Stabilimenta as parasols: shade construction by *Neogea* sp. (Araneae: Araneidae, Argiopinae) and its thermal behaviour

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Summary

Neogea sp. is active in sunlight on an opaque disc stabilimentum it constructs at the hub of the web. When the spider becomes too hot it shuttles to the other side of the disc and rests in its shade; the disc cuts the transmission of light by 60%, so reducing the body temperature of the spider by 1.8°C. On warming in the sun the spider undergoes a sequence of behavioural responses which should serve to reduce the body temperature — by increased convective cooling, by reduction of the body surface exposed to sunlight, and by seeking the shade of the disc, following which the first two behaviours may be repeated in the shade. The behavioural sequence involves "stilting", orientation and posturing and within each behaviour there is a gradation in intensity of the behaviour. The progression of behaviours occurs within the temperature range 35–40°C; above 40°C the spider becomes agitated and shuttles to the shaded side of the disc. The reduction in heat load produced by stilting, posturing, orientation, tracking and the disc shade is cumulative, hence *Neogea* sp. has a layered thermal defence; together they permit the spider to remain at the hub of the web under a wide range of ambient conditions. The use of spider-produced shade is novel and it raises the wider question about the function of stabilimenta. Both stilting and the use of stabilimentum-shade is added to the thermal-behaviour repertoire of spiders.

Introduction

Spiders which remain active by day at the hub of the web, even spiders in mid-latitudes or those inhabiting forest, may be exposed to very high levels of incident solar radiation. In the shade such spiders rest on the underside of the web with their body vertical and the prosoma pointing down. When exposed to the sun during hot weather they generally point their abdomen to the sun and track its apparent movement through the day. The standard interpretation of this behaviour relies on a simple physical model; posturing in this way reduced the silhouette area exposed to the sun and so lowers the equilibrium body temperature (but see Humphreys, 1986).

In such spiders thermoregulatory behaviour has largely been deduced but not demonstrated (Biere & Uetz, 1981; Blanke, 1972; Caine & Hieber, 1987; Carrel, 1976; Humphreys, 1991a; Krakauer, 1972; Robinson & Robinson, 1974, 1978). However, for some spiders thermal balance models have been developed (Riechert & Tracy, 1975; Tolbert, 1979) which show the thermal consequences of some behaviours. A few direct temperature measurements have been made of spiders in the field (Humphreys, 1974, 1978, 1987a,b), but those made on orb-weavers have not been associated with specific behaviours (Humphreys, 1991a).

I investigated the thermal behaviour of a tropical orb-weaving spider which builds an opaque disc stabilimentum at the hub of its web and, amongst other behaviours, uses the shade of the disc to keep cool in hot weather.

Methods

The work was conducted during April and May 1990 in a traditional garden of taro, sago and bananas, cleared in lowland rainforest on Nobanob hill, near Madang, Papua New Guinea (5°10′S), adjacent to regrowth forest that was being cleared.

Observations and recordings of spider temperature were made between 1100 and 1500 hours. The abdominal temperature was recorded of undisturbed spiders resting both above and below the hub of the web, both in the shade and in the sun. The temperature was recorded at intervals and as soon as possible (<3 s) when there was a change in behaviour. Spider behaviour changed according to the incident light; this varied because the site was sometimes shaded by trees or by clouds. To induce more behavioural sequences the spider was sometimes shaded artificially and the strength and direction of the incident sunlight adjusted using a plane or concave mirror.

Disc opacity was determined by focusing a fibre-optic light source into a Nikon camera, adjusting the exposure, and then intersecting the light-path with the disc from the web and readjusting the exposure.

Spider temperatures were read using a close-focusing 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. In addition, wind speed, air temperature, relative humidity and net solar radiation were measured using the same instruments described previously (Humphreys, 1991a). Voucher specimens were collected (Western Australian Museum 91/605-91/607).

