

## CRITERIA FOR IDENTIFYING THERMAL BEHAVIOUR IN SPIDERS: A LOW TECHNOLOGY APPROACH

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The widespread occurrence of thermal behaviour in diurnally active web spiders is either largely ignored or not recognised. Thus it obfuscates some explanations of the function of the stabilimentum on spiders webs. Thermal behaviours of four spiders (*Nephila edulis*, *N. maculata*, *Gasteracantha minax* and *Neogea* sp.) are examined using technology which is often inappropriate for field studies. Many thermal behaviours are recognised as well as behaviours which facilitate thermal behaviour. The thermal correlates of these behaviours are established. Some observational criteria are derived, which require only simple equipment, by which thermal behaviours may be recognised in the field and distinguished from other behavioural patterns. □ *Araneae, orb-weavers, thermal behaviour, thermoregulation, stabilimentum.*

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Many orb-web spiders remain active at the web hub during the day, where they can continue to feed, mate, and defend their web site from the same and other species, as well as produce or respond to attractant signals (acoustic, tactile, visual or chemical). The seasonal and diurnal duration of this activity can be extended by adopting behaviours that warm the spider (Robinson and Robinson, 1974, 1978; Biere and Uetz, 1981) when it would otherwise be too cold or else that prevent it from overheating (Lubin and Henschel, 1990; Humphreys, 1978, 1987a, 1991, 1992).

I consider below mainly behaviours that prevent overheating. In essence, in hot weather the spider postures so as to align the long axis of its body with the sun's rays and in this position it tracks the sun's apparent movement during the day. Such behaviour is not exclusive to spiders of open country nor in tropical climates but is found also in both temperate and tropical forest spiders (Biere and Uetz, 1981; Humphreys, 1991, 1992 and unpublished). The standard interpretation of this thermal behaviour relies on a simple physical model; posturing minimises the projected surface area (silhouette) exposed to the sun's radiation and so reduces the heat load (Fig. 1), lowering equilibrium body temperature (Willmer and Unwin, 1981: but see Humphreys, 1986) or, in an anti-predator hypothesis, minimising the silhouette against the brightest background, else the body area most brightly illuminated.

Recent observations have shed some light on this seemingly simple process and revealed a sequence of behaviours serving to reduce pro-

gressively the heat loading, behaviours that are themselves mostly graded (Humphreys, 1992). These include stilting, drooping, orientation, front leg raising, abdomen pointing, posturing, front leg rotation and web abandonment. Associated behaviours include silk laying and agitation (Humphreys, 1992 and unpublished). In addition, the use of a disc stabilimentum as a sun shade, suggested by Robinson and Robinson (1973: 283), is an effective thermal behaviour in *Neogea* sp. (Humphreys, 1992). Such behaviours not only maintain the animal within its heat tolerance range, but also serve to maintain the body temperature ( $T_b$ ) within a narrow range (presumably some optimum temperature) for extended periods of time (Humphreys, 1974, 1978, 1991). As body temperature has wide implications in physiological, behavioural, ecological and evolutionary contexts (Willmer, 1991), it is important to recognise thermal behaviour in spiders in order to allow different types of explanations for their behaviours.

That the thermal behaviour of spiders is not being recognised or is not being reported in the literature can be drawn from work on stabilimenta on spiders' webs. While stabilimenta have many different forms, they are mostly thought to provide mechanical support (Robinson and Robinson, 1973), to function as anti-predator devices (Eberhard, 1973, Edmunds and Edmunds, 1986; Lubin, 1986), to attract prey (Ewer, 1972; Craig and Bernard, 1990) or to collect water (Olive, 1980; see also Ewer, 1972; Robinson and Robinson, 1973: 283). *Neogea* sp. in

Papua New Guinea uses a disc stabilimentum as a parasol, which, together with a sequence of other behaviours, each themselves graded, reduces its heat loading (Humphreys, 1992). The demonstration that stabilimenta may be used in a thermoregulatory role raises questions concerning many observations which have been interpreted as supporting the anti-predator role of stabilimenta.

