 and shows the 'normal behaviour' seen in most spiders recorded with egg sacs. The changes from head up to head down posture caused the alternation in maximum temperature between the spider and egg sac but it did not occur when the egg sac reached any set point temperature; however, the spider was able to maintain the egg sac at fairly constant temperatures for long periods. It is suggested that these data are not consistent with there being a wide refractory zone in the spiders, rather they support the idea of two set points required for specific physiological or ecological purposes.
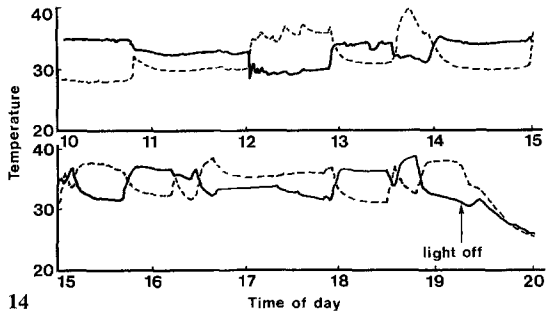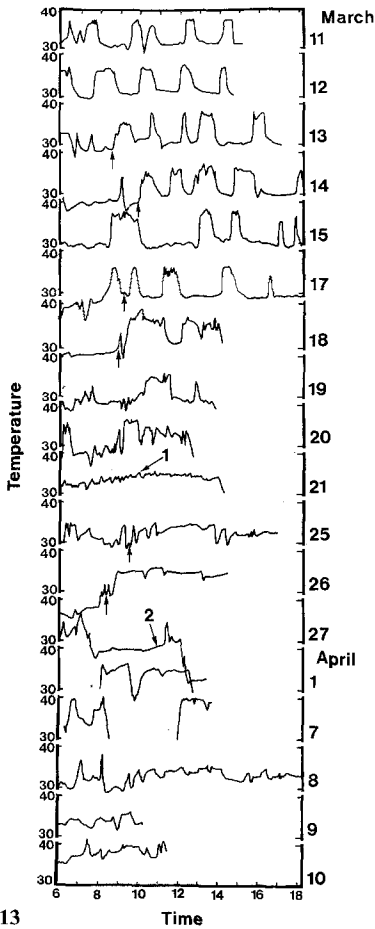
Fig. 13. Temperature (°C) trace during the thermoregulatory period on successive days of a female *Geolycosa godeffroyi* with egg sac. The first few days during which the trace is of a 'square wave' form are discussed in the text. Note the change of form at the time of the emergence of spiderlings and the effect of the provision of water to the spider *(arrows)*. The spiderlings started to emerge from the egg sac at *1* and most dispersed from the back of the female at *2*. Lack of trace is due to technical failure

Fig. 14. Simultaneous recording of cephalothorax *(continuous line)* and egg sac *(broken line)* temperatures (°C) from a female *G. godeffroyi*

Species Differences

The data obtained for six species of burrow dwelling lycosids belonging to four genera are summarized in Table 2. All the species examined have distinct thermoregulatory behaviour similar to that described for *G. godeffroyi* although the data obtained were based on few individuals. Intraspecific differences in temperature appear as great as interspecific differences but there are some inter-

Table 2. Mean temperatures of various species of burrow dwelling lycosids in Australia