Definitions

The definitions of spider behaviour given in Humphreys (1991a) need modification for *Neogea:*

Repose position: Spiders occupy the lower or upper surface of the disc with the prosoma pointing downwards; the anterior–posterior axis of the spider is parallel to the plane of the web.

Stilting: A term employed to describe the "standing on tiptoe" behaviour of scorpions used to prevent overheating (Southcott, 1955; Alexander & Ewer, 1958); it is used here to describe a similar behaviour in spiders.

Orientation: The angle of the sagittal 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

Parameter	Mean	S.D.	N
Relative humidity (%)	73	6	5
Net radiation (W m^{-2})	661	45	3
Air temperature (°C)	32.0	1.2	5

Table 1: Environmental conditions during the study. Wind speed was <2 m s^{-1}. Maximum elevation of the sun was 66° and the theoretical maximum incident solar radiation was 890 W m^{-2} with an atmospheric transmission coefficient of 0.75 (Beer, 1990).

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 (Humphreys, 1991a). Continued adoption of the Fabian position results in the long axis of the spider tracking the sun during the day.

Results

Environment and natural history

The garden was hot and humid but the air was generally still with occasional gusts up to 2 m s^{-1} (Table 1). The garden and cleared forest was *c.* 5°C hotter than the adjacent forest.

All individuals collected were juvenile *Neogea* sp., and from their distribution (Levi, 1983) probably *Neogea egregia* (Kulczyński) (weight 60 mg, body length 8 mm, width of abdomen 4.5 mm; largest individual). The spider builds an inclined orb web (50–70° to the horizontal), at the hub of which it constructs an opaque silk disc (see Levi, 1983: plate 2). The spider rests prosoma down at the hub of the web (repose position) but, unusually for an orb-weaver, it often rests on the upper surface of the web where it is highly conspicuous (unlike many spiders, e.g. *Philoponella* sp. G: Lubin, 1986) as it is black on a brilliant white background; the disc is sufficiently opaque that the spider cannot be seen through the disc.

Preliminary observations showed that on hot days *Neogea* 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; the spider also accurately tracks the sun. Such behaviours have frequently been reported in orb-web spiders which normally hang prosoma down below the hub of their vertical or inclined webs during the day (Humphreys, 1991a; Krakauer, 1972; Robinson & Robinson, 1974, 1978; Suter, 1981). However, *Neogea* exhibits a progressive behavioural response to increasing temperature and has novel behaviours.

Behaviour

As *Neogea* heats up in the sun it exhibits a progression of distinct behaviours, each of which is itself graded (Fig. 1) and which are associated with the temperature of the abdomen. When a spider in the repose position is heated by the sun it initially "stilts", as has been described for scorpions. The spider raises its body away from the disc surface until eventually it appears to be standing on tiptoe (Fig. 1b–c). This presumably removes the body from the boundary layer to enhance convective cooling, the role ascribed to abdominal pointing in another spider (Suter, 1981). Stilting itself is graded and full stilting is much more marked than represented in Fig. 1, involving full downward extension of all legs, thus removing the body of the spider as far as possible from the disc's surface.

On further heating the spider gradually rotates the long axis of the body until it is parallel to the incident radiation while maintaining its anterior–posterior axis in the plane of the web (Fig. 1d).

Next the spider gradually postures, starting with the abdomen; it rotates the tip of the abdomen towards the incident radiation and this minimises the projected surface area of the abdomen exposed to the sun (Fig. 1e). As the posturing develops further the prosoma also is aligned with the abdomen (Fig. 1e) so that the entire spider is orientated with its prosoma from the sun with minimal silhouette area exposed. Eventually the legs themselves are rotated forwards until they are parallel to the long axis of the spider, in which position they are in the shadow of the abdomen, as is the prosoma; this is the full

