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Thermal behaviour of a small spider (Araneae: Araneidae: Araneinae) on horizontal webs in semi-arid Western Australia

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Summary. The solar orientation response of a small spider (gen. nov.: Araneae: Araneidae: Araneinae) is examined at a semi-arid location in tropical Western Australia. The spiders rest beneath horizontal dome-shaped webs close to the ground surface on spinifex (*Triodia* sp.). The spiders are small (c. 5 mm long) and robust, being only twice as long as wide. Spider orientation, elevation, wind velocity, radiation and wet and dry bulb temperatures together with spider and egg-sac temperatures were measured throughout the day. The spiders orientated their long axis to the solar azimuth through much of the day and postured to the solar elevation; in so doing they tracked the apparent movement of the sun throughout the day with considerable precision, far exceeding that of other spiders studied. Stepwise regression indicated that the solar position was the most important environmental factor associated with the posturing and orientation. The variance in the orientation of the population was associated with a suite of environmental variables related to wind velocity and temperature. Spider (abdominal) temperature had a curvilinear relationship with ambient temperature, with a plateau at c. 35° C, whereas egg-sac temperature had a strictly linear relationship with ambient temperature. Stepwise regression indicates that both the spider and egg-sac temperatures are related mainly to net radiation and ambient temperature. The spiders can alter the incident radiation to which they are exposed by c. 2.2 times which represent the limits of the exposed silhouette area between full dorsal sunlight and the posterior (or anterior) aspect. Under hot conditions the spiders posture and orientate such that the long axis of the body is orientated abdomen towards the sun.

Introduction

Thermoregulation in spiders has largely been deduced from their behaviour (Humphreys 1987b) and there are

few direct measurements of spiders temperature in the field (Humphreys 1974, 1978, 1987a) and none on web inhabiting species, although sophisticated thermal modelling has been conducted on the sheet web spider (*Agelenopsis aperta* (Riechert and Tracy 1975)). Thermal behaviour has been examined in two categories of spiders; those which shuttle between sunlight and the more equitable thermal environment of a retreat (Fabre 1912; Humphreys 1974, 1975, 1978; Riechert 1976; Riechert and Tracy 1975), and those which remain during the day at the hub of a vertical web exposed to sunlight (Biere and Uetz 1981; Blanke 1972; Krakauer 1972; Robinson and Robinson 1974, 1978). The latter are usually well removed from the steep thermal gradients that occur close to the ground surface (Humphreys 1978), while the former escape to their retreats, or burrows (Humphreys 1983, 1986, 1987a, b; Riechert and Tracy 1975) where there is a thermal gradient in which to move. Suter (1981) examined posturing and reorientation in the 6 mg spider *Frontinella communis* (Linyphiidae); in the laboratory, but under conditions of very low insolation (0.98 W m⁻²), he showed that changes in the orientation of the spider caused the body temperature to vary by up to 0.5° C.

In this paper I examine orientation and posturing by a small spider (gen. nov., Araneidae: Araneinae – I will refer to it as ‘the new species’) to the sun and their relationship to spider temperature. The spider is of similar size, web and habits to *F. communis* but occurs in a semiarid tropical area with solar radiation greater by three orders of magnitude. Unlike *F. communis* (Suter 1981), the orientation of the new species is almost always prosoma away from the sun, a position that may have physiological implications (Humphreys 1987b). It builds webs on low spinifex tussocks (*Triodia* sp.: Poaceae) which in the study site forms almost the entire sparse ground cover between an occasional shrub overstory. The spinifex is low and, although the webs are constructed well within the periphery of the spiny leaves, they receive no shade. The webs are c. 30 cm above the

ground and in consequence the spiders inhabit a region of steep gradients in both wind velocity and temperature.

Air movement is one of the main factors determining the thermal balance of a body subjected to a radiant heat load. The temperature excess (equilibrium body temperature above that of the air) of a body subject to a radiant heat load is also directly proportional to the mass of body, other conditions being equal; very small bodies equilibrate rapidly with little temperature excess. Although such a small body has minimal thermal advantage in posturing, the small thermal advantage may be crucial, because, amongst other factors, it is more prone to water loss, having a high surface area to volume ratio.

Methods

Natural history. Little is known about the natural history of the new species. In my study site they are common from June through September when males and females are seen on webs and a series of egg sacs are produced. Adult female spiders are c. 5 mm long and weigh c. 6.8 mg. The abdomen is round seen from above and appears ovoid from the posterior and lateral aspects. The spiders hang beneath the horizontal surface of the web (which has a knock-down web above), and their resting position is horizontal (as in *F. communis*: see Suter 1981: Fig. 1). Preliminary observations showed that on hot days they seem to orientate their long axis towards the sun (the solar azimuth) and sometimes strongly posture away from the web elevating their long axis, abdomen first, towards the sun. Such postures have frequently been reported in orb web spiders which normally hang prosoma down at the hub of their vertical webs during the day (Krakauer 1972; Robinson and Robinson 1974, 1978; Suter 1981), although the converse orientation has been reported (Pointing 1965). In this study 70% of the spiders had egg sacs in their webs, one was mating on the web, and several caught prey.

