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A mathematical simulation of thermoregulatory behaviour in an orb-weaving spider

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Summary

1. In order to better document the thermoregulatory effectiveness of observed behaviours compared to other possible behaviours, we develop a model of interception of solar radiation. We demonstrate its use with data from a population of the orb-weaving spider *Nephila clavipes* inhabiting a mid-altitude Mexican desert.

2. *Nephila clavipes* exhibits three behaviours that appear related to thermoregulation in this extreme climate: microhabitat selection, orb–web orientation and postural adjustments.

3. Large females more often built in open spaces without shade and small juveniles built within shrubs in shaded web sites. Webs built by large females tended to have a north–south orientation, whereas among small juveniles there was no correlation in web orientation.

4. Only individuals in unshaded sites exhibit postural thermoregulation, in which the spider's abdomen tracks the elevation of the sun. The simulation revealed that interception of solar radiation by large females was reduced by solar tracking, but that the north–south orientation of the orb did not reduce the interception of solar radiation relative to an east–west orientation.

Key-words: Microhabitat selection, *Nephila clavipes*, solar radiation, Tetragnathidae, thermoregulation

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Introduction

In ectothermic animals such as arthropods, the temperature of the environment directly influences the animal's body temperature. Behaviours associated with maintaining the body temperature within the appropriate range alter the rate of heat acquisition, and include selection of appropriate microhabitats (e.g. sunny or shaded) and changes in posture while occupying a given site (reviewed in Heinrich 1993). The behaviour of a wide variety of insects in thermally extreme environments has been studied (Cloudsley-Thompson 1991; Heinrich 1993), but its effectiveness in controlling body temperature is difficult to determine. First, the behaviours involved in foraging, reproduction, defence and thermoregulation are often difficult to distinguish and not necessarily mutually exclusive (Cloudsley-Thompson 1991). It may also be impossible to determine the main purpose of any observed activity. Second, there are serious methodological problems in studying thermoregulation in very small organisms (Heinrich 1993). In part, this is because thermoregulatory behaviour is a dynamic process yet most quantitative methods of studying small animals require sacrificing the animal to determine its body temperature. Repeated observations of the same individual in a variety of situations are thus difficult to obtain. Also, it is often impossible to induce alternative responses to solar radiation, so that the thermal consequences of different behaviours cannot be easily determined (however, see Suter 1981). In this paper, we adapt a model developed for plants to calculate interception of solar radiation by an organism, presumed to be highly correlated with heat acquisition. This model can be used to compare the solar radiation intercepted by an animal using observed behaviour with hypothetical alternatives. We demonstrate the use of the model with data from an orb-weaving spider.

Spiders can alter their thermal environment in three ways: microhabitat selection, web orientation, and postural adjustments while on the web. Microhabitat use in orb–web building spiders tends to reflect patterns of differential tenacity at sites with different characteristics (Enders 1976). The orientation of the web within a site will affect the solar radiation felt by the spider (Krakauer 1972; Robinson & Robinson 1974; Moore 1977; Carrel 1978; Tolbert 1979; Hodge 1987; Higgins & McGuinness 1991). The posture that

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a spider assumes on the web can be very flexible, and is believed to influence the rate of heat absorption by either maximizing or minimizing exposure to solar radiation (Krakauer 1972; Robinson & Robinson 1974; Suter 1981).

The current study involves an unusual population of the large orb-weaving spider *Nephila clavipes* (Linn.) (Araneae: Tetragnathidae). Although this species is generally associated with lowland tropical forests, this population inhabits an environment with wide temperature extremes, a mid-altitude desert in Mexico. Following a description of the model, we compare microhabitat use and orb–web orientation by juveniles and adult females, and describe adult female postural thermoregulation. Using the model, it is possible to compare of the rate of interception of solar radiation by individuals using the mean observed behaviour (thermoregulatory postures on north–south webs) with alternatives: thermoregulatory postures on an east–west oriented web, or no thermoregulation (vertically oriented abdomen; orb orientation is not important). The simulation revealed that the mean behaviour does not always yield the greatest reduction in the interception of solar radiation. We end with a discussion of these results.