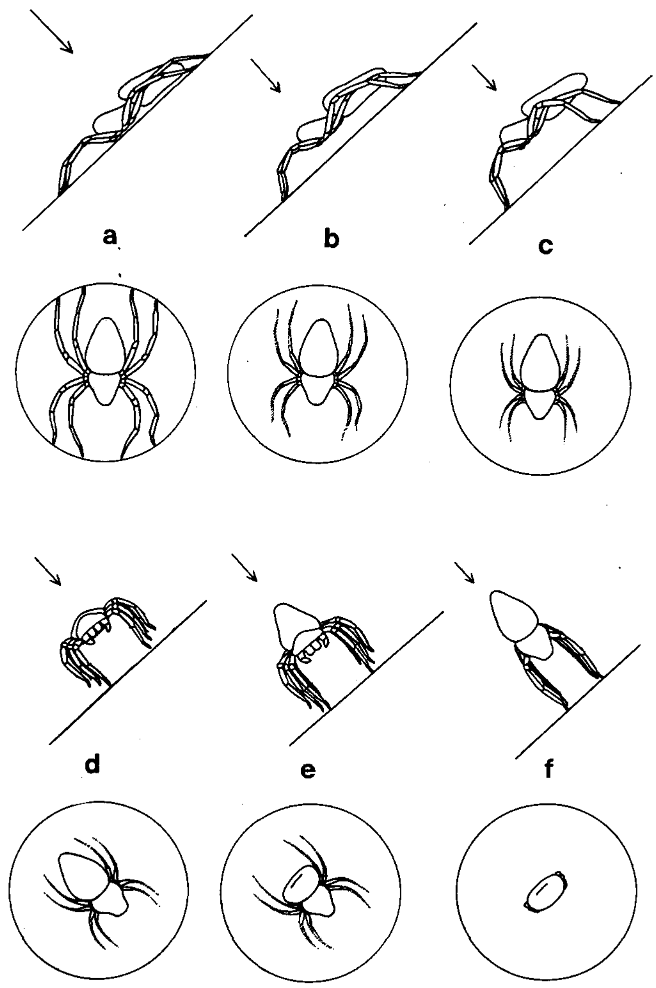

Fig. 1: Stylised drawing of the behaviours associated with increasing temperature in *Neogea* for a spider resting on the upper surface of the disc stabilimentum at the hub of the web. Below each view in the plane of the web is depicted the equivalent stance from the perspective of the direction of the incident radiation (arrow). *Neogea* is much less robust than depicted here, and in (**d**) and (**e**) the legs are on the disc surface; I am unsure of the position of the legs in (**f**).

A spider in the Repose position (**a**) heats up and progressively "stilts" (**b–c**); full stilting is much more marked than represented here and involves full downward extension of all legs. The spider then rotates the body (still in the plane of the web) so that the sagittal plane of the spider is aligned to the solar azimuth (**d**). On further heating the long axis of the abdomen alone is progressively aligned parallel to the incident radiation (**e**) and then the abdomen and prosoma are so aligned (**f**). At higher body temperature the legs are progressively straightened and rotated so that they point directly from the sun and lie in the shade of the body. In this final position only the posterior view of the abdomen is exposed to the sun and this represents 54% of the maximum silhouette area.

Fabian position from which the spider tracks the sun (Humphreys, 1991a).

As the spider heats further it eventually appears agitated, sometimes circling the whole body rapidly around the disc a number of times, moving to the edge of the disc, and briefly reposturing. This sequence may occur several times in rapid succession (within 10 s) before the spider shuttles through the web to the shade of the disc.

These behaviours form a graded series in that they appear in a predictable sequence associated with the intensity of the sunlight or with the duration of exposure to sunlight of high intensity. Each progression of behaviour is associated with a higher mean body temperature such that there is a significant overall temperature difference between behaviours (Table 2).

While a significant association between temperature and a progression of behaviours has been determined, much fine detail is unavailable from the field work. Owing to web movement in the wind the temperatures associated with most behavioural sequences could not be recorded; laboratory measurements would probably be required to examine the fine detail.