Field area. The work was conducted on 7–8 September 1989 at Learmonth on the North West Cape peninsula of Western Australia (22°15'S; 114°03'E), one of the most cloudless regions in the world. Twenty webs of mature females of the new species (Araneidae) were located, tagged and numbered voucher specimens of the spiders collected (Western Australian Museum 90/645 and 90/646). The area is semi-arid and lies in that part of Australia with the least predictable rainfall; both the constancy and contingency (sensu Colwell 1974) of the rainfall are low (see full discussion in Humphreys et al. 1989). The harsh climate of the region is ameliorated to some extent by the proximity of the site to the coast. Nonetheless the mean monthly maximum temperature at the site is >30°C for eight months of the year, of which four months exceed 35°C.

Techniques. At hourly intervals throughout the day I determined the compass orientation of the spider in the direction of the prosoma (using a prismatic compass) and the elevation of the body from the horizontal (using an inclinometer: – both by Suunto, Helsinki, Finland). The same instruments were used to determine the solar azimuth and altitude and the consistency of the data checked against Beer (1990). The spiders are small and only twice as long as wide so that accurate readings of the spider's orientation is difficult. Hence both compass direction and elevation were read to the nearest 5° of arc. The variance was also increased because the solar position was measured only in the middle of a series of readings of spider orientation, a process that took about 15 min. All readings were made of the direction to which the prosoma pointed and no correction was made for magnetic variation (c. 1.7° W). As some spiders were engaged in other activities at the

time of reading or were accidentally disturbed, not all data for each individual was recorded each hour (data were recorded for a mean of 19.6 spiders each hour).

Wet and dry bulb humidities were recorded one metre above the ground using a whirling hygrometer (Brannan, England), as it was impractical to take reading lower in the spinifex. Wind velocity was recorded at a height of 0.3 m using a hot wire anemometer (model TA2, Airflow Developments, High Wycombe, England), as was solar radiation using a net radiometer (Model 1612, Lambrecht, Göttingen, FRG) connected to a process monitor (Mann No. PM350) and process transmitter (Mann No. FTX/DMV). Spider temperatures were read using a close focussing infrared thermometer (Minolta/Land Cyclops 33CF; Sheffield, England) with a minimum target size of 2 mm at 17 cm working distance and reading the spectral band 7–30 μ. This instrument is working close to its limits with a spider of the size of the new species. The latter two instruments were calibrated against standards set to international standards.

Statistical methods. Least squares regression analysis was conducted using standard algorithms (Sokal and Rohlf 1981) and stepwise regressions following Draper and Smith (1981) and Montgomery and Peck (1982) as implemented in StatView 512+ (Abacus Concepts, CA, USA). Angular statistics were calculated using programs written following the algorithms of Batschelet (1965) and Mardia (1972). Two types of test are conducted. Firstly to determine whether the distribution of directions is uniform or whether it is unimodal with a preferred direction (the Rayleigh test). Secondly to determine whether the preferred direction is different from the hypothesised direction (Stephan's test), in this case the solar azimuth.

Definitions. Repose position: spiders occupy the underside of the web with their saggital plane horizontal and the dorsal surface down; the anterior-posterior axis of the spider is parallel to the plane of the web.

Orientation: the angle of the saggital plane of the spider with respect to the solar azimuth.

Posturing: change in the angle between the plane of the web and the anterior-posterior axis of the spider.

Fabian position: a spider which is aligned with its longitudinal axis parallel to the direction of incident sunlight with the prosoma facing away from the sun. This position may be achieved by reorientation and/or posturing. When the incident sunlight is parallel to the plane of the web then the Fabian position may be the same as the Repose position. The Fabian position is an allusion to the political philosophy of successive gradual change; here it describes the maintenance of the putative thermoregulatory position by gradual alteration of the spiders orientation and posture during the day while avoiding the presumption of thermoregulation. Continued adoption of the Fabian position results in the long axis of the spider tracking the sun during the day.

