THE IMPORTANCE OF THERMAL FACTORS FOR NEST-SITE SELECTION, WEB CONSTRUCTION AND BEHAVIOUR OF *STEGODYPHUS LINEATUS* (ARANEAE: ERESIDAE) IN THE NEGEV DESERT

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Abstract—1. We examined the thermal buffering effects of site selection and web structure of a diurnal desert-dwelling spider, *Stegodyphus lineatus*.
2. The spider's light colour and some of its microhabitats are thermally advantageous during heat.
3. Spiders construct hot, dense nests on the hottest side of shrubs, indicating the overriding importance of predator avoidance and prey capture.
4. Spiders respond to high nest temperatures by moving to the cooler entrance.
5. *S. lineatus* are heat-tolerant and capture prey more quickly during heat.

Key Word Index: Desert spiders; thermal ecology; nest-site selection; thermal tolerance; *Stegodyphus lineatus*

INTRODUCTION

Most desert-dwelling spiders escape the high temperatures and low humidities of these environments by burrowing and confining their above-ground activities to the night (Cloudsley-Thompson, 1983; Henschel and Lubin, 1992). In addition, many are large, and thus have small surface area:volume ratios, which minimizes evaporative water loss (Humphreys, 1974, 1975, 1987; Main, 1982; Henschel, 1990).

In contrast with these trends are the spiders of the eresid spider genus *Stegodyphus* (Aranae: Eresidae), 7 of the 18 species of which are found in arid environments. *Stegodyphus* species may be characterized by their: (1) exposed webs, often high in shrubs or trees, (2) activity during the hot season, (3) diurnal activity, and (4) relatively small size. The total body length of adult females, the larger of the two sexes, ranges from 5.2–23 mm (Kraus and Kraus, 1988).

Members of this genus thus provide a good opportunity to examine the importance of thermal considerations in the lifestyle and habitat selection of desert spiders because they do not appear to have any morphological or behavioural characteristics that would allow them to avoid the summer heat (Seibt and Wickler, 1990).

The web of *Stegodyphus* species consists of two elements: a sticky trap, or sheet, for flying insects and a retreat, or nest, in which the spider sits and waits to ambush insects caught in the trap. We propose that by providing an escape from unfavourable climatic conditions and protection from predators, the nest

constitutes the major adaptation of *Stegodyphus* to arid environments. Using *S. lineatus* in the central Negev Desert of Israel as a study species, we examined the thermal importance of the web as an adaptation to high ambient temperatures. In conjunction with this, we also examined effects of the selection of web-sites within the available habitat on the thermal biology of this species.

Natural history

In the Negev Desert, *S. lineatus* Latreille 1817 build conical or tubular nests near the top of shrubs (Levy, 1985). The capture sheet radiates from the mouth of the nest in a two-dimensional array of non-sticky, radial elements and sticky (cribellar) connecting silk threads (Fig. 1). The sheet has the appearance of an untidy orb web and traps flying insects. The nest is made of very dense, woolly silk with remains of prey and other debris embedded in its walls. The entire web of *S. lineatus* is a complex structure containing much silk. *Stegodyphus lineatus* seldom relocate their webs (Ward and Lubin, unpublished data). Given that the spiders may live 2 years (Levy, 1985), we expect that they will select web sites with regard to factors that are critical in the long-term, and that they adjust their webs and behaviour to accommodate short-term environmental changes.

Stegodyphus nests superficially resemble those of the desert widow spiders, *Latrodectus revivensis* and *L. pallidus* (Theridiidae), that are common in the Negev. These, too, are conical, debris-covered structures, suspended near the tops of shrubs (Shulov, 1948; Zilberberg, 1988; Lubin *et al.*, 1991). This prompts the question whether this is a case of convergent evolution of web structure because theridiids and eresids are widely separated phylogenetically