The mean thermal effect of shading by the disc was measured by inducing the spider to remain on one or other side; under these conditions the spider would go through the full range of behaviours. When the web is in shade the temperature of the spider did not differ whether it was above or below the disc ($Fs_{1,8}=0.313, p=0.59$). However, when the web is in bright sunlight, spiders in the shade of the disc are 1.8°C cooler than those in direct sunlight (Table 3); I interpret this as the thermal benefit of being on the shaded side.

Stilting

To examine the effect of stilting, a 22 mm diameter disc of waterproof paper was placed on a fine pointed wooden rod 30 cm above a grass surface. An ovoid of modelling clay (5 × 10 mm, 200 mg) was suspended on a hair above the disc and moved to and from its surface allowing it to reach thermal equilibrium each time.

The angle of the disc (horizontal or 35° from horizontal) had no effect on the temperature of the model ($Fs_{1,12}=0.74, p=0.41$). The model temperature (Y°C) fell according to the square root of the distance from the surface (X mm) such that $Y=38.9-0.39X$ ($r^2_{adj}=0.94$; $Fs_{1,15}=237$, $p<0.001$). Movement from the surface to 3 mm above the disc reduced the temperature of the model by 0.6°C to 38.2°C ($Fs_{1,9}=8.634, p=0.017$). At full stilt the body of *Neogea* is about 5 mm above the disc.

Stilting both removes the body from the steepest temperature gradients at the surface (Humphreys, 1975) and removes the body from the boundary layer to where the greater air movement will increase convective cooling. For spiders on the sunlit side of the web this effect will be enhanced by the abdominal pointing because it moves the abdomen yet further from the disc surface (cf. Suter, 1981); this possibly accounts for the spider sometimes remaining on the upper surface of the disc, which is unusual in orb-weavers.

Behaviour	Temperature (°C)		
	Mean	S.D.	N
Repose (on cooling)	35.2	—	1
Stilting	35.7a	1.88	5
Rotation	35.9a	0.63	4
Posturing	37.4a	1.85	14
Agitation	40.6b	2.10	3
Move to other side of disc	40.7b	1.85	5

Table 2: Abdominal temperatures of *Neogea* sp. at which various behaviours were observed on webs in the field. Common letters (a, b) denote values which do not differ significantly (Fisher's PLSD). ANOVA on spider temperatures: $Fs_{4,26}=8.167, p<0.001$.

Spider	Spider on disc			Spider under disc		
	Mean	S.D.	N	Mean	S.D.	N
1	41.5	1.03	19	39.9	1.20	10
2	41.2	0.74	15	39.2	0.80	8
All	41.4	0.91	34	39.6	1.07	18

Table 3: Abdominal temperature of *Neogea* exposed to the sun when on top of and under the disc. Two-way ANOVA — position of spider on web; $Fs_{1,48}=30.17, p<0.001$: Individual; $Fs_{1,48}=1.15, p=0.29$: Interaction; $Fs_{1,48}=0.008, p=0.93$.

Qualitative evidence

Neogea never stilts, rotates or postures when the web is shaded. However, if the intensity of the sun is low *Neogea* can be induced to perform this full behavioural repertoire on either side of the web by increasing the apparent intensity of the sun using an appropriately focused concave mirror. By moving the mirror to different distances from the spider the appropriate behaviour can be maintained, or the spider can be heated sufficiently for it to change to the other side of the web. Hence, the behaviour is clearly related to direct sunlight and the data indicate it is associated with temperature.

Although *Neogea* has a clear behavioural repertoire associated with temperature, in what way may the behaviour be thermoregulatory? The spider's behavioural sequence serves progressively to remove the body from the boundary layer and to reduce the projected surface area (silhouette) exposed to direct sunlight. A simple physical model will predict a reduction in the equilibrium body temperature under set conditions of solar radiation and wind speed. The extent of this effect depends on the body mass and on the ratio of the minimum to maximum projected surface areas (Humphreys, 1991a); in *Neogea* the projected surface area of the posterior view is 0.54 that of the dorsal view (by camera lucida).