Some observations and deductions have resulted in an anti-predator function being ascribed to the stabilimentum. However, in the absence of other information, these observations are equally open to interpretation in terms of thermoregulatory hypotheses (see Humphreys, 1992). For example -1. Only spiders that remain at the hub of the web during the day produce stabilimenta (Eberhard, 1973). 2. Spiders with stabilimenta may shuttle from one side of the web to the other (*ibid.*). 3. The legs assume an 'aligned posture' by day but not by night (*ibid.*). 4. The amount of silk used is directly related to openness of the habitat (Marson, 1947).

Eberhard (1973) found that *Uloborus diversus* Marx used more silk in its stabilimentum on light than on dark nights (see also 4. above). The trend for larger stabilimentum at brighter sites camouflaged those spiders most susceptible to attack. However, without pertinent behavioural data, it is not possible to refute the hypothesis that the open sites are more exposed to direct sunlight and thus that the stabilimenta are used to protect the spider from ultra violet light (but see Craig and Bernard, 1990) or to reduce its heat load.

Posturing by spiders that remain by day at the web hub is rarely mentioned in the literature on stabilimenta and defense mechanisms. For example, although Edmunds and Edmunds (1986: 83) found that species of *Argiope*, *Nephila*, *Leucauge*, *Cyrtophora* and the Gasteracanthinae remain at the hub of the web during the day, they made no mention of posturing. In the Australasian region species in all these genera readily posture and track the sun (Humphreys, 1991, 1992; W.F. Humphreys, unpublished).

Clearly, thermoregulation hypotheses need more consideration in field studies of diurnally active spiders. More recently this has occurred (Henschel *et al.*, 1992; Humphreys, 1991, 1992; Lubin and Henschel, 1990; Ward and Henschel, 1992) but such studies often require expensive equipment to examine the thermal behaviour. Such equipment may be inappropriate to a field biologist primarily interested in observation and manipulation to examine behavioural or

sociobiological problems. There needs to be some observational criteria using only low technology by which thermal behaviour may be recognised and distinguished from other behavioural patterns.

The examination of thermoregulation in orb-weaving spiders is problematical as most methods used on vagrant spiders (thermal preferendum apparatus, thermocouple implantation, temperature transmitters) are not appropriate. The most promising apparatus for such studies is the use of remote infrared telemetry (Suter, 1981; Humphreys, 1991, 1992), although model spiders may be effectively used to determine  $T_c$  (Riechert and Tracy, 1975; Henschel *et al.*, 1992).

Can criteria be established which would enable workers, using cheap and readily available equipment, to establish that spiders are behaving in a manner consistent with thermoregulation and to identify the thermal conditions under which they initiate such behaviour?

## METHODS

Observations on *Nephila edulis* (Labillardière) were made both on Rottneest Island and in Perth, on *Gasteracantha minax* Thorell in the south-west, of Western Australia, and on *Nephila maculata* (Fabricius) in mangrove at Port Benoa, Bali, Indonesia.

Spider temperatures were recorded from 1100-1500 hours using an infra-red thermometer, described elsewhere (Humphreys, 1991, 1992). The temperature was recorded of undisturbed spiders resting above and below the hub of the web, both in the shade and in the sun. It was recorded at intervals and as soon as possible (<3s) after 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 direction and strength of the incident sunlight adjusted using a mirror. A plane mirror was used to alter the apparent position of the incident radiation at about the same intensity as the natural sunlight and a concave mirror was used to alter the apparent position of the incident radiation and at an intensity continuously variable from greater to less than the intensity of the direct sunlight. In the field, control of intensity was crude in the wind owing to movement of the web, and hence the spider; control of the intensity

Behaviour	Mean	s.d.	n	Range
Repose in shade	32.6 a	2.10	12	29.0-35.1
Repose in partial sun	32.4 ab	1.59	19	29.2-34.3
Repose in sun	35.0 b	1.66	47	31.6-38.3

TABLE 1. Mean temperature ( $T_b$  °C) of *N. edulis* in Repose position on Rottnest Island, Western Australia.  $T_b$  of spiders in Repose differs according to energy intensities of their location (shaded, partly shaded, sunlight: ANOVA -  $F_{s, 2,75} = 19.895$ ,  $P < 0.001$ ). Common letters include means not differing significantly (Fisher's PLSD at  $\alpha = 0.05$ ).

of radiant energy is therefore relative and greater or less than the natural incident radiation.