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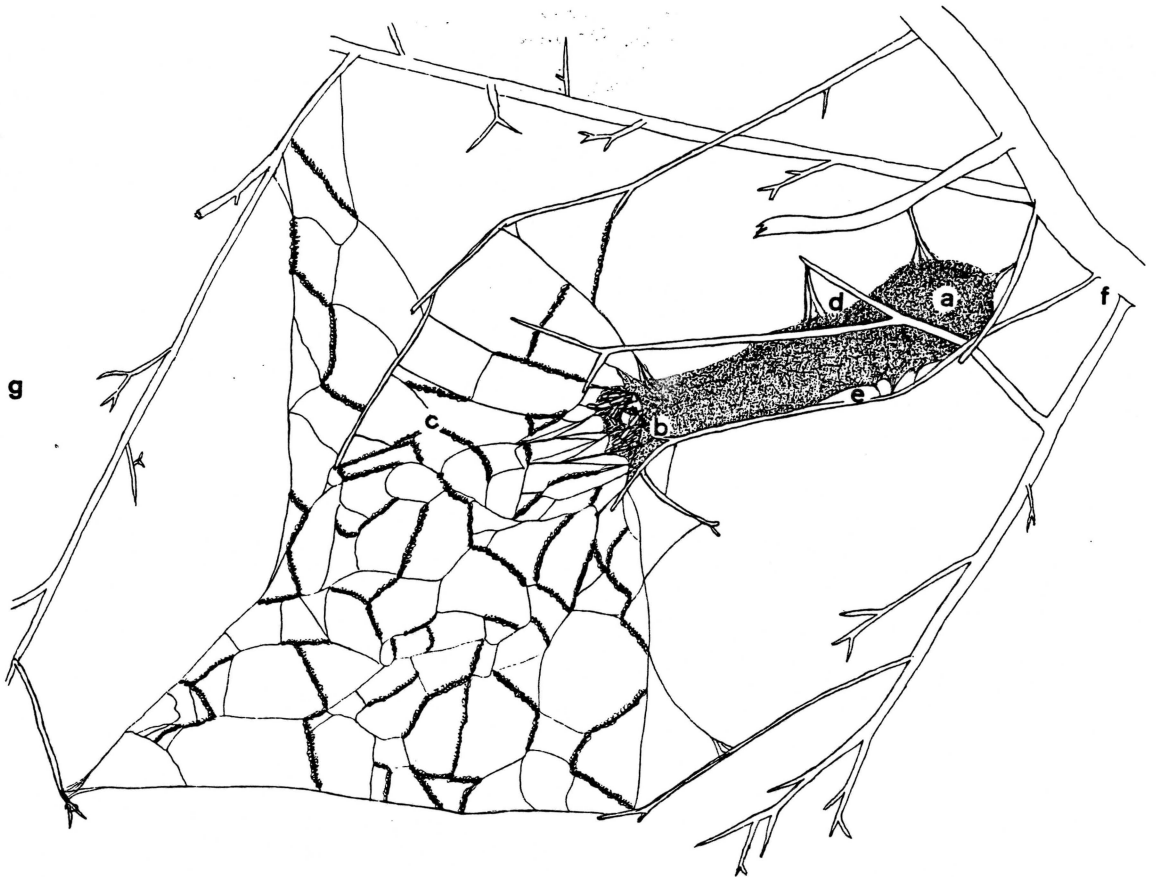
Fig. 1. Schematic representation of a web of *S. lineatus*, indicating the positions where temperature measurements were made in and near the web: a = nest; b = entrance; c = capture sheet; d = top of nest; e = under nest; f = under branch; and g = ambient.

(Foelix, 1982). We thus consider the hypothesis that these spiders have convergently evolved similar nest structures to withstand the same thermal conditions demanded by the desert environment.

We propose that *S. lineatus* nest structure, spider activity and colour is determined by microclimatic requirements. We tested this hypothesis by examining the following:

(1) The thermal insulation of the nest wall.
(2) The range of temperatures available in the nest for behavioural thermoregulation.
(3) How nest placement affects temperature.
(4) Whether the spider colour (mostly white) enhances the ability to stay cool.
(5) How spider foraging activity is affected by ambient and nest temperatures.

We predict that spiders at thermally unfavourable web sites will be less active in capturing prey and will obtain less food than spiders in thermally-favourable sites. This would mean that thermal constraints could ultimately affect spider development rate and fecundity, favouring natural selection of thermally-favourable nest sites.

