

HEAT SHUNTING IN SPIDERS

W.F. HUMPHREYS*

INTRODUCTION

Some diurnally active spiders alter their posture to track the apparent movement of the sun; such behaviour has been interpreted as, or shown to be, thermoregulatory (POINTING, 1965; KRAKAUER, 1972; HUMPHREYS, 1974, 1978, in press; ROBINSON & ROBINSON, 1974, 1978; RIECHERT & TRACY, 1975; TOLBERT, 1979; SUTER, 1981). Such behaviour serves to alter the equilibrium body temperature under given thermal conditions (CARREL, 1978; SUTER, 1981).

This study shows that diurnally active spiders, which are entirely ectothermic, can achieve some degree of physiological, as well as behavioural, thermoregulation.

BACKGROUND

Spiders have an open circulatory system and haemolymph is pumped from the heart in the opisthosoma through the pedicel into the prosoma where the vessels terminate; the haemolymph drains back through the pedicel and eventually returns to the heart (WILSON, 1967). The somata are insulated from each other by their spatial separation. This anatomy and the close apposition of the vessels in the pedicel offer the potential for heat shunting and counter-current heat exchange. In accord with these considerations heat is transferred forwards between the somata of *Lycosa tarentula* more rapidly than it is transferred backwards (HUMPHREYS, in press).

METHODS

Temperature was measured by implanting fine thermocouples into the prosoma and opisthosoma of spiders using previously described techniques (HUMPHREYS, 1974, 1978) and the thermocouple signal recorded on a 24-channel recorder (Bristol-Babcock) with a resolution of 18.5s and 0.1°C. Spiders were immobilized by securing their legs to a polystyrene sheet by glue and the required soma heated by a high intensity microscope lamp (Prior) focused so the thermocouple insertion was in the shade of the body; the unheated soma was shielded by aluminium foil. Circulation between the somata was restricted when required by tightening the noose in a fine thread around the pedicel. Heart rates were measured visually under magnification. Statistical analysis follows SOKAL & ROHLF (1981). Abbreviations used are: Tp = temperature of the prosoma; To = temperature of the opisthosoma; Teq = equilibrium temperature; Td = temperature differential between the somata.

*Department of Biogeography and Ecology, Western Australian Museum, Francis Street, Perth, W.A. 6000, Australia.

RESULTS

A) Data from *Schizocosa leuckartii* (Thorell) (Lycosidae) which is burrow inhabiting and thermoregulates at the burrow entrance (HUMPHREYS, 1978).

Effect of setae in heat loss:

Both somata when freely suspended lost heat ca. 17% faster ($P < 0.001$) when the setae covering the body surface were removed by shaving.

The role of legs in heat exchange:

The prosoma cooled 38% faster ($P < 0.001$) when water was placed only on their legs than when the legs were dry; T_p and T_o dropped steadily from T_{eq} after water was added and T_d declined (Fig. 1a). Heating the legs only and on one side raised T_p from 24.5 to 32.8°C while adding water to the contralateral legs resulted in a steady decline in T_p which was reserved on removal of the water; constriction of the pedicel increased T_p during both phases (Fig. 1b).

Changes in heating rates:

Heating the opisthosoma only of dead spiders showed that the somata are well insulated from each other with $T_d > 15$ C and resulted in smooth heating and cooling curves (Fig. 2a). In live spiders T_d was smaller and qualitatively different by not having smooth T_d curves (Figs. 2c,d). Constriction of the blood flow between the somata (T ; Figs. 2b,d) caused an increase in T_d and T_o , while T_p decreased. Restoration of the circulation (U) caused some heat transfer to the unheated soma in live (Fig. 2d) but not dead spiders (Fig. 2b).

Heating the prosoma alone of live spiders resulted in a T_d which increased when the blood flow was restricted and decreased when the blood flow was restored resulting in some heat transfer to the opisthosoma (Fig. 2e).

When the opisthosoma was heated the T_o curve levelled out between 35 and 40°C and lead to an increase in T_p ; this is seen most clearly in the T_d curves (Figs. 2c,d). When the prosoma was heated the T_p curve flattened between 32 and 37°C and lead to an increase in T_o as for examples Fig. 2f. This flattening in the heating curve was associated sometimes with brief stuggling by the spider and sometimes with pulsating movements in the opisthosoma; the latter is shown in Fig. 2c where the decline in T_d was associated with the onset of pulsating (P on the T_d curve) in the opisthosoma leading to the stabilization of T_o while T_p increased; when T_p reached 38°C it stabilized by heat transfer to the opisthosoma but when T_o reached 44°C stabilized at the cost of an increase in T_p .

The heart rate is not a simple function of the temperature of either soma as the heart rate was greater at a given temperature when the prosoma was heated than when the opisthosoma was heated (Fig. 1f). Individuals varied widely in their absolute response to changing temperature and an individual response is shown in Fig. 1g.