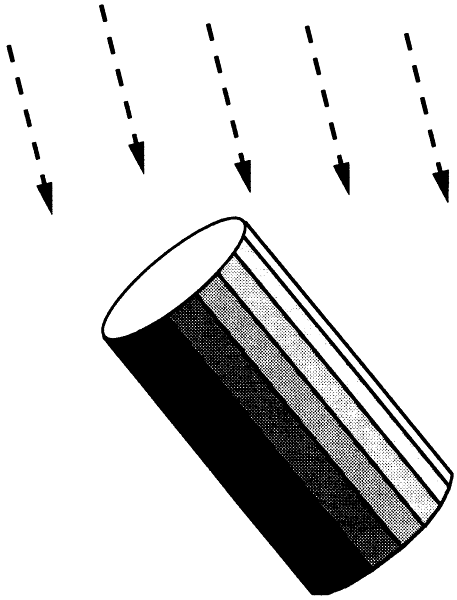

Fig. 1. The abdomen of the spider was simulated as a prism with 18 sides, a top and a bottom. The length of the prism was the mean abdomen length and the diameter was the mean abdomen width of the spiders found in the October census. The solar radiation intercepted by the entire abdomen was calculated as the sum over all sides of the solar radiation intercepted.

The model

This model was first developed to examine the solar radiation intercepted by plants and plant parts (Ezcurra, Montaña & Arizaga 1991; Ezcurra *et al.* 1992), and is readily adaptable to small ectothermic animals. The basic premise is that the solar radiation intercepted by an organism is correlated with heat acquisition, which has been demonstrated for a small linyphiid spider (Suter 1981). The amount of solar radiation intercepted is calculated from standard astronomical equations and the azimuth (magnetic orientation) and inclination (angle from the horizon) of the body over the course of the day. These calculations are described in Ezcurra *et al.* (1991, 1992); the theory is presented in Monteith & Unsworth (1990) and Gates (1980). A prism with the dimensions of the organism simulates its shape. For example, a triangular prism would well represent the shape of a katydid, and a rectangular prism, a grasshopper. Each of the faces of this prism intercepts an amount of solar radiation proportional to its relative area, determined as the projection of that side onto a plane orthogonal to the direction of the radiation. Faces that received no direct solar radiation (i.e. self-shaded) have values of zero. The total direct radiation intercepted by the prism at each time is calculated as the sum of radiation intercepted by all the rectangular faces and the top and bottom of the prism. In the case presented here, the abdomen of the spider was modelled as an 20-faced cylindrical prism of length equal to the mean abdomen length and diameter equal to the mean abdomen width of spiders in the October census (Fig. 1).

We made the following simplifying assumptions in adapting the model to this spider: (1) the abdomen is of uniform colour, so that it does not matter whether the radiation contacts the dorsal or ventral surface; (2) there is no difference in spider behaviour on orbs facing north *vs* south, or on orbs facing east *vs* west; (3) the mean inclination of the spiders does not differ among webs facing different directions; and (4) interception of solar radiation is correlated with heat acquisition. Assumptions (2) and (3) are supported by the field observations. Atmospheric transmittance was taken as 0·75, a value typical of desert areas.

Materials and methods

STUDY SITE AND ORGANISM

Tehuacan valley is a mid-altitude desert between the central and eastern ranges of the Sierra Madre Oriental in the states of Puebla and Oaxaca, Mexico. The spiders were studied at the botanical garden administered by the National Institute of Ecology (INE), located near the village of Zapotitlan, Puebla (1200 m altitude, 18 °20' N, 97 ° 28' W). The microclimatological characteristics of this site are described in depth by Peters-Recagno (1993), and a summary of pertinent data are presented here. The area used in this study has a mean annual precipitation of only 380 mm (Garcia 1973). The air temperature ranges seasonally from mean maximum and minimum of 35 °/1 °C in December to 37 °/13 °C in August (Peters-Recagno 1993). In the summer, the daily temperature at ground level cycles from 18 ° to 40 °C in the sun, but the daily maximum is much lower in the shade or 2 m above the ground (Valiente-Banuet *et al.* 1991; Peters-Recagno 1993).