The following temperatures are mentioned:  $T_a$  = of ambient shaded air;  $T_b$  = of the spider's body which by default is the abdomen ( $T_{ab}$ ), otherwise the thorax ( $T_{th}$ ). The environmental temperature ( $T_e$ ) which is used as a shorthand for the effective heat load on the spider taking account of all energy gains and losses. Means are followed in parentheses by the standard deviation of the mean, and sample size.

Definitions required for this discussion are given below (see also Humphreys, 1991, 1992).

*Abandon web*: the spider leaves the web, often after a sequence of very agitated movements, and moves to the shade provided by the objects to which the main anchor lines of the web are attached.

*Abdomen pointing*: the abdomen alone is orientated to the sun as a prelude to full posturing. This behaviour is strongly represented in some species (Humphreys, 1992).

*Agitation and body lift*: the spider appears agitated and circles its body around the web's hub and in the process the body is raised away from the web. The latter is sometimes seen on its own and they are included here under the same behaviour. This body lift is not comparable to stiling (Humphreys, 1992).

*Drooping*: the spider hangs limply from the back legs with apparent loss of hydrostatic pressure; the appearance is like that adopted by a spider immediately after moulting while the new cuticle is hardening.

*Fabian position* (Humphreys, 1991): the spider aligns its long axis parallel to the direction of incident sunlight with the prosoma facing away from the sun. This position may be achieved by orientation and/or posturing. When the incident sunlight is parallel to the web plane then the Fabian position may be the same as the Repose position (Humphreys, 1991). Continued adoption of the Fabian position results in the long axis of the spider tracking the sun during the day.

*Front legs raised*: legs I and II are raised off the web and aligned parallel to the incident radiation; this occurs as a graded sequence with the first pair being raised before the second pair.

*Orientation*: the angle of the saggital plane of the spider is rotated to lie parallel to the solar azimuth while the long axis of the body stays in the plane of the web.

*Part orientation*: the spider is not in the Repose position and has partly orientated its saggital plane between the Repose position and the orientated position.

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

*Repose position*: spiders occupy the lower or upper surface of the hub with the prosoma pointing downwards; the anterior-posterior axis of the spider is parallel to the plane of the web.

*Rotate front legs*: following front legs raising the legs are rotated forwards such that they are stretched out in front of the spider and lie in the shade of its body when it is fully postured; this may occur as a graded sequence with the first pair being rotated before the second pair.

*Silk laying*: adjusts the web structure near the hub apparently to aid leg placement the better to posture and orientate to achieve the full Fabian position. This facilitates subsequent thermoregulatory behaviour but is not itself thermoregulatory.

*Start to posture*: when the spider changes the angle between its anterior-posterior axis and the plane of the web such that its long axis is parallel to the incident radiation.

*Stiling*: describes the 'standing on tiptoe' behaviour of scorpions used to prevent overheating (Alexander and Ewer, 1958); here it describes similar behaviour in spiders (Humphreys, 1992).

## EVIDENCE

Statements otherwise unsupported are based on my unpublished observations.

### REPOSE POSITION AND THERMOREGULATION

Spiders adopt the repose position if  $T_e$  is below some critical level and they do so whether they are in shade or sun, hence, direct sunlight alone does not cause spiders to posture. However,  $T_b$  in sun is higher than in shade (Table 1). For example, during cool weather (low  $T_e$ ) in the sun and during hot weather in the shade all individuals are in the Repose position on their webs if not otherwise engaged in activities such as mating, web building, etc.

When  $T_e$  is not sufficient to cause posturing in *G. minax* the proportion of spiders in the Repose

position during daylight does not differ between sunlit (36/38) and shaded (32/33) sites ( $\chi^2_1 = 0.016, P = 0.90$ ).

The mean  $T_b$  temperature of *N. edulis* in the Repose position was directly related to the intensity of the incident radiation such that spiders in the sun were hotter than partly or fully shaded spiders (Table 1).