Species	Number of indi- viduals	Total number of days recorded	Mean daily temperature (°C ± S.E.)	Range of individual means (°C)	Range of daily means (°C)
Geolycosa godeffroyi					
juveniles – lab.	6	39	32.3 ± 1.34	28.5 – 35.0	25.5 – 39.0
♂♂ m – lab.	4	24	29.1 ± 1.50	28.4 – 31.0	17.1 – 35.9
♀♀ with egg sac	9	27	30.3 ± 0.58	29.4 – 31.8	29.2 – 33.3
Egg sacs	9	12	29.7 ± 0.29	29.6 – 30.2	26.8 – 32.2
Field – Kowan[a]	13	19	35.7 ± 1.56 (34.7 ± 1.94)		
Field – Plateau[b]	10	14	35.3 ± 0.68		
Field – Clouds Ck.	4	16	32.5 ± 0.57	31.6 – 33.5	28.2 – 35.6
Lycosa sp. nov. 1					
♀ m	1	3	29.0 ± 0.65	28.1 – 30.2	
Lycosa sp. nov. 2					
♀	1	8	34.4 ± 0.38	32.7 – 35.8	
L. speciosa					
♀♀ m	2	12	34.4 ± 0.35	34.2 – 34.4	32.4 – 35.4
Schizocosa leuckartii					
♀♀ m lab.	3	9	32.8 ± 0.38	30.3 – 34.1	27.5 – 33.9
♀ m field	1	5	32.3 ± 1.04	31.8 – 35.4	
♂ p	1	5	34.4 ± 1.28	30.9 – 37.8	
Venatrix fuscus					
♀♀ m	2	16	33.4 ± 0.71	28.8 – 33.7	27.4 – 37.4
♀ with egg sac	1	6	27.5 ± 3.11	18.3 – 34.8	

m = mature; *p* = penultimate instar

[a] Calculated from mean temperature of crests and troughs for spider temperatures > 30° C (> 20° C) respectively, for clear days only

[b] Constant temperatures > 1 h

specific trends. Data for *Schizocosa leuckartii* and *G. godeffroyi* show that field and laboratory mean temperatures were of similar magnitude within species. These species also show differences consistent with known feeding behaviour; penultimate instar males and nonbreeding females and juveniles, all of which feed normally, had high preferred temperatures while mature males and breeding females which feed much less, if at all, had low preferred temperatures. Both *G. godeffroyi* and *Venatrix fuscus* had lower preferred temperatures when carrying egg sacs than at other times.

Discussion

The lycosids discussed here have advanced behavioural thermoregulation similar to that used by many reptiles, especially the much studied lizards. *G. godeffroyi* basked in the morning following emergence, changed orientation, shuttled, both increased and avoided contact with the substrate and adopted shade and sun

seeking as has been described for various lizards and arthropods (e.g. Hardy, 1962; Stower and Griffiths, 1966; Regal, 1967; Bradshaw and Main, 1968; Pianka, 1969; Heath, 1970; Heatwole, 1970; Cogger, 1974; Veron, 1974; Reichert and Tracy, 1975).

Lycosids appear unable to change shape for increased surface contact or to expose a greater area to radiant heat as do some lizards (Cogger, 1974) but they use body contact and stilting to change the rate of heat transfer (unpublished data). They are cryptically coloured (Turnbull, 1973) and cannot undergo physiological colour change as reported for many arthropods (see Veron, 1974). Evaporative cooling had a negligible effect on temperature (unpublished data) and would be several orders of magnitude smaller than the heat exchange with external heat sources (Ahearn and Hadley, 1969); it would be unlikely as a normal thermoregulatory mechanism in an arthopod subject to rapid dehydration (Humphreys, 1975c).

Workers on lizard thermoregulation frequently caution about the lack of comparability between various measurements used to define the thermal regimes and the difficulty of comparing these measurements between species or within species from different studies (Cogger, 1974; Huey and Slatkin, 1976); they also caution about the use of photothermal gradients due to the effects of feeding, apparatus, acclimation, physiological and hormonal states, the presence of conspecifics and time of day and warn that preferred body temperatures derived thus can serve only as a crude index of optimal body temperature in the field (Huey and Slatkin, 1976). It may be added here that any discussion of 'physiological safety margins' or 'temperature tolerance' has little value if its relationship to time of exposure is not determined and then related to the probability of these conditions arising for that species under field conditions. An attempt in this direction was made by Nørgaard (1956) in his study of the spider *Theridion saxatile*. However, the survival of a population in an area requires that the probability of adverse thermal conditions must be low enough to sustain adequate reproduction; physiological safety margins could explain the absence not the presence of species.

It may be argued that the use of thermocouple implantation may change the behaviour of the spiders and negate the usefulness of the data collected. Several factors support the method: data from egg sacs recorded biotelemetrically were similar to those obtained from implanted thermocouples and activity periods obtained from field actographs were similar to those deduced from thermocouple implantation; the spiders were able to perform complex behaviour (egg sac construction, oviposition and incubation) with thermocouples implanted and it was possible with this technique to obtain consistent treatment differences.