This area supports a population of the orb-weaving spider *Nephila clavipes*. The orb webs of this species are slightly inclined from vertical and the hub is in the centre of the upper edge (see Levi 1980 for a photograph and complete description). The spiders spend almost all their time at the hub on the lower surface of the inclined orb (Higgins 1987). This side of the orb will be referred to as the dorsal side, as it corresponds to the dorsal surface of the spider. When relaxed, the spider is head down, with the long axis of the body held approximately vertically.

The thermoregulatory postures of this species have been thoroughly described by Krakauer (1972) and Robinson & Robinson (1974). The spiders orient the distal tip of the abdomen towards the sun, frequently but not always with the cephalothorax aligned as well. In order to accomplish this, they change their inclination from the vertical relaxed position, and may change the azimuth of the body as well.

MICROHABITAT USE

A census of spider microhabitat use was taken twice in 1991, once in July, during the peak abundance of unsexed emerging juveniles (leg I tibia + patella length, TPL, $\leq 0{\cdot}5$ cm), and once in October, during the peak of penultimate-instar and adult female abundance (TPL $\geq 1{\cdot}0$ cm). During each census, the following web-site characteristics were observed: height of orb-hub from the ground (up to 2 m); magnetic orientation of the dorsal side of the orb; whether or not the web was located within or below the canopy of a shrub, most commonly Mesquite (*Prosopis laevigata* M. C. Johnston) or Palo Verde (*Cercidium praecox* Harms). In addition, spider size (TPL), abdomen length and abdomen width were measured. From abdomen length and width, abdomen volume and surface area can be approximated using equations for a cylinder.

POSTURAL THERMOREGULATION

On October 15 1991, a survey was made of postural thermoregulation by nine large females occupying webs with different orientations. This was done by trap-line observations, where the posture of each individual was recorded every half hour from dawn to dusk. Owing to the rugged nature of the site, direct sunlight fell only between 0730 and 1730 h (throughout this paper, daily time in hours is given in Local Solar Time, i.e. time is referred to the celestial position of the sun with respect to the observer's meridian).

At each observation, the posture of the individual was determined as the azimuth (to the nearest 2°) and the inclination of the abdomen from the normal, vertical resting position (to the nearest 5°; Robinson & Robinson 1974). The azimuth was measured with a magnetic compass, and the inclination was measured with a protractor with an attached plumb-line. The long edge of the protractor was aligned with the long axis of the spider abdomen, and the angle read from the point where the plumb-line crossed the outer edge of the protractor. We noted if the individual was shaded, capturing prey or feeding at the time of the observation.

Results

MICROHABITAT USE

A total of 46 juveniles were observed in July and 37 penultimate-instar and mature females were observed in October. There was no overlap in size between the two censuses (Table 1). A significant shift in microhabitat use accompanied growth of spiders at Tehuacan (Fig. 2). Small spiders tended to build webs below a height of 2 m, in shaded spots within or below the canopy of shrubs. Large penultimate-instar and mature females tended to build webs above 2 m from the ground, outside of the shade (maximum likelihood ratios: height: $G = 39{\cdot}7$, d.f. = 3, $P < 0{\cdot}001$; shade: $G = 21{\cdot}7$, d.f. = 1, $P < 0{\cdot}001$).

The degree of correlation of magnetic orientation among webs differed significantly between the two age-groups of spiders (Fig. 2). For statistical analysis, the compass orientations were divided into four equal arcs of 90°C (i.e. north = 315° –45°). The distribution of observations among the four arcs was compared by χ^2 analysis. The juveniles, building in the shade, showed no significant correlation of web orientation. However, the larger females had a significant tendency to build in a southern orientation, i.e. the dorsal side of the orb and of the spider faced south (juveniles: $\chi^2 = 4{\cdot}6$, d.f. = 3, NS; adults: $\chi^2 = 16{\cdot}3$, d.f. = 3, $P < 0{\cdot}01$).