Spiders on non-horizontal webs almost invariably rest on the underside of the web with the prosoma pointing down. However, spiders resting in positions other than the Repose position should not be taken as proof of thermoregulatory behaviour because some species, such as *Verrucosa* and *Cyclosa*, reputedly adopt a head up stance (Foelix, 1982: 139), as does *G. minax* at night and *Argyrodes antipodianus* O.P. Cambridge, generally.

#### ORIENTATION AND POSTURING: EVIDENCE FOR THERMOREGULATORY FUNCTION

In hot weather, spiders orient or posture on the web to attain the Fabian position and then track the sun's apparent movement. They do this irrespective of web orientation. Heat and sunlight are needed to obtain these behaviours. On very hot days, spiders may leave the web altogether and seek shade. Large spiders assume Fabian posture earlier than small ones possibly because under given environmental conditions large spiders reach higher body temperatures. However, small spiders may have lower threshold  $T_b$ 's.

In hot weather an individual spider in the sun will use reorientation and/or posturing to align the anterior-posterior axis of its body parallel to the direction of incident sunlight with the prosoma facing away from the sun and thus achieve the Fabian position (Robinson and Robinson, 1974, 1978; Humphreys, 1991, 1992). The spider will adjust this position during the day and track the apparent movement of the sun (Humphreys, 1991). In hot weather all individuals in the sun orientate in the same direction irrespective of the orientation of their webs; namely they all assume the Fabian position by posturing and/or reorientation (Humphreys, 1991).

Heat alone does not cause the thermal behaviour because in hot weather under heavily overcast conditions spiders do not assume the Fabian position. However, if intermittent direct sunlight strikes the spider it assumes the Fabian position intermittently.

On very hot days spiders may assume the Fabian position in the morning and afternoon but leave the web to seek shade during the middle of the day.

Such activity patterns have been reported for many heliothermal spiders (Humphreys, 1973, 1987a, 1987b) and other taxa (e.g. reptiles: Heatwole, 1970).

*N. edulis* abandons the web at  $44.8^\circ\text{C}$  ( $\pm 0.50, 3$ ) and moves into shade. In Perth, Western Australia, when the shaded air temperature was extreme ( $46.2^\circ\text{C}$ ) many *N. edulis* failed to seek cooler places and fell dead from their shaded webs through heat stress (G.A. Harold, pers. comm., 1991).

Large spiders assume the Fabian position earlier in the day than do small spiders (e.g., *N. maculata*)—this is consistent with the thermoregulation hypothesis because larger bodies have a higher temperature excess (Willmer and Unwin, 1981). However, the threshold temperatures for given behaviours could be size related and lower in small than in large spiders. This is consistent with the seeming generality that the tolerance zones of animals are related to the temperatures experienced. For example, very small *N. edulis* start to posture at  $36.0^\circ\text{C}$  ( $\pm 2.39, 4$ ), significantly cooler, by an average of  $4.4^\circ\text{C}$  ( $F_{8,1,25} = 13.279, p = 0.002$ ), than adult spiders undergoing the same behaviour ( $40.4^\circ\text{C} \pm 2.16, 27$ ).

#### ORIENTATION AND POSTURING IN RESPONSE TO MANIPULATION

Experiments with redirected and intensified sunlight can be conducted to influence the behaviour of spiders to assist in determining whether the behaviour is thermoregulatory without having to measure body temperature. The results are consistent for several species including *Arachnura higginsi*, *N. edulis*, *N. maculata*, *G. minax* and *Neogea* sp.

In cool sunny weather when the spiders are in the Repose position, additional heating (by concentrating redirected sunlight using a concave mirror), results in the spider orientating—and/or posturing if necessary—to assume the Fabian position. The redirected sunlight does not alone alter the behaviour of the spider (sunlight redirected at natural intensity using a plane mirror). Hence, posturing is dependent on the intensity of the heat applied.

In hot weather a spider which has assumed the Fabian position will resume the Repose position if clouds obscure the sun or it is artificially shaded even if lower than the natural insolation is reflected onto it by means of a concave mirror.