Results

Spider orientation

Compass direction. The data at each reading were analysed using angular statistics to determine whether they had an orientation different from random (z of the Rayleigh test, Table 1), and whether the orientation of the spider was different from that of the solar azimuth (θ_{0-a} ; Table 1). Before 10:30 h the spiders were either not orientated (z) or their orientation differed from that of the solar azimuth (θ_{0-a} ; the 23:30 h reading cannot

Table 1. Significance of the compass orientation of the new species during one day. The tests of significance are Rayleigh tests for angular data (Batschelet 1965). Note that the direction to which the prosoma pointed was measured; hence the direction from which the prosoma pointed is given in the final column for comparison with the solar azimuth as the spiders posture prosoma-from-sun. The probability for significant difference between the spider's orientation and the solar azimuth are shown (θ_{o-x}). z approximates N if all individuals have the same orientation

Time of day	Mean direction prosoma°	Angular sd	Skewness	N	Rayleigh test z	P	Solar azimuth° θ_o	Prosoma from° θ_{o-x}	
								α	P
0630	10	74.3	0.03	18	0.453	NS	–	–	–
0730	304	53.2	–0.11	17	5.498	<0.01	78	124	<0.01
0830	330	67.7	–0.34	15	1.358	NS	73	–	–
0930	283	30.8	–0.31	18	13.164	<0.01	63	103	<0.05
1030	233	28.5	0.62	18	13.815	<0.01	52	53	NS
1130	212	30.3	0.71	19	14.035	<0.01	30	32	NS
1230	182	11.2	0.06	16	15.391	<0.01	356	362	NS
1330	157	45.3	–0.55	19	8.956	<0.01	335	337	NS
1430	131	10.6	–0.92	19	18.347	<0.01	310	311	NS
1530	120	17.6	–0.73	20	18.148	<0.01	295	300	NS
1630	104	27.5	–0.29	19	14.856	<0.01	287	284	NS
1730	85	54.6	0.02	20	5.944	<0.01	280	265	NS
1830	74	57.2	0.13	19	4.771	<0.01	270	254	NS
2330	67	49.7	0.05	17	6.598	<0.01	–	247	–

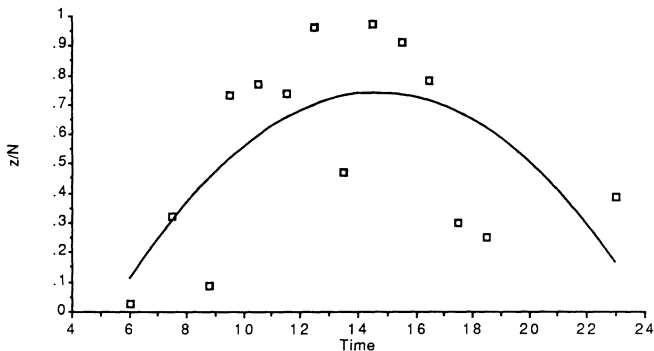


Fig. 1. Graph of the change in the magnitude of z/N of the Rayleigh test during the day; if all individuals are orientated in the same direction then z/N is c. 1.0. The data are fitted by a polynomial regression of power two ($F_{s2,11}=4.228$, $P=0.043$; $r^2=0.435$. X , $P=0.014$; X^2 , $P=0.016$)

be tested this way). In addition the value of z , a measure of the consistency of the orientation, generally increased towards the hottest part of the day and decreased thereafter (Fig. 1). Hence the spiders were not orientated with respect to the sun in the early morning but became highly orientated thereafter (if all individuals have the same orientation then z approximates N ; see Table 1).

The resolution of the tracking was examined by plotting the orientation of the spiders against the solar azimuth and elevation. There is a significant regression of spider direction on solar azimuth ($F_{s1,252}=86.50$, $P<0.001$), but there is a wide scatter of points in the early morning and late afternoon (Fig. 2a). I excluded this 'noise' in the data by examining only those data for the period when orientation was strongly directed ($z/N > 0.47$), namely from 0930 h through 1630 h (Table 1). The resulting regression is linear with narrow confidence intervals (Fig. 2b; $F_{s1,146}=320.7$, $P<0.001$) with a