STUDY AREA

The study was conducted during the summer months May–June 1990, early in the breeding season

of *S. lineatus*. The study area was located in the central Negev region near Sede Boqer (30°50′N, 34°46′E) in an area of rocky slopes and dry, sandy washes, or wadis. This area is arid with variable winter rainfall averaging 92 mm annually (Evenari *et al.*, 1982; Zangvil and Druian, 1983). The vegetation on the rocky slopes consists of scattered, perennial dwarf shrubs of mean ± SE height 30.1 ± 0.7 cm ($N = 731$; mainly *Artemisia* spp., *Zygophyllum dumosum*, *Noaea mucronata*, *Hammada scoparia*) and numerous annuals and geophytes that occur seasonally. Webs of *S. lineatus* were situated on these shrubs. We selected a study site along 60 m of a 20-m wide wadi running W–E and 70 m up the flanking northern and southern hill slopes.

METHODS

Equipment

Temperatures were measured using gauge 34 copper–constantan thermocouples that were calibrated against a mercury thermometer (±0.1°C; approved by the U.S. National Bureau of Standards). Temperatures were recorded every 5 s and averaged every 15 min with a Campbell CR21X datalogger. These averaged values were used because the time constant of the thermocouples is shorter than that of a spider and therefore each temperature measurement would otherwise constitute pseudo-replication.

The wind-speed profile near the nests was measured with Campbell model 03101-5 R.M. Young Wind Sentry Anemometers. The wind-speed sensor consists of three hemispherical plastic cups (40 mm diameter) with a threshold sensitivity of $0.2 \, \text{m s}^{-1}$ stall speed. Wind-speed sensors were located 100, 50 and 25 cm above the ground on a single pole about 2 m from any shrubs. Anemometers were calibrated in a wind tunnel using a pitot tube and Airflow Developments Ltd. Type 5 manometer and EDM 2500M micromanometer. The dimensions of the wind tunnel were 700 mm diameter and height; total length 10.7 m; two-dimensional 7:1 contraction cone and axial flow fan (Pye and Tsoar, 1990).

Continuous data sets of temperature and wind were obtained for periods of 1–3 days. Spot readings of temperature were also obtained with a Baily Bat recorder, using copper–constantan thermocouples with small (3 mm diameter), white (reflective) tips.

Spider mass was determined with a Mettler balance ($\pm 0.1 \, \text{mg}$).

Experiment 1: Thermal characteristics of spider models

We tested effects of spider colour and size using painted aluminium models attached to thermocouples. Two cylindrical model sizes were used: 10 mm long × 4 mm diameter and 6 mm long × 3 mm diameter, chosen to approximate spider size and shape as closely as possible. The temperature of the model represents operative spider temperature (T_e) (Bakken, 1976), i.e. the equilibrium temperature attained by a body of the same size and shape as a spider. Models of each size were painted either creamy white (approximate spider colour) or black (to contrast with spider colour). We compared temperatures recorded by models of each size and colour with thermocouple tips (3 mm) that were coloured either cream, black, white or silver by placing them adjacent to each other at 25 cm height above the ground in the sun for one day. White thermocouples and cream-coloured spider models were used in all subsequent tests.

Experiment 2: Nest location in the environment

To infer the thermal conditions in a natural population of *S. lineatus*, we mapped the distribution of all *S. lineatus* webs in the wadi and 70 m up on both slopes. For each web, we recorded the location, height above ground of the lowest part of the nest, the side of the shrub, the shrub species, orientation of the entrance (up, horizontal or downwards) and the status of the occupant (immature or adult female, presence of egg cocoon or juveniles, parasitoids or signs of predation.

To determine the thermal effects of nest location in the study area at large, we placed thermocouples at 25 cm height above the ground (T_{25}) in the wadi, and at eight positions at 20-m intervals up both flanking slopes (Bailey Bat recordings at 2-h intervals).

Experiment 3: Nest height and orientation

We tested the effects of height above the ground on temperature (1, 10, 25, 50, 100 and 200 cm height) and wind (25, 50 and 100 cm height) in the wadi. The thermal effects of compass orientation of the nest in a shrub were determined by placing thermocouples at 25-cm height on four quadrants of two shrubs (SE, SW, NW and NE).

We compared the temperatures of eight nests differing in height and degree of shelter from prevailing northwesterly winds. We used the data logger and small spider models placed inside the nest, at the entrance, and on the capture sheet. Wind was recorded simultaneously at three heights (25, 50 and 100 cm) with the data logger.