Spiders in the Fabian position in the sun will, if artificially shaded, assume a new Fabian position

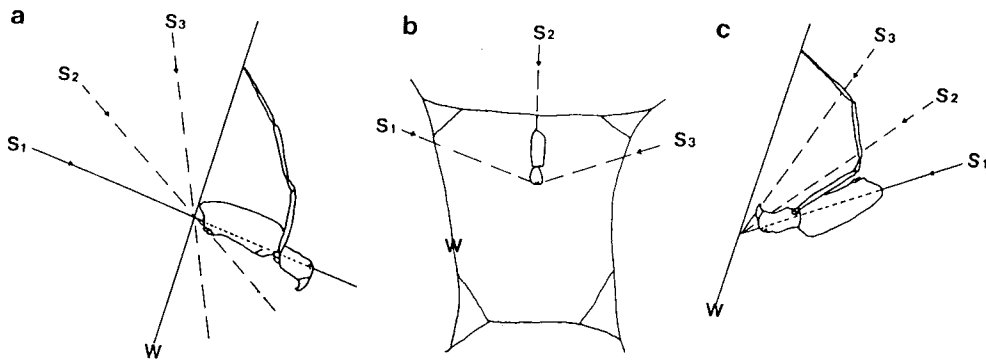


FIG. 1. Thermoregulatory postures adopted by golden web spider, *N. clavipes*. Lines projecting from three successive positions of sun ( $S_1$ ,  $S_2$ ,  $S_3$ ) indicate corresponding orientations of long axis of spider's body. Lateral views (a,c) and plan view (b) of web show posture assumed in response to ventral (through the web) insolation; b lateral insolation; c dorsal insolation (redrawn from Robinson and Robinson, 1974).

if the direction of the sun is artificially changed by means of a mirror.

In hot weather when the spiders are in the *Repose* position in the shade, redirection of unconcentrated sunlight, by means of a plane mirror or a concave mirror, results in the spider orientating and/or posturing if necessary to assume the *Fabian* position.

In hot weather, when the spiders are in a *Fabian* position, adding reflected sunlight from a plane mirror results in the spider orientating with respect to the mean angular direction of the two sources of incident radiation (when angle  $< 90^\circ$ ). A spider posturing between two heat sources will turn towards the one increased in intensity and *vice versa*. Hence, the *Fabian* position moves towards the incident radiation of the mirror if the heat reflected from the mirror is increased and towards incident radiation of the sun if the heat reflected from the mirror is decreased.

If redirected light comes from above the horizontal plane of the web spiders rapidly change their *Fabian* position; if redirected light comes from below the horizontal plane of the web, a naturally impossible position, spiders appear confused and change position frequently and some species never achieve the *Fabian* position (e.g. *N. maculata*).

#### CASCADING BEHAVIOURS

Many thermally related behaviours that have been categorised are themselves graded so that they each develop progressively rather than switch from one state to another.

For example as *Neogea* sp. warms in the sun, it exhibits a progression of distinct behaviours, each of which is graded and which are associated with

increasing temperature of the abdomen (Humphreys, 1992). When a spider in the *Repose* position on the disc stabilimentum is heated by the sun it initially 'stilt', as has been described for scorpions. The spider gradually raises its body away from the disc surface until it has full downward extension of all legs and seems to be standing on 'tiptoe', thus removing the body of the spider as far as possible from the disc's surface.

On further heating, *Neogea* sp. progressively orientates its body and then 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. As the posturing develops the prosoma also is aligned with the abdomen so that the entire spider is orientated 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 *Fabian* Position from which the spider tracks the sun (Humphreys, 1991, 1992). By these means the spiders potentially can obtain very fine control of their silhouette area and hence on their temperature.

In *N. edulis* many behaviours were recognisable as similar to those observed in other spiders (e.g. orientation, posturing, agitation: Humphreys, 1991, 1992), whereas others have not previously been reported or recognised (e.g. drooping). Some behaviours recognised may be components of the same behavioural sequence. For example, Agitation, in which the spider circles around the hub, involves the body being raised slightly from the

web, a behaviour sometimes seen on its own. Both behaviours are included here under the same category. Thermally there appears little difference between three categories recognised here as different behaviours (agitation and body lift, front legs raised, and start to posture). Work conducted under more controlled conditions in the laboratory may separate thermally these behaviours or allow their pooling using more rigorous criteria.