The subtleties of the behaviour are demonstrated by the effect of slight air movement which may result in the spider ceasing to stilt or to posture, only for the behaviour to be resumed when the gust has passed. Such changes may be rapid and, for example, the cycle from stilting–repose–stilting may take only several seconds.

After shuttling to the shaded side of the disc, in very strong sunlight the spiders may again progress through the series of graded behaviours on the shaded side; this can be induced on less sunny days by means of a mirror focused through the disc. Hence, the reduction of heat load provided by the disc stabilimentum is added to that resulting from stilting and from the components of the Fabian position. Hence, *Neogea* has a layered thermal defence more sophisticated than other spiders examined. Together these factors should permit the spiders to extend the period during which they can monitor the web in hot weather.

Neogea can achieve appropriate posturing and orientation even when redirected sunlight comes from a biologically impossible position, i.e. from an angle well below horizontal. Many species seem confused under this condition and orientate correctly only in terms of biologically possible solar positions (e.g. some *Nephila* spp. and *Gasteracantha* spp.: W. F. Humphreys, unpublished).

Disc

One disc removed intact on a frame was *c.* 22 mm in diameter and was structurally complex, comprising three concentric bands. Under magnification (×40) the core (11 mm diam.) is a continuous, thin, parchment-like silk layer, not unlike the outer covering of a lycosid egg sac. The middle band (5 mm wide) is thinner and is formed of omnidirectional swathes of silk. The thin outer band (6 mm wide) appears to be made from single swathes of silk. The whole disc is underlain by the radial and spiral framework which provides structural support for the disc. Surrounding the disc there is a gap of about 10 mm in the spiral framework through which the spider shuttles from one side of the disc to the other. The disc blocks *c.* 60% of the transmission of white light. Artificial local shade (intercepting the direct sunlight with a wooden board) reduced the temperature by 3.1°C to 34.0°C ($Fs_{1,12}$= 111.5; $p<0.001$).

Smaller individuals of *Neogea* produce a much less dense disc such that the spider's shadow is projected through the disc on to leaves below; the spiders normally rest on top of the disc but eventually move below the disc if strongly heated. The spiders readily switch sides if heated with a mirror, but are difficult to induce to switch sides by "predator simulation" (unlike in many species: Edmunds, 1986). The discs are much less opaque (<40%) than those produced by larger individuals and so provide less shade. When strongly heated, individuals gradually protrude their body over the edge of the disc, with the body parallel to the web, until only the hind legs are left in contact with the disc (Fig. 2); in this position convective cooling would be maximum.

Discussion

Thermal behaviour

Thermally associated behaviours are not exclusively found in open country or in tropical climates. Both temperate and tropical forest spiders may orientate their webs appropriately for thermoregulation (Biere & Uetz, 1981) or adopt the full Fabian position even when exposed to sunlight only briefly during the day (Humphreys, 1991a, and unpublished).

The thermal behaviour of *Neogea* is much more complex than that recorded in other spiders (Humphreys, 1991a), adding both stilting and hub-shade use to the thermal-behaviour repertoire of spiders. While no spider previously has been reported to use its own silk for shade, it is usual for spiders that build stabilimenta to rest at the hub of the web during the day (Edmunds, 1986), often adding egg sacs or debris (prey or plant remains) to the web (Carico, 1986). In addition, during times of extreme heat, *Nephila edulis* (Labillardière) may shelter in the shade provided by the debris (W. F. Humphreys, unpublished).

The thermal benefit to *Neogea* from using the shade of the disc is greater than the 0.5°C benefit achieved by posturing in the 6 mg spider *Frontinella communis* (Hentz) (Linyphiidae) in the laboratory (Suter, 1981). The thermal benefit of the disc shade is cumulative with the progressive thermal benefits resulting from stilting and from the silhouette reduction behaviour (see Humphreys, 1991a). Together these determine the maximum heat load on *Neogea* and hence its occupancy of the web hub during hot weather.