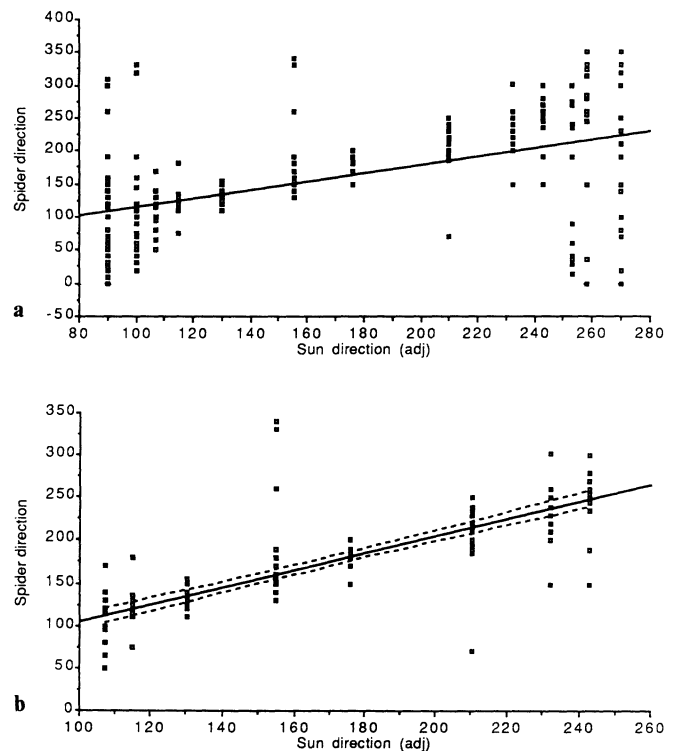


Fig. 2a, b. Graphs of solar azimuth against the compass orientation of the new species. **a** all the data. **b** data from 0930 h to 1530 h inclusive where the 9.5% confidence intervals of the true mean Y are shown. Points in any column denote individuals ($n=15$ to 20; Table 1) and the same individuals were measured at different solar azimuths. Note that many of the outlying points are close to 180° on the y -axis from the majority of the data; these result from individuals adopting a prosoma-towards-sun rather than the normal prosoma-from-sun orientation (see Humphreys 1986). To enable plotting the solar azimuth data have been adjusted by $+180^\circ$ if originally less than or equal to 180° and by -180° if originally greater than 180° . Hence, in the fig. the morning is to the right and the evening to the left of the x -axis

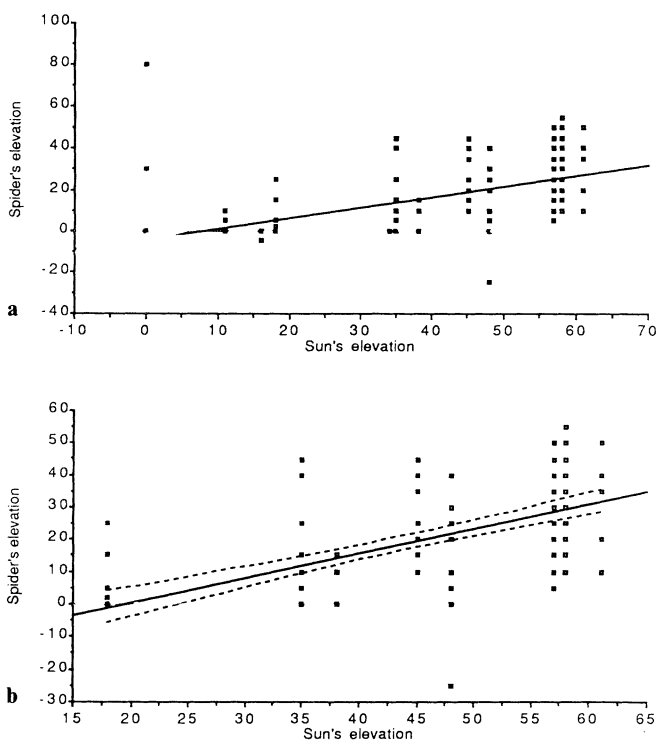


Fig. 3a, b. Graphs of solar elevation against the elevation of the new species. **a** all the data. **b** data from 0930 h to 1530 h inclusive; the upper line is the isotherm. The 95% confidence intervals of the true mean Y are shown

slope (Spider orientation = 1.007 Solar azimuth (adj.) + 3.75; $r^2 = 0.69$) not differing from 1.0 (SE $b = 0.056$, $P > 0.1$).

There is also a significant regression of spider elevation on solar elevation ($F_{s,1,219} = 137$, $P < 0.001$; $r^2 = 0.39$), but, as with compass direction, there is a wide scatter of points (Fig. 3a). Examination of the data from only that period when $z/n > 0.47$ (Table 1), that is when most spiders were orientated, results in a regression with narrow confidence intervals (Fig. 3b; $F_{s,1,116} = 52.2$, $P < 0.001$) and a slope (Spider elevation = 0.769 Solar elevation - 14.88; $r^2 = 0.38$) that differs from 1.0 (SE $b = 0.084$, $P < 0.05$).

Important environmental variables

The composite plot of significant environmental parameters (Fig. 4) shows the very low relative humidity (33%) reached during the middle of the day during winter in this semi-arid area and the relatively mild maximum temperature of 32.2° C.

Stepwise multiple regression was used to separate the important environmental variables for each behavioural attribute from amongst those measured. The parameters included are given in the relevant tables. In no analysis did the individual variation contribute significantly to the explained variance.