Continuous recording of body temperature used here showed a strategy not previously reported in the behavioural thermoregulation of ectotherms, that employed by those individuals whose temperature records were of the square wave form, alternating between two temperatures with long periods of constant temperature between the rapid temperature changes. While such behaviour would not have been recorded in the continuous temperature traces from *Varanus varius* (Stebbins and Barwick, 1968) due to their large thermal capacity (weight 4200 g), the common use of spot temperature measurements

in smaller lizards could result in similar behaviour being overlooked. Bimodal temperature distribution has been found in the iguanid *Tropidurus albermarlensis* (Stebbins et al., 1967).

The preferred temperature of these Australian spiders contrasts markedly with the implications of a study on energy flow through a forest floor spider community in Tennessee. This indicated that the spider populations (which included lycosids) went into negative production when the temperature exceeded 20.5°C for small spiders (< 1 mg dry weight) or about 18°C for large spiders (> 10 mg dry weight) (Moulder and Reichle, 1972). The mean daily temperature of *G. godeffroyi* was in excess of 25°C during January and February and was the time of most rapid production (Humphreys, 1973, 1976). Under suitable laboratory conditions the spiders selected temperatures in excess of 30°C continuously.

There are no direct measurements of spider temperatures with which to compare this study but various indirect methods have been used to examine the thermal biology of spiders. The most significant of these was conducted on an Agelenid, *Agelenopsis aperta,* using thermal balance equations and showed that 50% of the spiders were active at predicted body temperatures between 21 and 35°C with a preferred maximum of 31°C (Reichert and Tracy, 1975). *Nephilia claviceps* (L.) pointed its abdomen to the sun to reduce thermal input at temperature greater than about 35°C and exuded water to produce evaporative cooling (Krakauer, 1972). The array of postural changes in this species, presumed to be associated with thermoregulation, allowed the spiders to orientate so as to reduce insolation whatever the position of the sun or orientation of the web (Robinson and Robinson, 1974).

The thermal tolerance of *Theridion saxatile* eggs was lower than the spiders and the spiders removed egg sacs from their nests into the sun to keep them cool as their nests, located on south facing banks in Denmark, heated excessively in the sun. The web to where they were moved had a mean temperature of 31.3°C compared with nest temperatures of 42.3°C.

In thermal gradient apparatus lycosids show a wide range of preferred temperatures between species and usually intraspecific differences between breeding females and others (Table 3). Field studies also suggest thermoregulatory behaviour. *Lycosa lugubris* (Walckenaer) exhibited seasonal changes in habitat preference and when females produced egg sacs they moved from shaded to unshaded areas where they sunned their egg sacs; the smaller instars also inhabited these open areas until the autumn (Edgar, 1971a). *Pardosa pullata* (Clerck) and *P. nigriceps* (Thorell) underwent a vertical seasonal migration with juveniles and females with egg sacs occupying exposed upper layers of vegetation; both species sun their egg sacs (Vlijm and Kessler-Geschiere, 1967). If these behavioural strategies are connected with thermoregulation they would permit rapid egg incubation and may reduce egg sac parasitism (which may be high in lycosids, Edgar, 1971b) and permit a rapid development of the juveniles which, as suggested by Edgar (1972) may reduce overwintering mortality.

Agelenopsis aperta selects web sites which are relatively mild as excessive temperature reduces the time available for prey handling on the sheet of the web. This species captures small prey directly but those prey which require

Table 3. Information on possible thermal preferences of spiders from diverse methods