Stilting as a thermal behaviour has not previously been reported in spiders (though it has as a defensive behaviour: Tolbert, 1975), but it is not unique to *Neogea*, having been seen also in other spiders associated with continuous surfaces such as leaf-curling spiders (Amaurobiidae), which move their bodies away from the leaf surface when they are heated (W. F. Humphreys, unpublished). Indeed, if the thermal interpretation of stilting in orb-weaving spiders is correct, then the behaviour is appropriate only to spiders associated with surfaces and should not be seen in spiders on webs lacking some surface (disc or leaf).

Stilting behaviour was described initially in scorpions (Southcott, 1955: the term is used also for a stance adopted by scorpions during parturition), and it serves to cool the body owing to increased convection; it allows the scorpion to extend the prey-catching period into the heat of the day (Alexander & Ewer, 1958), as with *Neogea*.

Behaviour causing a change in convective cooling has been reported previously for spiders. The removal of egg sacs from the retreat into the sun by *Theridion saxatile* C. L. Koch (Nørgaard, 1956) probably serves to increase convective cooling. The small spider *F. communis* reduces its abdominal temperature by posturing its abdomen away from the boundary layer associated with its sheet web (Suter, 1981). The field data for *Neogea* are consistent

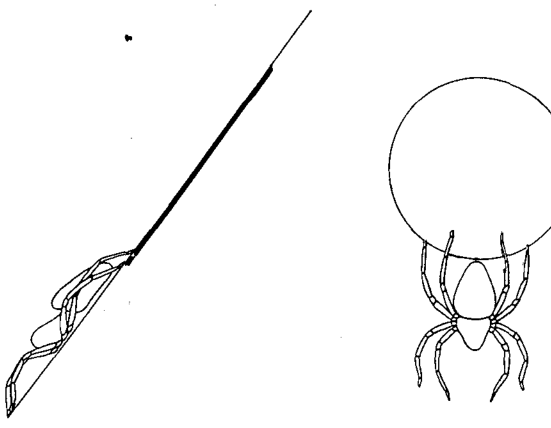

Fig. 2: *Neogea* sp. maintaining contact with the disc with only the hind legs; this position would provide maximum convective cooling.

with these laboratory observations, but the boundary layer associated with the solid disc of *Neogea* should be more marked than that found in the sheet web. The stilting behaviour seen in *Neogea* has not previously been reported as part of the thermal behaviour of spiders, but it serves the same function without the spider having to posture; posturing commences only at higher temperatures. Hence, the thermal load on *Neogea* can be reduced by both orientation and stilting before the spider has to assume the complex positions associated with posturing; such postures, because the leg placement is less symmetrical, could lead to a reduction in the efficiency of web monitoring for prey or intruders.

Spiders may posture on the web for non-thermoregulatory purposes but they are not in a Fabian position. A species of *Gasteracantha* in New Guinea regularly hangs horizontally upside-down away from the web (W. F. Humphreys, unpublished). *Cyclosa caroli* (Hentz) may cling to the stabilimentum, projecting the body at right angles to the web, and in that position shake the web violently (Comstock [1940] cited in Levi, 1977: 84).

Nonetheless, most spiders examined that are exposed to sunlight adopt the full Fabian position: *Gasteracantha minax* Thorell, *G. fornicata* (Fabr.), *G. sacerdotalis* L. Koch, *G. westringi* Keyserling, *G. quadrispinosa* O. P.-Cambridge, *G. taeniata* (Walckenaer), *G. theisi* Guérin, *Psechrus* sp., *Arachnura higginsi* (L. Koch), *Nephila maculata* (Fabr.), *N. edulis* (Labillardière), *Nephila* sp., an undescribed genus of Araneinae (Humphreys, 1991a), *Poltys* spp., *Cyrtophora citricola* (Forskål), *Argiope protensa* L. Koch (see Humphreys, 1991b), *Argiope* spp. and *Leucauge* sp. However, orientation and abdomen pointing alone occur in *Psechrus* sp. (Psechridae), and *Argyrodes* spp. have not been observed to respond to sunlight. Many of these species do not produce a stabilimentum (e.g. *Nephila* and *Leucauge*) or do not produce one that could be used as a parasol (*Argiope* sometimes and Gasteracanthinae). Hence, there appears to be a sequence in the development of thermally associated behaviours: orientation, to which is added abdomen pointing and then full posturing (solar tracking would naturally occur in all three). Although stilting starts the sequence in *Neogea*, it is an added behaviour that is applicable only to surface-associated spiders. The use of the disc as a parasol is probably derived from other functions of the stabilimentum.