The spider's compass direction overall was related to the solar azimuth and net radiation which explained

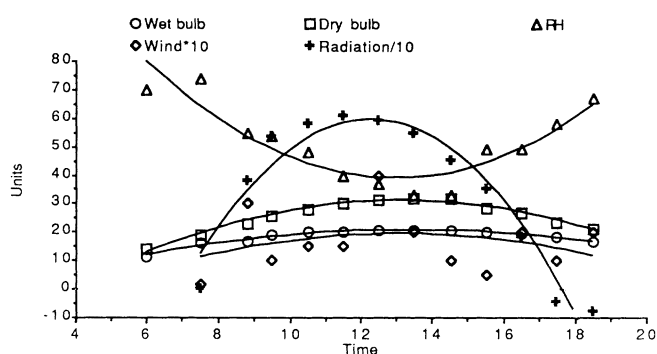


Fig. 4. Composite plot of environmental factors throughout the day with the curves fitted by polynomial regressions of the second order. The units are as follows: - Radiation (watts $m^{-2}/10$); Wind velocity = $ms^{-1} \times 10$; Temperature (°C) and Relative Humidity (%)

Table 2. Results of stepwise regression analysis to predict the compass direction and elevation of the new species from the environmental variables for the entire data set and for the subset of data between 0930 h to 1630 h inclusive. The parameters included were spider individual, spider compass direction, spider elevation, solar azimuth, solar elevation, wet and dry bulb temperatures, relative humidity, net solar radiation and wind velocity. Statistics are given only for the significant variables ($P < 0.05$)

Parameter	Value	r^2 adj	D.F.	F_s
<i>Spider direction</i>				
All data				
Intercept	42.17			
Solar azimuth	0.64	0.30	1, 217	96.4
Net radiation	0.04	0.32	2, 216	51.6
0930–1630 h only				
Intercept	3.753			
Solar azimuth	1.007	0.685	1, 146	321
<i>Spider elevation</i>				
All data				
Intercept	-46.57			
Dry bulb temperature	0.93	0.52	1, 200	219.39
Solar elevation	1.67	0.55	2, 199	124.27
Net radiation	-0.05	0.60	3, 198	102.47
0930–1630 h only				
Intercept	-85.64			
Dry bulb temperature	2.93	0.41	1, 129	89.3
Solar elevation	0.42	0.46	2, 128	57.1

only 32% of the variance (Table 2). Examination of the subset of the data when the spider population was strongly orientated (0930 h to 1530 h inclusive) showed the spider's direction to be significantly ($P < 0.05$) related only to the solar azimuth (Table 2) which alone accounted for 69% of the variance.

The spider's elevation overall was related mainly to two temperature related parameters, namely dry bulb temperature and net radiation, and partly to solar elevation (Table 2) which between them accounted for 60% of the variance. Between 0930 h to 1530 h inclusive, the elevation of the sun and dry bulb temperature were the

Table 3. Results of stepwise regression analysis to examine the association between the environmental variables and the consistency of the orientation of the spiders. Because z of the Rayleigh test approximates N when all individuals have the same orientation the measure of consistency used is $(\log(z/N))$; Table 1). a) The entire data set. b) The subset of data from 0930 h to 1630 h inclusive. The parameters included were spider individual, wet and dry bulb temperatures, relative humidity, net solar radiation and wind velocity. Statistics are given only for the significant variables ($P < 0.05$)

Parameter	Value	r^2 adj	D.F.	F_s
All data				
Intercept	-5.181			
Wind velocity	-0.057	0.86	3, 230	492
Dry bulb temperature	-0.086	0.83	2, 231	578
Wet bulb temperature	0.381	0.69	1, 232	511
0930–1630 h only				
Intercept	-4.984			
Wind velocity	-0.027	0.47	4, 154	36.28
Net radiation	-0.0002	0.04	1, 157	7.38
Dry bulb temperature	0.374	0.08	2, 156	8.23
Wet bulb temperature	-0.085	0.42	3, 155	39.08

only environmental variables significantly related the spider elevation (Table 2). Hence both the orientation and posture of the spiders appear to be influenced by the position of the sun and by temperature related measures (air temperature or net radiation).

The consistency of the orientation of the spiders is measured by z of the Rayleigh test. z_{\max} is related to the sample size and $z/n=c$. 1.0. Hence, z/n standardises z as a measure of the consistency of orientation within the population. To examine the factors related to this spread in the orientation at each reading during the day a stepwise regression was conducted of the environmental variables (see above) on z/n . Three environmental variables were significantly associated with z/n , namely, wind velocity and both wet and dry bulb temperatures (Table 3) which between them accounted for 86% of the variance of z/n . Between 0930 h and 1530 h the same parameters plus net radiation explained significant amounts of the variance in z/n (Table 3), accounting for 47% of the variance.