B) Data from *Nephila edulis* (Labillardiere) (Argiopidae) which is an orb-weaver exposed to the sun during the day at the hub of the web.

Recently dead *N. edulis* showed a much larger T_d when either the prosoma or opisthosoma were heated (Fig. 1c) than did live individuals (Figs. 1d,e). T_d increased markedly when the pedicel was constricted and fell when heanolympf flow was restored (Figs. 1d,e).

DISCUSSION

The legs comprise 50% of the prosomal mass and play a large role in heat exchange. While it is unclear whether this results from haemolymph circulation in the legs as suggested by CARREL (1978), it seems unlikely that the small contact surface between

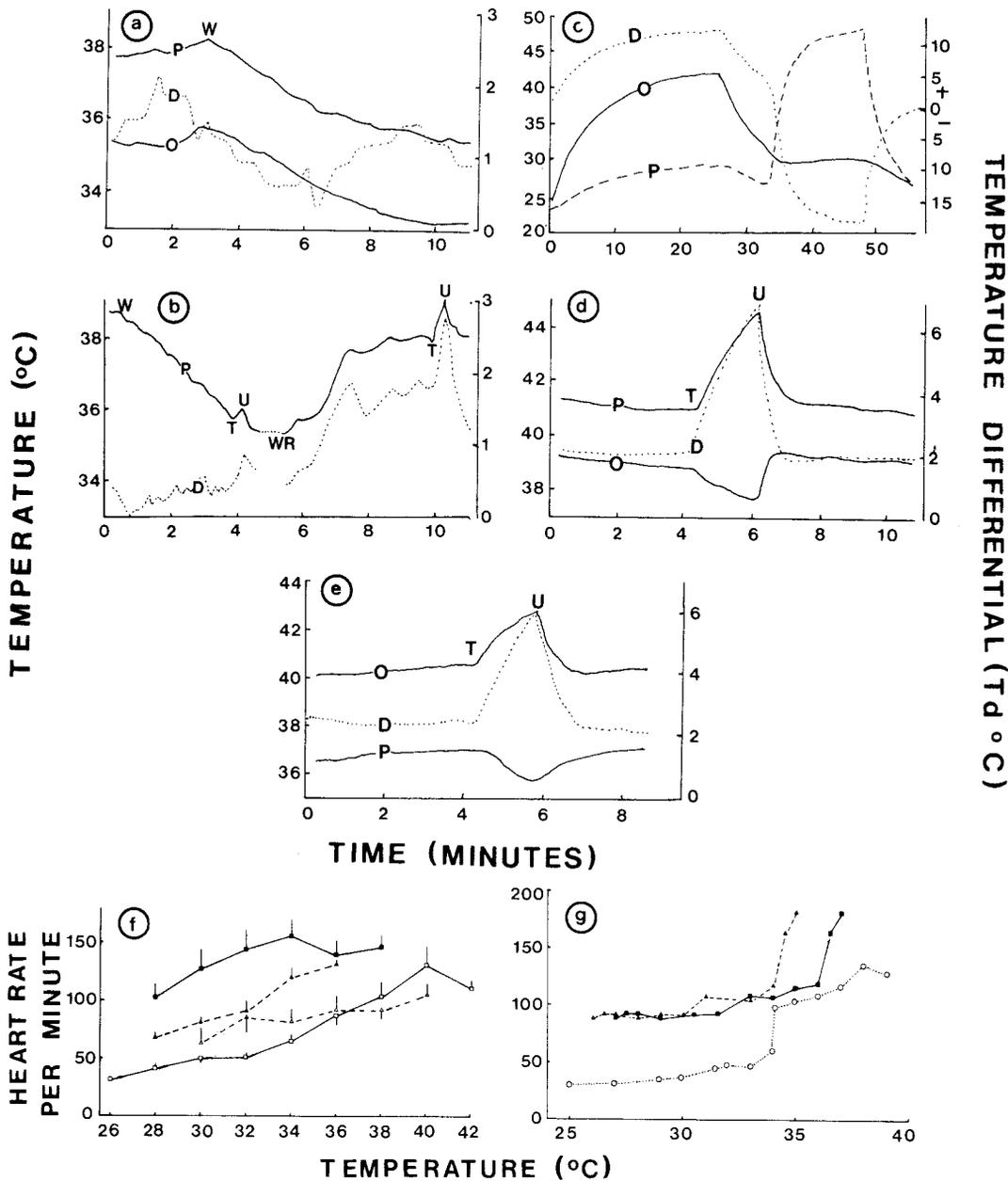


Figure 1. Records of temperatures and heart rates from *Schizocosa leuckartii* and *Nephila edulis*. External heat was applied to one soma using a focused microscope lamp. P = prosoma; O = opisthosoma; S = spider struggled; W = water added only to legs; WR = water removed from legs; D = temperature differential between the somata, haemolymph flow was stopped by tightening a noose around the pedicel at T and the noose released at U. a: Live *Schizocosa* heated on the prosoma, water was added (W) to the legs and the same heat input maintained. b: Live *Schizocosa* heated via the legs of one side and water added to the contralateral legs (W) and later removed (WR); pedicel constriction was applied briefly during both stages. c: Dead *Nephila* heated successively on the opisthosoma and the prosoma. d: Live *Nephila* heated on the prosoma