Species	Con-ditions	Preferred temperature (°C)	Authority
Lycosids			
Pardosa nigriceps	1	21	Almquist (1970)
P. chelata (O.F. Müller)	1	24	Hallander (1970)
P. pullata	1	25–27	Hallander (1970)
Pirata piraticus	1	18–24	Nørgaard (1951)
Pirata piraticus with egg sac	1	26–32	Nørgaard (1951)
Lycosa pullata	1	28–36	Nørgaard (1951)
Lycosa pullata with egg sac	1	No change	Nørgaard (1951)
L. amentata	8	egg sac > female	Vlijm et al. (1963)
Geolycosa godeffroyi	2	32–38	Humphreys (1974)
Geolycosa godeffroyi with egg sac	2	28–32	Humphreys (1974)
Other spiders			
Agelenopsis aperta	3	30.9 ± 1.9[4]	Riechert and Tracy (1975)
Theridion saxatile	5	35.7 and 20.6[6]	Nørgaard (1956)
Forest floor spider population	7	18–20.5	Moulder and Reichle (1972)
Frontinella communis	9	31	Pointing (1965)
Nephilia claviceps	10	36	Krakauer (1972)

1 = laboratory thermal gradient; 2 = field measure of actual spider or egg sac temperatures; 3 = energy exchange model; 4 = moved from sun to shade; 5 = field measurement of microenvironment; 6 = eggs moved out of and into nest respectively; 7 = went into negative energy balance above indicated temperatures; 8 = behavioural observations; 9 = black bulb temperature at postural change; 10 = gave postural changes and evaporative thermoregulation

wrapping in silk either to subdue them or prevent injury to the spider, can not be handled under hot conditions as the time required is sufficient to subject the spiders to thermal stress (Reichert and Tracy, 1975). Lycosids do not wrap prey but rapidly subdue them by force so that the thermal restraints on hunting depend on whether they are warm enough to move efficiently and can maintain a position suitable for hunting, either at the mouth of the burrow or on vegetation adjacent to the burrow. Behavioural thermoregulation may put the spiders at a locomotory advantage over their non thermoregulating prey and increase their chance of prey capture.

This study has shown that the preferred body temperature of some lycosids both in the field and laboratory, was related to species, breeding state, sex, availability of food, water and radiant heat and that the methods of achieving these temperatures are comparable with those used by other ectothermic animals, especially lizards. Whether these preferred temperatures were related to optimal temperatures is unknown; they were lower than the temperature of a maximum metabolic rate (Humphreys, 1977b) and permitted the spiders to obtain a size at maturity forty times greater than that of some European lycosids with a similar life cycle duration (Humphreys, 1976). It is probable that lycosids of

a size and life cycle duration similar to *G. godeffroyi,* for example the North American *Lycosa carolinensis* (Walckenaer), also thermoregulate.

The two set point temperatures for *G. godeffroyi* are interesting because it has been suggested that organisms may have different thermal optima for different physiological processes; in lizards (Bustard, 1967) this is untenable (Huey and Slatkin, 1976) and in plankton (McLaren, 1963; Kerfoot, 1970) the concept is not necessary (McLaren; pers. comm.) and not supported empirically (Swift, 1976). In toads short daily access to a photothermal gradient enhanced growth more than expected from constant temperature relationships (Lillywhite et al., 1973). Herpetologists now consider that mean body temperature is a compromise between physiology and ecological reality (Huey and Slatkin, 1976). In most groups of ectothermic vertebrates advantage may be gained from high preferred temperatures in digestion rate, conversion efficiency and growth but under conditions of food shortage a lower preferred temperature may reduce maintenance costs (Licht et al., 1969; Skoczylas, 1970; Brett, 1971; Lillywhite et al., 1973).

In *G. godeffroyi* the growth rate, utilization efficiency (due to spiders having external digestion this is closely equivalent to assimilation efficiency in other animals, Humphreys, 1977a) and feeding rate increased with temperature but assimilation and production efficiencies were temperature independent within the range tested (Humphreys, 1977a). Cycling temperature *per se* increased the respiration rate (Humphreys, 1975b), the number of feeds taken (Humphreys, 1977a) and enhanced growth rate more than expected (unpublished data). Under conditions of food shortage the metabolic rate dropped markedly (Humphreys, 1977b) and, as shown here, feeding was associated with a change in temperature preference. While temperature influenced a number of the gross physiological measurements mentioned above the temperature measurements indicate two preferred temperatures and are supported by the constancy of the preferred temperature during prolonged starvation (e.g. 26 days during egg sac incubation, Fig. 12).