POSTURAL THERMOREGULATION

Spider mean orientation (azimuth) was highly correlated with web orientation (Fig. 3). In general, spiders varied their abdominal inclination more than azimuth. Spider inclination roughly tracked the elevation of the sun between 0900 and 1430 h, and the abdomens were held vertically before and after those times (Fig. 4). The inclination of the abdomen towards the sun was similar in all orb-web orientations, supporting assumptions (2)

Table 1. Mean spider size in each census

	July (1 SD)	October (1 SD)
Tibia–patella (cm)	0·23 (0·12)	1·24 (0·25)
Abdominal length (cm)	0·27 (0·13)	1·73 (0·4)
Abdominal width (cm)	0·12 (0·04)	0·82 (0·28)
Abdominal volume (cm^3)	0·003	0·93
Abdominal surface area (cm^2)	0·11	4·99

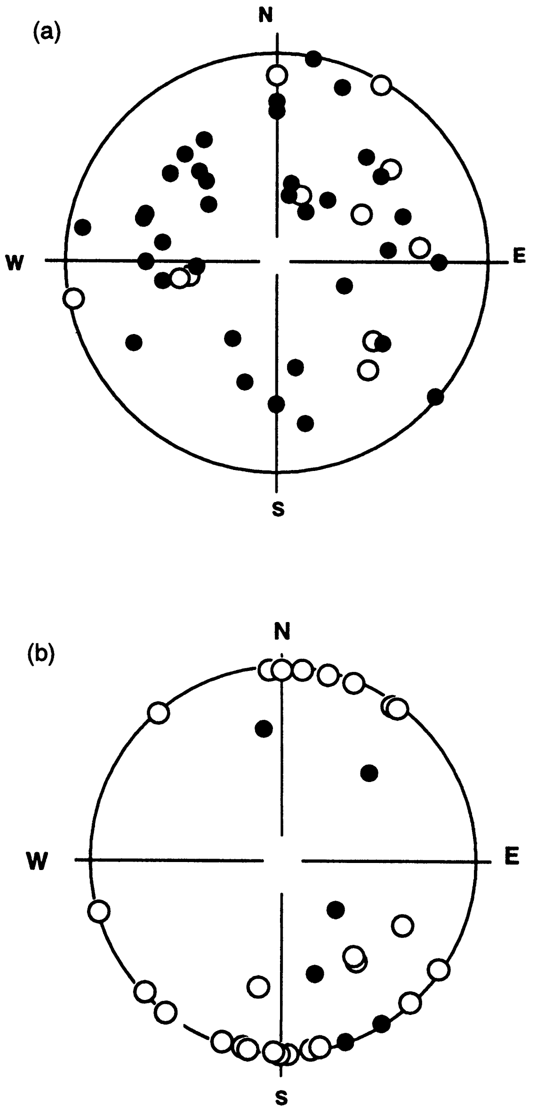

Fig. 2. Orb-web height and orientation of juveniles (a) and large females (b) in the field in July and October, respectively. The compass direction is indicated by the angle from vertical and the height from the ground by the radius. Heights at or above 2 m are indicated by points on the circle. Solid circles, shaded web sites; open circles, unshaded web sites.

and (3). Because the azimuth of the abdomen was primarily determined by web orientation, only abdominal inclination was used as the measure of thermoregulatory behaviour in the simulation of solar interception. However, not all data could be included in the simulation. All observations made when a spider was shaded or capturing prey were discarded, because these individuals are not orienting their abdomens. One individual was shaded for more than four observations (2 h), and most inclinations by another were more than 1 SD from the mean of the population (Fig. 4); the data from these individuals were not included in the simulation.

Simulation

The simulation was used to contrast two alternative strategies with the mean behaviour observed in the field. First, spiders could remain in the normal, vertical resting position (web orientation is unimportant in this case) or could track the sun. Second, spiders that did track the sun could build their webs in either an east–west or north–south orientation. The simulation revealed that spiders that track the sun intercepted significantly less radiation than spiders that do not track the sun (Fig. 5). The spiders in east–west webs intercept less radiation than those in north–south webs in the early morning and evening, and more radiation at midday. These differences are more than one SD from the mean for most of the morning and afternoon; differences are not significant at midday (Fig. 5a).

In order to place these results into the context of the spiders' biology, the median observed difference in intercepted solar radiation (+20 W m^{-2}) was used to estimate the hourly increase in body temperature, assuming that all radiation is absorbed. We take the specific heat of the tissue to be 3·34 J g^{-1} °C^{-1} (Heinrich 1993), and estimate mean spider weight as 0·84 g (as in Higgins 1992). If the spider that does not orient towards the sun intercepts solar radiation on half of its abdominal surface area (2·5 cm^2), it is intercepting 0·005 W more than the thermoregulating spider. Assuming no significant heat loss, the intercepted solar radiation would increase the spider's temperature by 4·5 °C every hour, a substantial contribution to the individual's overall energy balance.