and the pedicel constricted at T and then released at U. e: Live *Nephila* heated on the opisthosoma and the pedicel constricted at T and released at U. f: Mean heart rate (plus or minus 1 SE) of 6 *Schizocosa* as a function of temperature when the prosoma or the opisthosoma was heated upper two lines = prosoma heated, lower two lines = opisthosoma heated, continuous lines = heating phase, dashed lines = cooling phase. g: The heart rate of individual *Schizocosa* as a function of temperature; upper two lines = prosoma heated with the solid line = Tp and the dotted line = To, lower curve is To when the opisthosoma was heated.

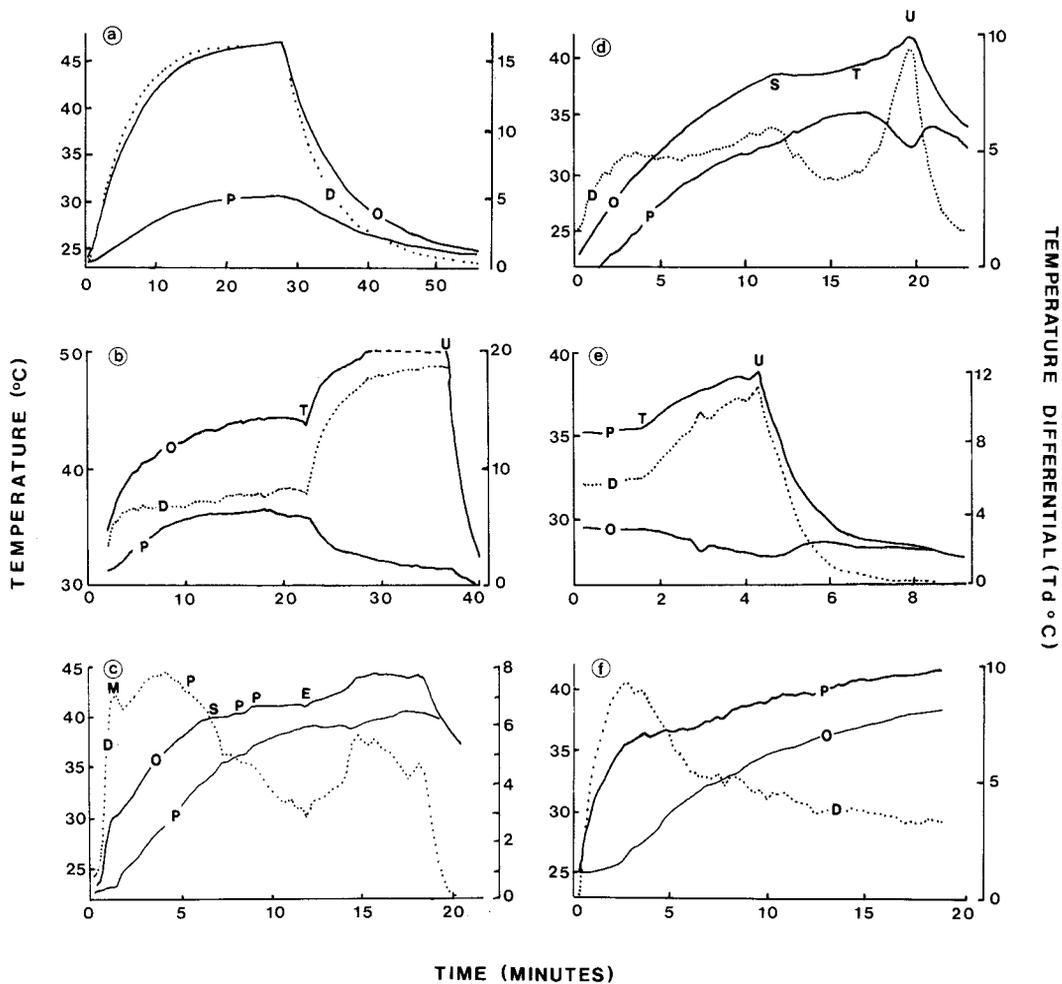


Figure 2. The temperatures of *Schizocosa leuckartii* during various treatments; symbols as for Fig. 1. a: A dead spider when the opisthosoma alone was heated; the temperature drop results from the lamp being turned off. b: A live spider when the opisthosoma alone was heated, the pedicel was constricted at T, released at U and the lamp turned off, the broken section of curve O is above the range of the instrument. c: As Fig. 2b; note the successive flattening of the To and Tp curves associated with changes in Td (see text). d: As Fig. 1b; note the flattening of curve To at about 38°C. e: A live spider when the prosoma alone was heated; the pedicel was constricted at T, released at U and the lamp turned off. f: As Fig. 1e; note the flattening of curve Tp at about 36°C.

the legs and the body could support this level of heat exchange by passive heat transport alone.