Huey and slatkin (1976) put forward the first synthetic theory of lizard thermoregulation but their theory is applicable to any ectothermic species using similar behavioural mechanisms to achieve a degree of thermal independence from its environment. They suggest that few conceptual advances have been made because the subject has been dominated by static concepts such as: the evolution of optimal body temperature is conservative within taxa, that most lizards thermoregulate carefully, that thermoregulation is normally beneficial. They cite recent work showing that 'optimal' body temperatures are in fact quite diverse and evolve rapidly in some genera, that some lizards are passive to thermal conditions, that careful thermoregulation may be maladaptive and conclude that the behaviour of lizards cannot be understood solely from physiological considerations; the latter were reviewed by Dawson (1975).

Too few comparative data are available for spiders to discuss in the terms of Huey and Slatkin. However different species in the lycosidae cover the full range of activity periods and habitat types used by lizards and in addition individuals, especially breeding females, may change both their habitat and thermal preferences through the year. Huey and Slatkin distinguish between

high and low cost habitats in relation to thermoregulation but hardly mention
seasonal changes in habitat cost; Heatwole (1970) showed short term weather
related changes in the relative temperatures of *Amphibolurus inermis* and its
environment similar to those shown for *G. godeffroyi* on a seasonal basis (Fig. 7).
Differential changes in the relative cost of thermoregulation are possible on
a seasonal basis depending on the change in density of the associated flora;
seasonal changes within habitats may be greater than the differences between
habitats. Huey and Slatkin (*op.cit.*) considered that a change in net energy
gain could shift optimal strategy from one of complete thermal passivity to
one of complete thermoregulation. While food changed the preferred tempera-
ture in *G. godeffroyi*, it did not result in complete passivity.

The relationship between spider communities and factors in the environment,
particularly microclimate and phytosociology, remains controversial. While it
has often been claimed that microclimate is important (see Turnbull, 1973)
much of the evidence is correlative and few experimental studies have been
conducted. These have shown the importance of thermal environment in the
field (Nørgaard, 1956; Reichert and Tracy, 1975) for single species. Huhta
(1971) attributed changes in forest floor spider communities in Finland after
clear cutting mainly to changes in the physical environment. Nevertheless the
changes were long term (over 7 years) while the changes in the physical environ-
ment were rapid. Community analyses often concentrate on the more abundant
species and should some be relatively independent of a measured microclimatic
variable (eg by behavioural thermoregulation) then attempts to relate community
composition to physical factors may be frustrated; the interception of sunlight
or continuity of the canopy may be more important than plant species composi-
tion *per se*.

The role of behavioural thermoregulation has probably been underestimated
in arthropod populations; it need not be of the overt type described here for
lycosids, as suitable choice of substrate such as ground or leaf surfaces (Burrage,
1971), even in temperate and arctic regions, may produce body temperatures
considerably in excess of air temperatures. It has been shown that the life
cycle of the heteropteran *Pyrrhocoris apterus* L. may be synchronized by the
larvae selecting sites which do not exceed 24°C (Honěk and Šrámková, 1976)
but the significance of thermal microhabitat selection has been demonstrated
for few species of arthropod.

Huey and Slatkin (1976, their Fig. 14) used published data to relate the
mean preferred temperature of lizards directly with mean environmental temper-
ature and inversely with altitude. If the lizards they considered had a constant
refractory zone then these relationships would be expected *a priori* as the animals
would cool faster in cold environments after reaching the upper temperature
of the refractory zone and the mean temperature would shift to the lower
end of the refractory zone. These data do not therefore support a shift in
optimal temperature with differing thermal environments; only a comparison
of individuals from different areas under identical thermal conditions could
demonstrate such a shift.