Discussion

Many aspects of the behaviour of *N. clavipes* at Tehuacan appear related to mitigating thermal stress in an extreme environment. The differences in microhabitat use by juveniles versus penultimate-instar and adult females and the postural adjustments by individuals exposed to the sun can be interpreted as reducing the amount of solar radiation intercepted. Our simulation allows the effectiveness of the mean observed behaviour to be compared with alternative behaviours. This simulation may be easily adapted to a variety of small ectothermic organisms, allowing investigation of the consequences of observed and alternative behaviours.

The difference in microhabitat use between small juvenile and large female spiders can be most simply

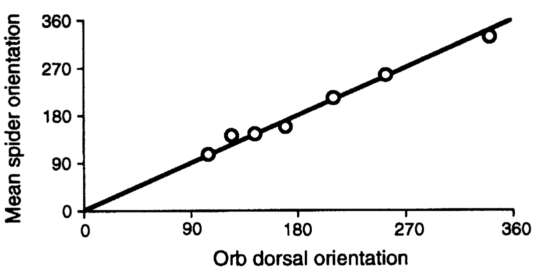

Fig. 3. Correlation of mean spider azimuth with the orientation of the dorsal side of the orb web, $y = 13{\cdot}7 + 0{\cdot}93\ x$, $R^2 = 0{\cdot}987$.

explained as a compromise between heat acquisition and the different spatial requirements of the webs. At Tehuacan, both shade and increased height from the ground reduce the daily fluctuations in temperature (Valiente-Banuet *et al.* 1991; Peters-Recagno 1993). The juveniles built orbs of less than 10-cm radius, that fit into spaces within the canopies of shrubs and were shaded. The larger females at this site built orbs of up to 50-cm radius, and the spaces required for these webs were available primarily in unshaded areas between

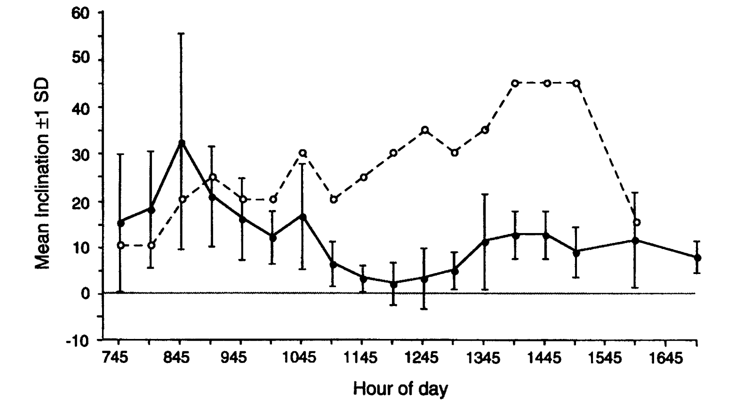

Fig. 4. The mean inclination of the spiders' abdomens from vertical (± 1 SD). A value of zero indicates that the spider is sitting with the abdomen held vertically. One individual, indicated by open circles, deviated significantly from the mean behaviour and was not included in the simulation.