Experiment 4: Position in and around the web

We compared temperatures at various positions within or near the nest (Fig. 1) with changing ambient temperature. Two sizes of cream-coloured spider models were placed in different webs and temperatures recorded with a data logger. Placement of the two sets of model sizes were reversed between webs on consecutive days to enable between-web and within-web comparison of model sizes. We used webs with nests that were at the average height (25 cm above ground; following Ward and Lubin, unpublished data: mean $\pm$ SE of 104 nests = 24.4 $\pm$ 1.8 cm). Models of each size were placed at two positions in the nest (and temperature records are referred to accordingly):

(1) In the distal closed end of the nest (T_{nest}).
(2) At the nest entrance (T_{entr}).

In order to determine whether the nest provided any buffering effect against high ambient temperatures, we placed thermocouples in the following exposed positions:

(1) In the centre of the capture sheet (T_{web}).
(2) Directly below the nest (T_{under}).
(3) On top of the nest (T_{top}).
(4) Below a nearby branch of the shrub (T_{branch}).

Ambient temperature (T_a) was recorded at the height of the nest entrance placed 10 cm away. Reference temperature (to enable comparison between all sets of readings) was recorded at 25-cm height (T_{25}) 1 m from the nest in an open area. The thermocouples used for T_{25} and T_a were unshaded and painted with reflective white paint. This is the most accurate means of measuring air temperature in field studies (Christian and Tracy, 1985).

Analysis of temperature data

All experiments were controlled for T_{25}, thus direct comparisons could be made between different treatments. We found that the only differences in temperature between thermocouples and models within any nest was during the middle of the day (see e.g. Fig. 6). For this reason, we made comparisons only for data between 10.00 h and 17.00 h, when differences between thermocouples were consistently $>1\,°C$.

For comparison of treatments where T_{25} differed among days and experiments we used analyses of covariance. ANCOVA is appropriate where there is a significant independent effect of the covariate on the treatments. Using ANCOVA with T_a as the covariate, we were able to control statistically the problem that T_a differed among days. We found, however, that during the 10.00 h–17.00 h period chosen for comparisons, there was not always a significant correlation between the temperature recorded by a specific

thermocouple and T_{25}. In such cases, we used either analyses of variance or paired t-tests where data for different treatments were recorded at the same time. Where use of ANCOVA was appropriate, we compared data using both paired t-tests and ANCOVA and found the results to be identical in all cases.

We plotted least-squares linear regression lines for T_{nest} and T_{entr} against T_{25} for each of the two groups for all nests tested. Examination of residuals of the linear regression equations revealed homogeneity of variance across the range of the independent variable (T_{25}), and thus no transformation of the data was required (Steel and Torrie, 1981).

Results are given as mean $\pm$ SE; unless otherwise indicated, significance levels were $P < 0.05$.

Experiment 5: Thermal discomfort

Levels of thermal discomfort were determined for 19 spiders of a wide range of body sizes (40–400 mg). These spiders were captured in the field one day before the experiment and were not fed. In a controlled-temperature laboratory (26°C), we suspended a smooth, stainless steel panel (50 × 85 cm) above a 60 W bulb in such a way that the centre of the panel reached 60°C, and top surface temperatures declined to room temperature (26°C) towards the periphery. Lighting was even on both sides of the panel. We put spiders into small plastic cups with thin paper bases and waited for the spiders to become inactive. We placed the cups on the panel surface and moved these stepwise at 1-min intervals closer towards the hot centre until the spiders indicated stress by sudden vigorous activity. We immediately removed the spider and recorded the temperature at their last position with a thermocouple sensor.

To test which temperatures were selected by spiders out of an available range (the range of temperatures was based on measurements obtained in the field), we used the same stainless steel panel in the same position as in the previous experiment. The metal surface was covered with thin sheets of paper to facilitate spider movement. Long, narrow enclosures (2 cm × 85 cm) were constructed across the surface by means of 1 cm high plastic strips as side barriers and a transparent plastic sheet as roof. As above, the panel was heated with a light bulb from below, so that the hottest place (48°C) was in the centre of each enclosure. One spider was released at a random position into each enclosure. The spiders were free to move along the enclosures. After 3 h we noted each spider's position and measured the temperature at that site. This was repeated four times.