References

Ahearn, G.A., Hadley, N.F.: The effects of temperature and humidity on water loss in two desert tenibrionid beetles, *Eleodes armata* and *Cryptoglossa verrucosa*. Comp. Biochem. Physiol. **30**, 730–749 (1969)

Almquist, S.: Thermal tolerances and preferences of some duneliving spiders. Oikos **21**, 230–236 (1970)

Barnett, J.L., How, R.A., Humphreys, W.F.: The mammals of Clouds Creek, north-eastern New South Wales, and their distribution in pine and native forest. Aust. Zoologist **19**, 23–34 (1976)

Bradshaw, S.D., Main, A.R.: Behavioural attitudes and regulation of temperature in *Amphibolurus* lizards. J. Zool., Lond. **154**, 193–221 (1968)

Brett, J.R.: Energetic responses of salmon to temperature. A study of some thermal relations in the physiology and freshwater ecology of Sockeye Salmon (*Oncorhynchus nerka*). Am. Zool. **11**, 99–113 (1971)

Burrage, S.W.: The microclimate at the leaf surface. In: Ecology of leaf surface micro-organisms (C.H. Dickinson, ed.). New York-London: Academic Press 1971

Bursell, E.: Environmental aspects: temperature. In: The physiology of insecta, Vol. 1 (M. Rockstein, ed.). New York: Academic Press 1964

Bustard, H.R.: Activity cycle and thermoregulation in the Australian gecko *Gehyra variegata*. Copeia **1967**, 753–758 (1967)

Cloudsley-Thompson, J.L.: Microclimates and the distribution of terrestrial arthropods. A. Rev. Ent. **7**, 199–222 (1962)

Cogger, H.G.: Thermal relations of the Mallee Dragon *Amphibolurus fordi* (Lacertilia: Agamidae). Aust. J. Zool. **22**, 319–339 (1974)

Dawson, W.R.: On the physiological significance of the preferred body temperatures of reptiles, pp. 443–473. In: Perspectives in biophysical ecology. (D.M. Gates, R.B. Schmert, eds.). Berlin-Heidelberg-New York: Springer 1975

DeVoe, R.D., Small, R.J.W., Zvargulis, J.E.: Spectral sensitivities of wolf spider eyes. J. Gen. Physiol. **54**, 1–32 (1969)

Digby, P.S.B.: Factors affecting the temperature excess of insects in sunshine. J. Exptl. Biol. **32**, 279–298 (1955)

Edgar, W.D.: The life cycle, abundance and seasonal movement of the wolf spider, *Lycosa (Pardosa) lugubris,* in central Scotland. J. Anim. Ecol. **40**, 303–322 (1971a)

Edgar, W.D.: Aspects of the ecology and energetics of the egg sac parasites of the wolf spider *Pardosa lugubris* (Walckenaer). Oecologia (Berl.) **7**, 155–163 (1971b)

Edgar, W.D.: The life-cycle of the wolf spider *Pardosa lugubris* in Holland. J. Zool. (Lond.) **168**, 1–7 (1972)

Hackman, W.: Studies on the ecology of the wolf spider *Trochosa ruricola* Deg. Cemmentat. Biol. **16**, 1–34 (1957)

Hadley, N.F.: Micrometeorology and energy exchange in two desert arthropods. Ecology **51**, 434–444 (1970)

Hagstrum, D.W.: Physiology of food utilization by the spider *Tarentula kochi* (Araneae: Lycosidae). Ann. Ent. Soc. Am. **63**, 1305–1308 (1970)

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

Hardy, D.F.: Ecology and behaviour of the six-lined racerunner, *Cnemidophorus sexlineatus.* Univ. Kansas Sci. Bull. **43**, 3–73 (1962)

Heath, J.E.: Behavioural thermoregulation of body temperature in poikilotherms. Physiologist **13**, 399–409 (1970)

Heatwole, H.: Thermal ecology of the Desert Dragon *Amphibolurus inermis*. Ecol. Monogr. **40**, 425–457 (1970)

Holm, E., Edney, E.B.: Daily activity of Namib desert arthropods in relation to climate. Ecology **54**, 45–56 (1973)

Honěk, A., Šrámková, K.: Behavioural regulation of development cycle in *Pyrrhocoris apterus* L. (Heteroptera: Pyrrhocoridae). Oecologia (Berl.) **24**, 277–281 (1976)

How, R.A.: The ecology and management of *Trichosurus* species (Marsupialia) in New South Wales. Ph.D. thesis, University of New England, Armidale (1972)