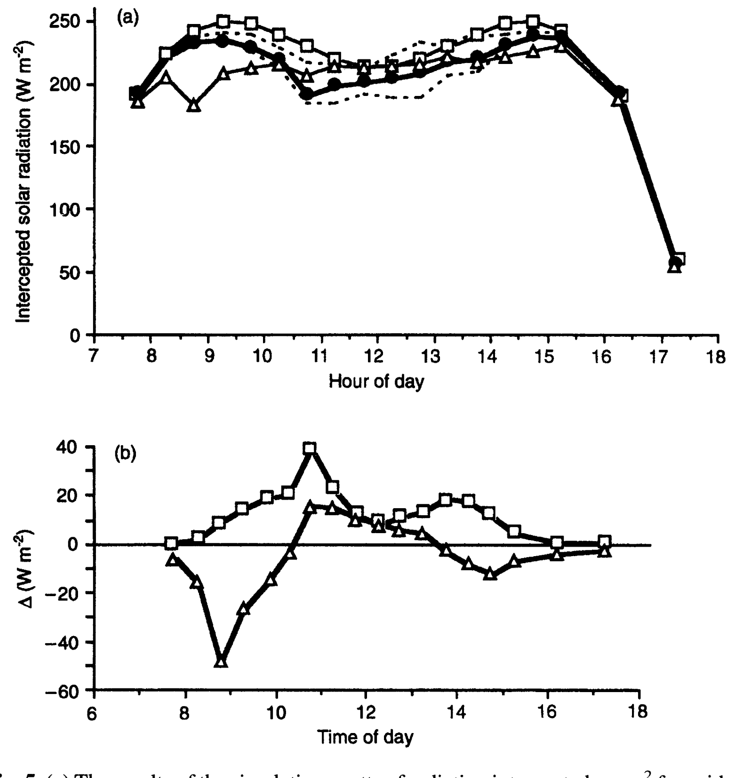

Fig. 5. (a) The results of the simulation; watts of radiation intercepted per m^2 for spiders utilizing the mean orientation behaviour (solid circles) (±1 SD; dotted lines) on a web facing north–south compared to radiation intercepted for a spider utilizing the mean orientation behaviour on a web facing east–west (open triangles) or a spider not tracking the sun (open squares). (b) The difference between the mean behaviour and alternative behaviours in watts of radiation intercepted per m^2. Open triangles: thermoregulatory postures on an east–west web; open squares, no thermoregulatory postures.

shrubs and amongst columnar cacti (L. E. Higgins, personal observation). These females tended to build their webs 2 m or more from the ground, at which height the extreme fluctuations in temperature are reduced (Peters-Recagno 1993). Building in unshaded spots, these individuals must deal with the heat acquired through insolation.

The simulation shows that both the orientation of the spider's body on the web and the orientation of the web in an unshaded web site alter the amount of solar radiation intercepted, supporting prior interpretations of these behaviours (Krakauer 1972; Robinson & Robinson 1974; Moore 1977; Carrel 1978; Biere & Uetz 1981; Suter 1981; Hodge 1987). The mean behaviour among the adult females at this site, tracking the path of the sun with their abdomens, reduces the amount of solar radiation intercepted relative to the alternative behaviour of not tracking, regardless of the orientation of the web. Orb-web orientation perpendicular to the north–south axis further reduces heat acquisition at midday. A spider on an east–west web that utilizes postural thermoregulation acquires less morning and evening heat and more midday heat than a spider on a north–south web. The increased early morning and late evening exposure to the sun in north–south webs compared with east–west webs may be less disadvantageous than the increased exposure in the middle of the day, or may be actually advantageous. As in many mid-altitude deserts, the nocturnal temperatures at Tehuacan are low, and increased interception of solar radiation would allow these spiders to achieve higher body temperatures in the morning and evening when the atmospheric temperatures are lower. Similarly, locusts and grasshoppers in desert environments orient the long axis of the body approximately perpendicular to the sun in the early morning, which has been interpreted as a means to increase body temperature after chilly nights (reviewed in Cloudsley-Thompson 1991). The maximum difference in solar radiation intercepted by *N. clavipes* on north–south webs in the morning, about 50 W m^{-2}, could increase body temperature by 11 °C h^{-1}.

Most studies of thermoregulatory behaviour in arthropods are purely descriptive, with few experiments to determine the thermal consequences of the behaviours observed. Often, in thermally extreme environments, behaviours that change with diurnal or seasonal changes in temperature are assumed to have thermoregulatory function, but this is difficult to demonstrate. The model we have developed can be easily adapted to other organisms whose shape can be estimated by prisms and whose behaviour can be described by measurement of inclination and azimuth. Such thought experiments allow one to escape from the difficulties of interpreting static data to describe dynamic processes. More importantly, they allow the comparison of the observed behaviour with alternative behaviours that are not as common, or perhaps not seen at all. In combination with empirical studies, they permit testing of the interpretations of the roles of behavioural responses in physiological function.