Spider temperature

A plot of the spider temperature on ambient temperature shows a curvilinear relationship with the spider temperature increasing above ambient and then reaching a plateau (Fig. 5) at 34.9°C ($sd = 2.44$, $N = 38$). This temperature is close to that adopted by a number of spider species exhibiting behavioural thermoregulation (Humphreys 1978, 1987a, b). The regression is significantly improved up to a third order polynomial (see Fig. 5 for the statistics for the subset of data between 0930 and 1630 h) and shows clearly the curvilinear form of the regression. It is the plateau rather than the absolute temperature which is indicative of a thermoregulatory response.

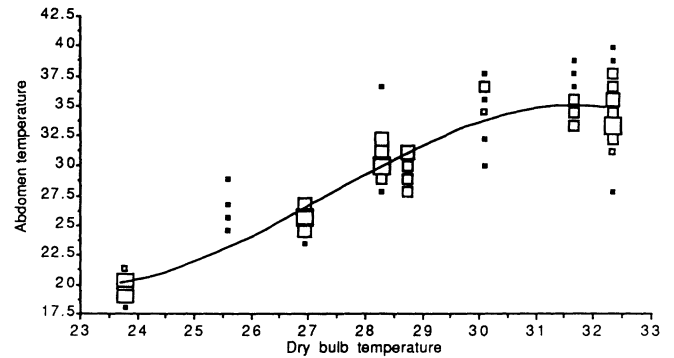


Fig. 5. Regressions of spider temperature on dry bulb air temperature. The fine straight line is that along which both axes are equal. Symbol size is proportional to the number of overlapping points. The curved line was fitted using a third power polynomial regression to the data between 0930 h and 1530 h inclusive. $r^2 = 0.53$, $F_{3,92} = 73.98$, $P < 0.001$. X , $P < 0.001$; X^2 , $P < 0.001$; X^3 , $P < 0.001$

Table 4. Results of stepwise regression analysis to examine the association between the environmental variables and temperature of both the spider (abdomen) and of the egg-sacs. Analysis is given for the entire data set and for the subset between 0930 h and 1630 h inclusive. The parameters included were spider individual, wet and dry bulb temperatures, relative humidity, net solar radiation and wind velocity. Statistics are given only for the significant variables ($P < 0.05$)

Parameter	Value	r^2 adj	D.F.	F_s
<i>Spider temperature</i>				
All data				
Intercept	18.535			
Dry bulb temperature	1.648	0.74	1, 112	319
Net radiation	0.012	0.86	2, 122	327
Wet bulb temperature	-2.043	0.87	3, 110	253
0930–1630 h only				
Intercept	-9.448			
Net radiation	0.011	0.64	1, 94	166
Dry bulb temperature	1.212	0.75	2, 93	143
<i>Egg-sac temperature</i>				
All data				
Intercept	-11.032			
Dry bulb temperature	1.319	0.78	1, 53	185
Net radiation	0.007	0.81	2, 51	115
0930–1630 h only				
Intercept	-12.125			
Net radiation	0.008	0.62	1, 47	80.2
Dry bulb temperature	1.342	0.67	2, 46	49.9

Stepwise regression of spider temperature on the environmental variables shows that three parameters are significantly related to spider temperature, namely wet and dry bulb temperatures and net radiation (Table 4). However, using the subset of the data between 0930 h and 1630 h shows only net radiation and dry bulb temperature to have significant effects (Table 4) accounting for 75% of the variance in spider temperature.

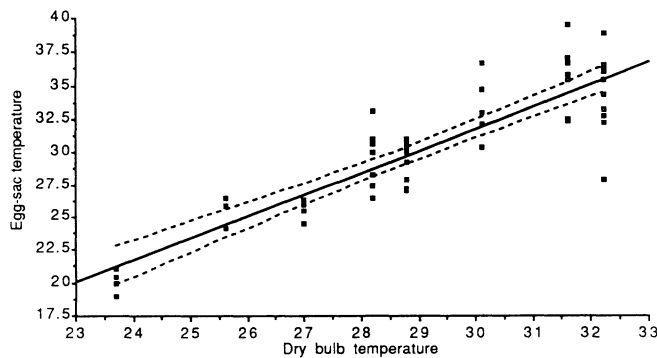


Fig. 6. Regression of egg-sac temperature on ambient temperature for the new species. The 95% confidence intervals of the true mean Y are shown

Egg sac temperature

Some individuals of the new species had egg sacs attached to their webs just above where the spiders rested. However, within the population the egg-sacs covered about the same vertical range as the spiders and were thus exposed to sunlight of similar duration and intensity. The egg sacs are of an ovoid spindle shape but is not known whether they are orientated with respect to compass direction. Because the egg-sacs are not moved by the spiders and as they cannot posture or reorientate, they serve as controls for the form of the regression of spider temperature on ambient temperature. Hence any difference in the form of the curve between the spiders and their egg sacs results from the movement of the spiders. However, it does not serve as controls for the actual temperature level because the egg-sacs may have different reflectivity and mass.