Huey, R.B., Slatkin, M.: Cost and benefit of lizard thermoregulation. Quart. Rev. Biol. **51**, 363–384 (1976)

Huhta, V.: Succession in the spider communities of the forest floor after clear-cutting and prescribed burning. Ann. Zool. Fenn. **8**, 483–542 (1971)

Humphreys, W.F.: The environment, biology and energetics of the wolf spider *Lycosa godeffroyi* (Koch, 1865). Doctoral dissertation, Australian National University, Canberra, 353 pp. (1973)

Humphreys, W.F.: Behavioural thermoregulation in a wolf spider. Nature (Lond.) **251**, 502–503 (1974)

Humphreys, W.F.: The food consumption of a wolf spider, *Geolycosa godeffroyi* (Araneae: Lycosidae), in the Australian Capital Territory. Oecologia (Berl.) **18**, 343–358 (1975a)

Humphreys, W.F.: The respiration of *Geolycosa godeffroyi* (Araneae: Lycosidae) under conditions of constant and cycling temperature. Physiol. Zool. **48**, 269–281 (1975b)

Humphreys, W.F.: 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 (1975c)

Humphreys, W.F.: The population dynamics of an Australian wolf spider, *Geolycosa godeffroyi* (L. Koch, 1865) (Araneae: Lycosidae). J. Anim. Ecol. **45**, 59–80 (1976)

Humphreys, W.F.: Variables influencing laboratory energy budgets of *Geolycosa godeffroyi* (Araneae). Oikos **28**, 225–233 (1977a)

Humphreys, W.F.: Respiration studies on *Geolycosa godeffroyi* (Araneae: Lycosidae) and their relationship to field estimates of metabolic heat loss. Comp. Biochem. Physiol. **57A**, 255–263 (1977b)

Kerfoot, W.B.: Bioenergetics of vertical migration. Am. Nat. **104**, 529–546 (1970)

Krakauer, T.: Thermal responses of the orb-weaving spider *Nephilia claviceps* (Araneae: Argiopidae). Am. Midl. Nat. **88**, 245–250 (1972)

Licht, P., Hoyer, H.E., Van Oordt, P.G.W.J.: Influence of photoperiod and temperature on testicular recrudescence and body growth in the lizards, *Lacerta sicula* and *Lacerta muralis*. J. Zool. (Lond.) **157**, 469–501 (1969)

Lillywhite, H.B., Licht, P., Chelgren, P.: The role of behavioural thermoregulation in the growth energetics of the toad *Bufo boreas*. Ecology **54**, 375–383 (1973)

List, R.J.: Smithsonian meteorological tables. Smithson. Misc. Collns. **114**, 1–527 (1968)

Macfadyen, A.: Methods of investigation of productivity of terrestrial ecosystems. In: Secondary productivity of terrestrial ecosystems (Principles and methods) (K. Petrusewicz, ed.), pp. 383–412. Warsawa-Kraków: Polish Academy of Sciences Institute of Ecology and International Biological Programme P.T. 1967

McKay, R.J.: The wolf spiders of Australia (Araneae: Lycosidae): 1. The bicolor group. Mem. Qd. Mus. **16**, 375–398 (1973)

McLaren, I.A.: Effects of temperature on growth of zooplankton and the adaptive value of vertical migration. J. Fish. Res. Board Can. **20**, 685–727 (1963)

Miyashita, K.: Effects of locomotory activity, temperature and hunger on the respiratory rate of *Lycosa T-insignita* Boes. et Str. (Araneae: Lycosidae). Appl. Ent. Zool. **4**, 105–113 (1969)

Moeur, J.E., Eriksen, C.H.: Metabolic responses to temperature of a desert spider, *Lycosa (Pardosa) carolinensis* (Lycosidae). Physiol. Zool. **45**, 290–301 (1972)

Moulder, B.C., Reichle, D.E.: Significance of spider predation in the energy dynamics of forest-floor arthropod communities. Ecol. Monogr. **42**, 473–498 (1972)

Nakamura, K.: The ingestion in wolf spiders. II. The expression of degree of hunger and amount of ingestion in relation to spider's hunger. Res. Popul. Ecol. **14**, 82–96 (1972)