The setae covering the general body surface are important in heat exchange, hence experiments on thermoregulation which involve disrupting the setae (ROBINSON & ROBINSON, 1978) may produce anomalous results by altering T_{eq} .

The spiders transport considerable amounts of heat between the somata and to some extent can regulate physiologically this heat transport. I am unaware of other data showing physiological thermoregulation in small, entirely ectothermic, animals; even in small lizards the control of thermal conductance is not effective in thermoregulation (FRASER & GRIGG, 1984). The role of the heart in heat transport is ambiguous at this stage and the elevation in heart rate when the prosoma is heated may not have thermoregulatory significance.

When one soma is heated the spider develops initially a large T_d which starts to decline only when the temperature of the soma reaches temperatures similar to those the spiders maintain in the field (HUMPHREYS, 1978); heat shunting would serve to prevent overheating. There is no evidence to suggest that heat gain in a soma may be sequestered there to accelerate heating from sub-optimal temperatures although it should be advantageous for the prosoma to reach rapidly the temperature at which the locomotor organs are most efficient as they are required in prey capture. The evidence suggests that heat sequestering does not occur for when heat is removed T_d in live spiders falls to zero much faster than in dead spiders (Fig. 2).

If the function of posturing under hot conditions serves only to minimize the silhouette area exposed to the sun then prosoma-to and prosoma-from the sun postures are equivalent and wide flat spiders should orientate laterally to the sun to minimize their silhouette area, as occurs in some *Gasteracantha* (ROBINSON & ROBINSON, 1978). There are, however, few reports of prosoma-to sun orientation (POINTING, 1965) and *Gasteracantha minax* in Australia, while adopting lateral posturing on occasion, always adopt a prosoma-from sun posture when heated further (W.F. HUMPHREYS, unpublished).

Spiders have clear functional separation between the somata; the prosoma contains the locomotor and digestive organs and the main nerve ganglia, while the opisthosoma contains the reproductive organs, the heart and lung-books. Hence prosoma-to and prosoma-from the sun postures, despite the equal silhouette area they expose to the sun, may not be functionally equivalent for a number of reasons:

1) The opisthosoma of spiders is generally bulbous and larger than the prosoma which has a complex morphology; in combination these factors produce a surface to volume ratio in the prosoma which is substantially greater than that of the opisthosoma, hence the prosoma will have a lower equilibrium temperature under given thermal conditions.

2) Posturing prosoma-to or prosoma-from the sun will result in self shading of one soma. If the thermal problem is one of overheating it will be advantageous to posture so that the prosoma is shaded and pump excess heat into the prosoma from where it will be dissipated more rapidly than in the observe posture.

3) Spiders do show postural changes which serve or should serve to increase heating rates (CARREL, 1978, HUMPHREYS, 1978; TOLBERT, 1979). If the thermal problem is to heat rapidly to optimize the temperature within a soma then sequestering heat within that soma should be beneficial; at this stage, however, there is no evidence of heat sequestering although counter-current heat exchange may be expected from anatomical considerations.

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ZUSAMMENFASSUNG

Die Morphologie und die zirkulatorische Anatomie der Spinnen haben das Potential einer Wärmeübertragung und Wärmeverteilung, wenn die Spinnen einseitig erhitzt werden wie, beispielsweise, bei Wolfspinnen, die sich in der Sonne erwärmen und überhaupt, wenn Spinnen tagsüber an ihrem Netz tätig sind. Die alleinige Erwärmung des vorderen, beziehungsweise des hinteren Körperteils bei den *Schizocosa leuckartii* (Lycosidae) oder den *Nephila edulis* (Argiopidae) führt zu einer massiven Wärmeübertragung von dem erwärmten zu dem kälteren Teil des Körpers; wenn der erhitzte Körper höhere Temperaturen erreicht, wird der Wärmeaustausch reguliert, um eine Überhitzung zu verhindern. Der Puls der *S. leuckartii* ist bei einer bestimmten Temperatur, wenn der vordere Körperteil allein erwärmt wird, schneller als bei der alleinigen Erwärmung des hinteren Körperteils. Die Beine und die Borsten, welche die Körperoberfläche von *S. leuckartii* bedecken, spielen bei der Wärmeübertragung eine wichtige Rolle.