Eleven behavioural categories are recognised in *N. edulis*, ranging from *Rest* to web abandonment which occur between  $T_b$  of 33.9 and 44.8°C (Table 2). The spider temperature associated with many of these behaviours is significantly different from others. Some of these behaviours reduce the projected body surface area exposed to the sun and thus, under the predictions of the physical model, should result in lower equilibrium body temperature, all else being equal (e.g. orientation, posturing, leg raising, leg rotation and web abandonment). Other behaviours may not be thermoregulatory but are associated with the onset of the next behaviour in the graded series (e.g. agitation and body lift) or facilitate a subsequent stage (e.g. silk laying to enable correct leg placement for full posturing).

As in *Neogea* sp. (Humphreys, 1992), some behaviours themselves form a graded series which should proffer gradually increased thermoregulatory effects. Both front leg raising and front leg rotation occur initially in the front legs followed by the second pair of legs. In addition contralateral legs are not necessarily lifted or rotated at the same time.

## DISCUSSION

Two classes of observation refute the hypothesis that posturing serves an anti-predator role as stated in the introduction.

Firstly, if the Fabian position reduce the silhouette area against the brightest part of the sky as an anti-predator defense (i.e. to make them less visible) then they should posture to the sun under clear conditions irrespective of the intensity of the sunlight; they do not. Furthermore, under conditions of patchy heavy clouds (cumulus and cumulo-status) against a clear sky, the spiders should assume a Fabian position with respect to the brightest sector of the sky; they do not.

Secondly, many thermally related behaviours are themselves graded so that they are exhibited progressively as the spider warms. This provides the strongest evidence for the thermoregulation hypothesis because partial stiling, posturing or

Behaviour	Mean	s.d.	n	Range
Rest - see Table 1	—	—	—	
Part orientation	33.9	0.57	6	33.1-34.7
Drooping	36.5	1.57	8	35.4-38.8
Orientation	38.7a	2.30	9	34.2-40.3
Agitation and body lift	38.7a	2.09	21	35.2-43.5
Front legs raised	38.9a	2.84	11	35.0-43.3
Start to posture	40.4b	2.16	27	34.8-43.6
Silk laying	41.1bc	1.34	6	39.3-42.6
Rotate front legs	42.4cd	0.99	10	41.2-44.3
Abandon web	44.8d	0.50	3	44.3-45.3

TABLE 2. Mean temperature ( $T_b$ , °C) of *N. edulis* on Rottneest Island, Western Australia, associated with different behaviours (ANOVA -  $F_{8,93} = 15.233$ ,  $P < 0.001$ ). Common letters include means not differing significantly (Fisher's PLSD at  $\alpha = 0.05$ ).

orientation (Humphreys, 1992) makes no sense under alternative hypotheses but is entirely consistent with, and predicted from, the thermoregulation hypothesis.

The body temperature of a spider is a complex function of many intrinsic factors (size, morphology, attitude, physiology, reflectance, etc.) as well as factors extrinsic to the individual (e.g. wind speed, turbulence, air temperature, incident radiation and its spectral characteristics; Monteith and Unsworth, 1990). It is because  $T_b$  is a complex function of intrinsic and extrinsic factors that makes  $T_a$  a poor predictor of thermal behaviour. Hence, the observation that a spider may not always assume the Fabian position (or other presumptive thermoregulatory behaviour) at the same  $T_a$  does not imply that the behaviour has no thermoregulatory significance. For example, *Lycosa godeffroyi* Koch in Canberra began basking at much lower  $T_a$  in winter (4°C) than in summer (17°C) and reached 35°C on clear winter days at  $T_a$  of 11°C (Humphreys, 1974, 1978); the latter shows the dominant role of boundary layer effects for such surface dwelling spiders. Although orb-weaving spiders are often high above the ground, such boundary layers may assume more importance in those orb weaving spiders that incorporate a surface in their web (e.g. *Neogea* sp. and leaf curling species; Humphreys, 1992).