Alternative hypotheses about the function of the Fabian position were considered elsewhere (Humphreys, 1991a). *Neogea* provides additional evidence supporting the thermal hypothesis; partial posturing or partial orientation make no sense in the anti-predator hypothesis but are entirely consistent with the thermoregulation hypothesis.

Stabilimenta

The stabilimenta of spiders' webs have many different forms, which may vary even within individuals (Marson, 1947; Ewer, 1972; Eberhard, 1973; Lubin, 1986), and may include opaque discs at the hub (Hingston, 1927; Edmunds, 1986; Lubin, 1986). Silk stabilimenta are mostly considered to be anti-predator devices (Eberhard, 1973; Edmunds & Edmunds, 1986; Lubin, 1986) and detritus and egg-sac stabilimenta are generally conceded (Eberhard, 1973) to function to protect the spider from visual predators (Gertsch, 1949), to attract prey (Craig & Bernard, 1990) or to collect water (Olive, 1980).

The use of stabilimenta in a thermoregulatory role raises questions concerning many observations which have been interpreted as supporting the anti-predator role of stabilimenta. In the absence of other information some of these observations are equally open to interpretation in terms of thermoregulatory hypotheses: only spiders that remain at the hub of the web during the day produce stabilimenta (Eberhard, 1973); spiders with stabilimenta may shuttle from one side of the web to the other (Eberhard, 1973); the legs assume an "aligned posture" by day but not by night (Eberhard, 1973); the amount of silk used is directly related to openness of the habitat (Marson, 1947); on vertical or inclined orb webs the spiders rest prosoma down at the hub of the web (see Humphreys, 1986).

I examine one of these assertions in more detail. Eberhard (1973) found that *Uloborus diversus* Marx uses more silk in its stabilimentum on light than on dark nights; he argued that "Webs at such [bright] sites . . . [are] most exposed to . . . predators . . . and . . . trends in stabilimentum size . . . may . . . provide . . . camouflage for . . . spiders most susceptible to attack . . .". The argument can equally be made that open sites are more exposed to direct sunlight and the stabilimenta are used to protect the spider from ultraviolet light (but see Craig & Bernard, 1990) or to reduce its heat load.

In considering the function of stabilimenta, failure to consider possible temperature effects means that appropriate data which could preclude temperature as a factor are not presented. The lack of consideration of temperature in the large literature on stabilimenta is surprising; for example, in a study of defence mechanisms Edmunds & Edmunds (1986: 83) found that species of *Argiope, Nephila, Leucauge, Cyrtophora* and the Gasteracanthinae remain at the hub of the web during the day; however, no mention is made of posturing. In the Australasian region, species in all these genera readily adopt the Fabian position (Humphreys, 1991a, and unpublished).

Of the spiders examined, shuttling behind the stabilimentum is unique to *Neogea* and is presumably derived. Use of the disc's shade, to supplement other heat-load reducing behaviours, enables *Neogea* to extend the range of ambient conditions within which it can maintain suitable operating temperatures. Thus, *Neogea* extends the time during which it can monitor its web from the hub. What benefit accrues from this is unknown, but presumably it is associated with the ability to detect and locate other organisms on the web, be they potential prey, predators, competitors or mates.

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