The egg sac temperature has a linear relationship with ambient air temperature (Fig. 6; $b = 1.67$; $F_{s1,52} = 185$, $P < 0.001$) which is significantly greater than a slope of 1.0 (SE $b = 0.122$, $P < 0.05$). The fit is not improved by a polynomial regression for the entire date set or for the rising and falling ambient temperature subsets (for X^2 , $P > 0.09$), hence the regression is strictly linear and shows no evidence of the plateau in the curve seen at high ambient temperature for the spider body temperature alone (Fig. 5).

Stepwise regression of egg sac temperature on the environmental variables shows, for the entire data set, that only the temperature related variables, dry bulb temperature and net radiation to be significant (Table 4). For the subset of the data between 0930 h and 1630 h only the same variables are significant and account for 67% of the variance (Table 4).

Overall the spider temperature was 0.5°C greater than the egg sac ($t_{s51} = 3.142$, $P = 0.003$; paired t -test, two-tailed). During rising ambient air temperature the spider was 0.6°C hotter than the egg sac ($t_{s38} = 2.717$, $P = 0.010$), but during falling ambient temperature the spider and egg sac temperatures were similar ($t_{s16} = 1.941$, $P = 0.070$). While in the field there are fractional differences in temperature between the spider and egg sac temperatures, this difference is not related to ambient

temperature ($F_{s1,50} = 0.14$, $P = 0.71$), or any other environmental factor.

Discussion

During the day when the temperature and the net radiation are high the spiders precisely track the solar direction and altitude. This is evidenced by the narrow confidence intervals for the regressions (Figs. 2 and 3) and the slope of 1.0 for the regression of spider direction on solar azimuth. The measured spider elevation is between 20° and 30° below that of the sun (Fig. 3); this may reflect only my misinterpreting the axis giving minimal silhouette area in this short and small spider.

The new species exhibits a precision of orientation to the solar azimuth and altitude far exceeding that of any other spider studied (e.g. spiders: Suter 1981; web orientation: Biere and Uetz 1981; Caine and Hieber 1987). The spider also accurately tracks the sun. The compass direction of the spiders throughout the day is primarily determined by the solar azimuth and temperature but after the spiders have started to orientate only the solar azimuth is of importance (Table 2). The closeness of the orientation of the spiders to the solar azimuth (the magnitude of z/n) during periods when most spiders are orientating is related to a range of environmental variables (Table 3). Elevation of the spiders is primarily associated with solar elevation, net radiation and temperature (Table 2). The spiders do not posture as close to the solar altitude as they do to the solar azimuth and they quickly return to the *Repose* position if shaded.

The webs of the new species are horizontal dome webs so that they have no compass orientation. Hence, changing the web orientation would *per se* change the thermal balance of the spider which must rely for this on changing its posture and orientation. This is unlike the vertical orb webs previously examined in this context where web orientation is both relevant and changeable according to the seasonal position of the sun (Biere and Uetz 1981; Caine and Hieber 1987; Carrel 1978).

The form of the temperature curve for the spider departs from that expected from the air temperature as well as that of the eggs sacs, the latter having no behaviour by which to adjust their temperature. The data suggest that posturing, which becomes more intense under more adverse thermal conditions, serves to reduce the heat load and thus the equilibrium temperature of the spider.

Effect of posturing. Long wave radiation from the ground surface directly beneath the spider will be much reduced because the spinifex provides good ground cover from this aspect. I want to discuss the potential effects of posturing in terms of the exposed silhouette area of the spider, as it is this measure that determines the amount of direct solar radiation received by the spider. As a first approximation I exclude the legs although in some spiders they are involved in thermal posturing (e.g. *Argiope protensa* Koch and *Nephila* spp.; W.F. Humphreys, unpublished). The silhouette area of a ma-