These many classes of observation support the hypothesis that the posturing and/or reorientation that spiders undergo in intense sunlight is of thermoregulatory significance. Many are not alone adequate to support unequivocally the thermoregulation hypothesis (e.g. Table 3: 4, 6, 9), some, in combination with others, support the

Condition at spider	Manipulation	Behavioural response and thermal consequences
1 <sup>a</sup> Cool weather in shade	Nil	Repose; $T_b = T_a$
2 <sup>a</sup> Cool weather in sun	Nil	Repose; $T_b > T_a$
3 <sup>a</sup> Cool weather in sun	=S	Repose; $T_b > T_a$
4 <sup>a</sup> Cool weather in sun	>S	Orientate and/or posture; $T_b > T_e$
5 <sup>a</sup> Hot weather in shade	Nil	Repose; $T_b = T_a$
6 <sup>a</sup> Hot weather in shade	=s or >s	Fabian
7 <sup>a</sup> Hot weather in sun	Nil	Orientate and/or posture X tracks sun; minimise $T_b$
8 Hot weather in sun	<<S	Repose
9 Hot weather in sun	=S or >S	Fabian
10 Very hot day in shade	Nil	Repose; <i>in extremis</i> may suffer heat death without posturing
11 Very hot day in sun	Nil	Seeks shade
12 Population in hot sun	Varied web orientation	All spiders orientate in same direction; minimise $T_b$
13 Population in hot sun	Large & small spiders	Large spiders posture earlier in day than small
14 Hot weather in sun	=S perpendicular to sun	Spider postures mid-way between two incident heat sources
15* Grade n-1 behaviour	>S	Grade n behaviour; behavioural cascade culminating in Fabian
16 Hot weather in sun	=S below horizontal	Apparent confusion in some species; $> T_b$
17 Cool weather in shade	=s	Posture to > exposure to heat source; $T_b > T_a$

TABLE 3. Summary of characteristics of thermoregulatory behaviour in orb-weaving spiders. *Definitions:* Spiders assume Fabian position in hot but not in cold weather. S denotes sunlight redirected onto the spider at about intensity of natural sunlight using a plane mirror (=S) or at greater or less than natural intensity using a concave mirror (>S or <S). The spider is simultaneously artificially shaded (s) or not (S). Numbers with \* are considered alone, and numbers followed by common letters are considered together, to support strongly the thermoregulation hypothesis.

hypothesis (e.g. 1-7), while others support no other hypothesis (e.g. 15).

While the emphasis here has been on behaviours that reduce the heat load, spiders should use behaviours to warm them in order to enhance the time they are at optimal temperatures. This is the case in burrow dwelling lycosids (Humphreys, 1974, 1978, 1987a, 1987b) as well as in orb web spiders which may seasonally orientate their webs to maximise the projected surface area to warm more or faster (Carrell, 1978; Tolbert, 1979).

While there is an indication of size related effects in thermoregulatory behaviour in *Nephila* spp., as may be expected theoretically using a simple physical model, no such size effect was observed in *Stegodyphus lineatus* Latreille (Henschel *et al.*, 1992).

While the thermal behaviour of spiders is much more sophisticated than has been accepted, the presumed advantages of such fine tuning are not understood. None the less, the recognition of such behaviour is an important aspect of field studies and the means to do so are required, especially for smaller spiders which are intractable subjects for direct recording of temperature in the field. However, the sensible use of this schema should allow easy appraisal of the overt body positions of spiders in the field as to their likely thermoregulatory significance and it should assist in disen-

tangling thermoregulatory from other behaviours.

A thermoregulator with the battery of finely graded behaviours seen here should, under ideal conditions, be able to maintain a near constant body temperature under a wide range of environmental conditions. In practice their temperatures fluctuate markedly with every air movement, at least partly owing to their small thermal capacity. If the spiders are innately incapable, owing to their small mass, of precise thermoregulation, why have they developed such a wide range of sophisticated behaviours which should permit precise thermoregulation?

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