Experiment 6: Attack response and prey handling

We examined the activity of spiders in the field by testing their reaction to a stimulus using musical tuning forks (440 Hz) to simulate the vibrations of captured winged insects. On one day, at 2–3 h intervals from sunrise to sunset (06.00–20.00 h), we tested the reaction of 45 spiders to such stimuli. We recorded the initial positions in the nest of spiders and of their egg cocoons (if present) and the occurrence of an attack response to the vibration stimulus. Air temperature at a height of 25 cm and humidity were recorded at the same time.

The time latency to attack and subdue prey in relation to ambient temperature was tested by placing mealworm beetles *Tenebrio molitor* into 45 spider capture sheets in the field. The test was conducted during a cool period in the morning (09.00 h) and a hot period in the early afternoon (14.00 h). For each test, we recorded the time that it took a spider to make first contact with the prey on the capture sheet and the time when it returned to the nest with the immobilized prey.

RESULTS

Experiment 1: Thermal characteristics of spider models

There was no significant difference in temperature between white, black, cream or silver-coloured thermocouples (ANOVA, $P > 0.05$). Cream-coloured thermocouples were used for all further measurements in spider nests because they most closely resembled the colour of the spiders. These thermocouples were not exposed to direct solar radiation.

Temperature did not differ significantly between small and large spider models of the same colour (paired t-tests; $N = 57$; $P > 0.05$). However, colour of models was important; cream-coloured models (approximate colour of *S. lineatus*) were significantly cooler than black models (large cream vs large black: 23.6 ± 0.32°C vs 26.2 ± 0.45°C, $N = 57$, $P < 0.0001$; small cream vs small black: 23.7 ± 0.37°C vs 27.3 ± 0.48°C; $N = 57$, $P < 0.0001$). Cream-coloured spider models were used for all subsequent T_e measurements in and near spider nests.

Large and small models were compared by inserting them into the same spider nests on subsequent days and computing the temperature differential $(T_{nest} - T_{25})/T_{25}$. Only values during the hot hours when T_{nest} was > 1°C hotter than T_{25} were compared. In two nests, the gradient was significantly greater for small models than for large models (ANOVA, $P < 0.003$), while in a third nest there was no significant difference between the models (ANOVA; $P > 0.05$). Small bodies thus sometimes became hotter than large bodies in the same nest. Small spider models were used when examining thermal characteristics of different spider nests to minimize the possibility of damaging small nests.

Experiment 2: Web location in the environment

Conditions in the wadi differed from both north- and south-facing hillsides, but the location up each slope made little difference [Fig. 2(a)]. Overnight, the wadi was 3°C cooler than both hillsides. At 06.30 h there was no difference between any of the localities, but by 08.00 h, the wadi was 2°C hotter than the other sites. After 11.00 h, the wadi and south-facing slope were 4°C hotter than the north-facing slope [Fig. 2(a)].

The wadi had the highest concentration of spiders. Although the wadi comprised only 14% of the study area, 30% of the spiders nested in this comparatively hot region [Fig. 2(b)]. Another 50% of the spiders lived on the cooler north-facing flank, while the
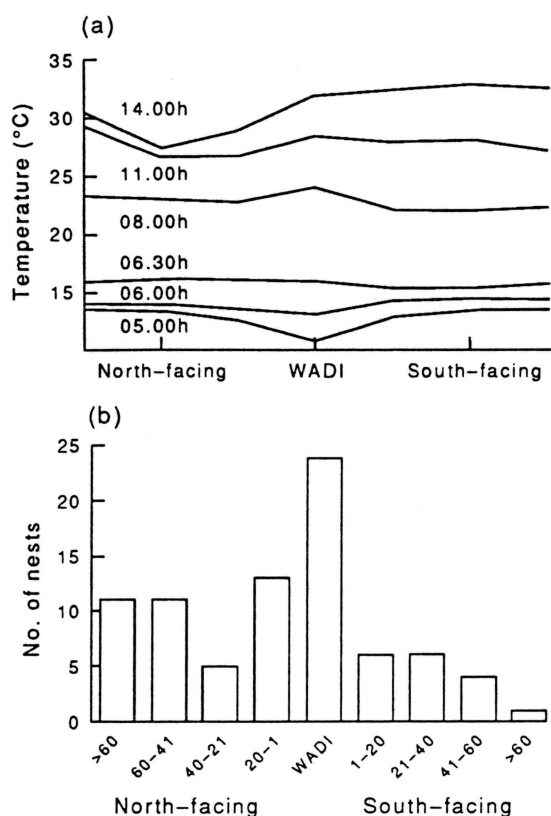
(a)

(b)

Fig. 2. Temperatures (°C) measured at 25 cm at various times of day (a) and number of *S. lineatus* counted (b) at locations in the 20-m wide wadi and up the north- and south-facing hill slopes flanking the wadi. m = metres from the wadi.

equally-sized south-facing flank contained only 20% of the spiders.