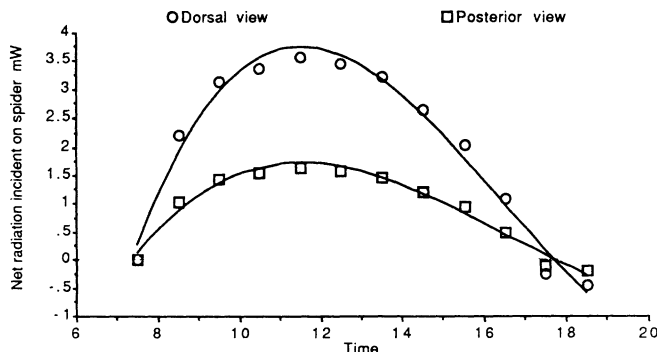


Fig. 7. Estimated net solar radiation incident on an individual of the spider fitted by a polynomial regression of the third order. The upper curve is for the sun incident on the dorsal surface (5.8 mm^2) and the lower curve is for the sun incident on the posterior surface (2.7 mm^2) of the spider. As such the curves set the maximum and minimum values of incident radiation with which the spider must operate at the hub of the web. Posturing by different amounts exposes varying silhouette areas of the spiders to the incident radiation; the limits determine the extent of behavioural thermoregulation by purely physical means

ture female was measured using a camera lucida. The ventral or dorsal surface has a silhouette area of 5.8 mm^2 , while the silhouette area of the posterior view, that presented towards the sun during full posturing, is 2.7 mm^2 . Hence posturing reduces the exposed silhouette area by up to 46% of the silhouette area of a non-postured spider. This ratio (minimum: maximum exposed silhouette area: Fig. 7) determines the scope for postural thermoregulation, that is the extent to which a spider can control its body temperature by purely physical means without moving from the hub of the web. Any thermal advantage resulting from heat shunting (Humphreys 1986) would supplement these physical effects and permit the spider a greater latitude of thermal conditions before being forced off the web.

Examination of the curves in Fig. 7 indicates that the scope for postural temperature adjustment is greater in the morning than in the afternoon. This could have implications if spiders warm up in the morning by posturing to increase their incident radiation; such processes have been described on a seasonal basis for web orientation (Biere and Uetz 1981; Carrel 1978). The magnitude of the thermal effect on the spiders resulting from these postural changes in incident radiation are unknown and experimental work is required to determine them. However, posturing in this harsh thermal environment serves to maintain the upper temperature of the spiders close to that reported for other species using different mechanisms (Humphreys 1978, 1987a, b).

Under low radiant heat loads in the laboratory *F. communis* heated when the wind speed was slow and then postured prosoma-to-sun (Suter 1981). This posture is unlike that of the new species or any spider species previously examined in this respect (Humphreys 1986 and unpublished). Suter (1981) considered that this attitude projected the abdomen into a region of increased forced convection and so cooled the spider. However, this argument may be inconsistent with to the physical

facts. The rate of heat exchange increases with increased surface to volume ratio ($s:v$); hence, to maximise heat loss, the spider should project the prosoma away from the web (it having a much greater $s:v$) and minimise heat gain by projecting the almost spherical abdomen (minimum $s:v$) to the sun.

The assumption that the posturing and reorientation shown by diurnally active web building spiders is of thermoregulatory significance is open to criticism. A number of alternative hypotheses may be stated: –

1. The Fabian position serves to reduce predation by minimising the silhouette area against the brightest sector of the sky.

2. The Fabian position serves to reduce predation by minimising the silhouette area that is brightly illuminated.

3. The Fabian position serves to turn the eyes away from the sun preventing saturation of the photoreceptors; spiders have no screening pigments or irises to protect their eyes (Blest 1985).

1) and 2) are refuted because the spiders adopt the Fabian position only when the intensity of sunlight reaches a high level, although at other times they will still be exposed against the brightest sector of the sky or else the brightly illuminated area of the body will not be minimal.

3) is refuted because some individuals adopt the reverse Fabian position (Fig. 2) which is inconsistent with the hypothesis, although it is consistent with a temperature regulation model depending only on physical factors. In addition turning away from the sun may be unnecessary as spiders can reduce the available photopigment during the day by an order of magnitude by removing photoreceptor membrane (Land 1985).

This single study of spiders on horizontal webs is insufficient to make general comparison with spiders on vertical webs, nor is there adequate information for either category so to do. However, it is becoming clear that ground living spiders, as well as those living on vertical and horizontal webs have many similar behaviours. Although this study was conducted in a hot and arid climate, similar behavioural tactics can be seen in a wide range of species and habitats, including lowland tropical rainforest where exposure of spiders on the forest floor to direct sunlight is both brief and intermittent, and temperatures are not extreme. In addition to the much studied *Nephila* spp. (Carrel 1978; Krakauer 1972; Robinson and Robinson 1974, 1978), these include: – in lowland rainforest – *Gasteracantha fornicata* (Fabr.), *G. sacerdotalis* Koch, *G. quadrispinosa* O.P. Cambridge, *Poltya* sp., *Argiope* sp. and *Psechrus* sp.; in semi-arid areas – *Argiope protensa*; in Mediterranean climates – *Arachnura higginsii* Koch and *Gasteracantha minax* Thorell (Humphreys, unpublished).

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