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References

Biere, J. M. & Uetz, G.W. (1981) Web orientation in the spider *Micrathena gracilis* (Araneae: Araneidae). *Ecology* **62,** 336–344.

Carrel, J.E. (1978) Behavioral thermoregulation during winter in an orb-weaving spider. *Symposium of the Zoological Society of London* **42,** 41–50.

Cloudsley-Thompson, J.L. (1991) *Ecophysiology of desert arthropods and reptiles.* Springer-Verlag, New York.

Enders, F. (1976) Effects of prey capture, web destruction and habitat physiognomy on web-site tenacity of *Argiope* spiders. *Journal of Arachnology* **3,** 75–82.

Ezcurra, E., Arizaga, S., Valverde, P.L., Mourelle, C. & Flores-Martínea, A. (1992) Foliole movement and canopy architecture of *Larrea tridentata* (DC.) Cov. in Mexican deserts. *Oecologia* **92,** 83–89.

Ezcurra, E., Montaña, C. & Arizaga, S. (1991) Architecture, light interception, and distribution of *Larrea* species in the Monte Desert, Argentina. *Ecology* **72,** 23–34.

Garcia, E. (1973) *Modificaciones al Systema de Classificación Climatica de Köppen.* Universidad Nacional Autonoma de Mexico Press, Mexico City.

Gates, D.M. (1980) *Biophysical Ecology.* Springer. New York.

Heinrich, B. (1993) *The Hot-blooded Insects: Strategies and mechanisms of thermoregulation.* Harvard University Press. Cambridge, MA.

Higgins, L. (1987) Time budget and prey of *Nephila clavipes* (Linnaeus) (Araneae: Araneidae) in southern Texas. *Journal of Arachnology* **15,** 401–417.

Higgins, L. (1992) Developmental plasticity and reproduction in the orb-weaving spider *Nephila clavipes. Journal of Arachnology* **20,** 94–106.

Higgins, L. & McGuinness, K. (1991) Orientation behavior of the orb-weaving spider *Nephila clavipes* in southeastern Texas. *American Midland Naturalist* **125,** 286–293.

Hodge, M.A. (1987) Factors influencing web site residence time of the orb weaving spider *Micrathena gracilis. Psyche* **94,** 363–371.

Krakauer, T. (1972) Thermal responses of the orb-weaving spider, *Nephila clavipes* (Araneae: Argiope). *American Midland Naturalist* **88,** 245–250.

Levi, H.W. (1980) The orb-weaver genus *Mecynogea*, the subfamily Metinae and the genera *Pachygnatha, Glenognatha* and *Azilia* of the subfamily Tetragnathinae north of Mexico (Araneae: Araneidae). *Bulletin of the Museum of Comparative Zoology* **149,** 1–75.

Monteith, J.L. & Unsworth, M.H. (1990) *Principles of Environmental Physics.* Edward Arnold, London.

Moore, C.W. (1977) The life cycle, habitat and variation in selected web parameters in the spider *Nephila clavipes. American Midland Naturalist* **98,** 95–108.

Peters-Recagno, E.M. (1993) *Variaciones microclimaticas de un desierto intertropical en el centro de México: Algunas implicaciones sobre la vegetación.* Unpublished licenciatura thesis. Universidad Nacional Autonoma de México.

Robinson, M.H. & Robinson, B. (1974) Adaptive complexity: The thermoregulatory postures of the golden-web spider *Nephila clavipes* at low latitudes. *American Midland Naturalist* **92,** 386–396.

Suter, R.B. (1981) Behavioral thermoregulation: Solar orientation in *Frontinella communis* (Linyphiidae), a 6-mg spider. *Behavioral Ecology and Sociobiology* **8,** 77–81.

Tolbert, W.W. (1979) Thermal stress of the orb-weaving spider *Argiope trifaciata* (Araneae). *Oikos* **32,** 386–392.

Valiente-Banuet, A., Bolongaro-Crevenna, A., Briones, O., Ezcurra, E., Rosas, M., Nuñez, H., Barnard. G. & Vazquez, E. (1991) Spatial relationships between cacti and nurse shrubs in a semi-arid environment in central Mexico. *Journal of Vegetation Science* **2,** 15–20.

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