Nørgaard, E.: Økologiske Undersogelser over nogle danske Jagteddekopper. Flora Fauna, Aarhus, **51**, 1–37 (1945)

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

Nørgaard, E.: Environment and behaviour of *Theridion saxatile*. Oikos **7**, 159–192 (1956)

Parry, D.A.: Factors determining the temperature of terrestrial insects in sunlight. J. Exptl. Biol. **28**, 445–462 (1951)

Parry, D.A.: On the drinking of soil capillary water by spiders. J. Exptl. Biol. **31**, 218–227 (1954)

Pianka, E.R.: Sympatry of desert lizards (*Ctenotus*) in Western Australia. Ecology **50**, 1012–1030 (1969)

Pointing, P.J.: Some factors influencing the orientation of the spider *Frontinella communis* (Hentz.), in its web (Araneae: Linyphiidae). Can. Entomol. **97**, 69–78 (1965)

Regal, P.J.: Voluntary hypothermia in reptiles. Science (Wash.) **155**, 1551–1553 (1967)

Reichert, S.E., Tracy, C.R.: Thermal balance and prey availability: bases for a model relating web site characteristics to spider reproductive success. Ecology **56**, 265–284 (1975)

Robinson, H.M., Robinson, B.C.: Adaptive complexity: the thermoregulatory postures of the golden-web spider, *Nephilia claviceps,* at low latitudes. Am. Midl. Nat. **92**, 386–396 (1974)

Seymour, R.S., Vinegar, A.: Thermal relations, water loss and oxygen consumption of a North American Tarantula. Comp. Biochem. Physiol. **44A**, 83–96 (1973)

Sinclair, J.G.: Temperature of the soil and air in a desert. Mon. Weath. Rev. U.S. Dep. Agric. **50**, 142–144 (1922)

Skoczylas, R.: Influence of temperature in gastric digestion in the grass snake, *Natrix natrix* L. Comp. Biochem. Physiol. **33**, 793–804 (1970)

Stebbins, R.C., Barwick, R.E.: Radiotelemetric study of thermoregulation in a lace monitor. Copeia **3**, 541–547 (1968)

Stebbins, R.C., Lowenstein, J.M., Cohen, N.W.: A field study of the Lava Lizard (*Tropidurus albemarlensis*) in the Galapagos Islands. Ecology **48**, 839–851 (1967)

Stower, W.J., Griffiths, J.F.: The body temperature of the desert locust (*Schistocerca gregaria*). Ent. Exp. & Appl. **9**, 127–178 (1966)

Swift, M.C.: Energetics of vertical migration in *Chaoborus trivittatus* larvae. Ecology **57**, 900–914 (1976)

Turnbull, A.L.: Ecology of the true spiders (Araneomorphae). A. Rev. Ent. **18**, 305–348 (1973)

Veron, J.E.N.: The role of physiological colour change in the thermoregulation of *Austrolestes annulosus* (Selys) (Odonata). Austr. J. Zool. **22**, 457–469 (1974)

Vlijm, L., Kessler, A., Richter, C.J.J.: The life history of *Pardosa amentata* (Cl.) (Araneae: Lycosidae). Ent. Ber. (Amst.) **23**, 75–80 (1963)

Vlijm, L., Kessler-Geschiere, A.M.: The phenology and habitat of *Pardosa monticola, P. nigriceps* and *P. pullata* (Araneae: Lycosidae). J. Anim. Ecol. **36**, 31–56 (1967)

Wellington, W.G.: Effects of radiation on the temperatures of insectan habitats. Scient. Agric. **30**, 209–233 (1950)

Whitcomb, W.H., Eason, R.: A technique for determining the period of egg incubation in wolf spiders. Turtox News **42**, 301–302 (1964)

Williams, C.B.: Some bioclimatic observations in the Egyptian Desert. In: Biology of deserts (J.L. Cloudsley-Thompson, ed.). London: Institute of Biology 1954

Woodward, R.H., Goldsmith, P.L.: Cumulative sum techniques. Mathematical and statistical techniques for industry Monograph, No. 3. London: Oliver & Boyd 1964