Experiment 3: Nest height and orientation

We found, as is almost universally true (Geiger, 1965; Campbell, 1977), that air temperature decreased with height off the ground [Fig. 3(a)]. This is due to an increase in convection with height [Fig. 3(b)]. During midday, there is a sharp gradient between ground level and 10 cm. Most nests were on the sides of shrubs, with the height of the lowest part being 19.6 ± 1.48 cm ($N = 112$).

We tested our expectation that nests be located on the coolest sides of shrubs. The mean orientation of 105 nests on the side of shrubs was $179.7 \pm 11.5°$, but 10 nests were located in the middle of shrubs and 7 were in the open, away from vegetation. Divided among the four quadrants of shrub sides, 54% of the nests were in the southeast quadrant, 29% in the southwest quadrant, and only 16% on the northern half of shrubs [Fig. 4(b)]. This distribution of nests contradicts our initial expectation, as the southeast side, where most nests were situated, was significantly hotter than all other sides [ANOVA, $F > 3.6$, $P < 0.01$, $N = 35$; Fig. 4(a)]. There was no significant difference between any combination of pairs of thermocouples in the remaining three quadrants (ANOVAs; $P > 0.05$).

In order to determine the combined effects on T_{nest} of height and degree of wind-shelter we made comparisons between:

(1) Four nests at heights of 20–40 cm in open shrubs.
(2) A nest at ground level away from vegetation.
(3) A nest at ground level under a rock.
(4) Two nests at the mean height but in sheltered sites in a clump of dense vegetation.

We found no significant difference in temperature between the exposed nest at ground level and the two sheltered nests in dense vegetation. These three nests were significantly hotter than the nests at greater height in open shrubs, which in turn were hotter than the nest at ground level against a rock (ANOVA, $F = 94.87$; $P < 0.0001$; Fig. 5). Thus, nests that were higher and exposed to the wind tended to be cooler, although a rock provided more protection from high temperatures than height or convection.

Experiment 4: Position in and near the web

If a function of the nest is to provide thermal buffering for the spider, we postulated that the spider would be significantly cooler inside than outside the nest. We found, however, that, for both large and small models, T_{nest} was significantly higher than T_{branch} and T_{under}, and not significantly different from T_{top}. We conclude that the nest does not confer a thermal benefit and is often hotter than exposed positions elsewhere in a shrub.

In all comparisons T_{entr} was significantly cooler than T_{nest} (ANOVAs, $P < 0.05$; e.g. Fig. 6, Table 1); mean diurnal temperatures differed by as much as 7°C. This is to be expected, as spiders at the entrance were able to cool convectively while being shaded from direct solar radiation. However, shade may not be very important, because the sun-exposed T_{web} was not significantly different from the shaded T_{entr}.

The entrance was not the coolest position in a shrub available to a spider. We found that T_{branch} was significantly cooler than T_{entr} (paired t-tests; $P < 0.001$). During hot days the mean temperatures could differ by as much as 5°C (e.g. Table 1).

For most nests of immature spiders (72%, $N = 38$), the entrance was at the same height above the ground or lower than the closed end of the nest (Fig. 1). When the spiders had eggs or young, however, they usually extended their nest upwards (63%, $N = 41$), thus raising the nest entrance by 20 cm. The walls of these vertical extensions were very thin and appeared to be permeable to wind, facilitating both convective cooling and concealment.

Experiment 5: Thermal discomfort

In the laboratory, we exposed spiders in small cups to steadily increasing temperatures. Attempts to flee were interpreted as indicative of thermal stress. Nineteen spiders responded at $50.2 \pm 0.7°C$ (range 44.2–55.5°C). However, no spider survived more than 30 min at temperatures greater than 48°C ($N = 6$). At 48°C, one spider died, while another survived more than 30 min. All spiders survived temperatures of 47°C and less ($N = 11$).

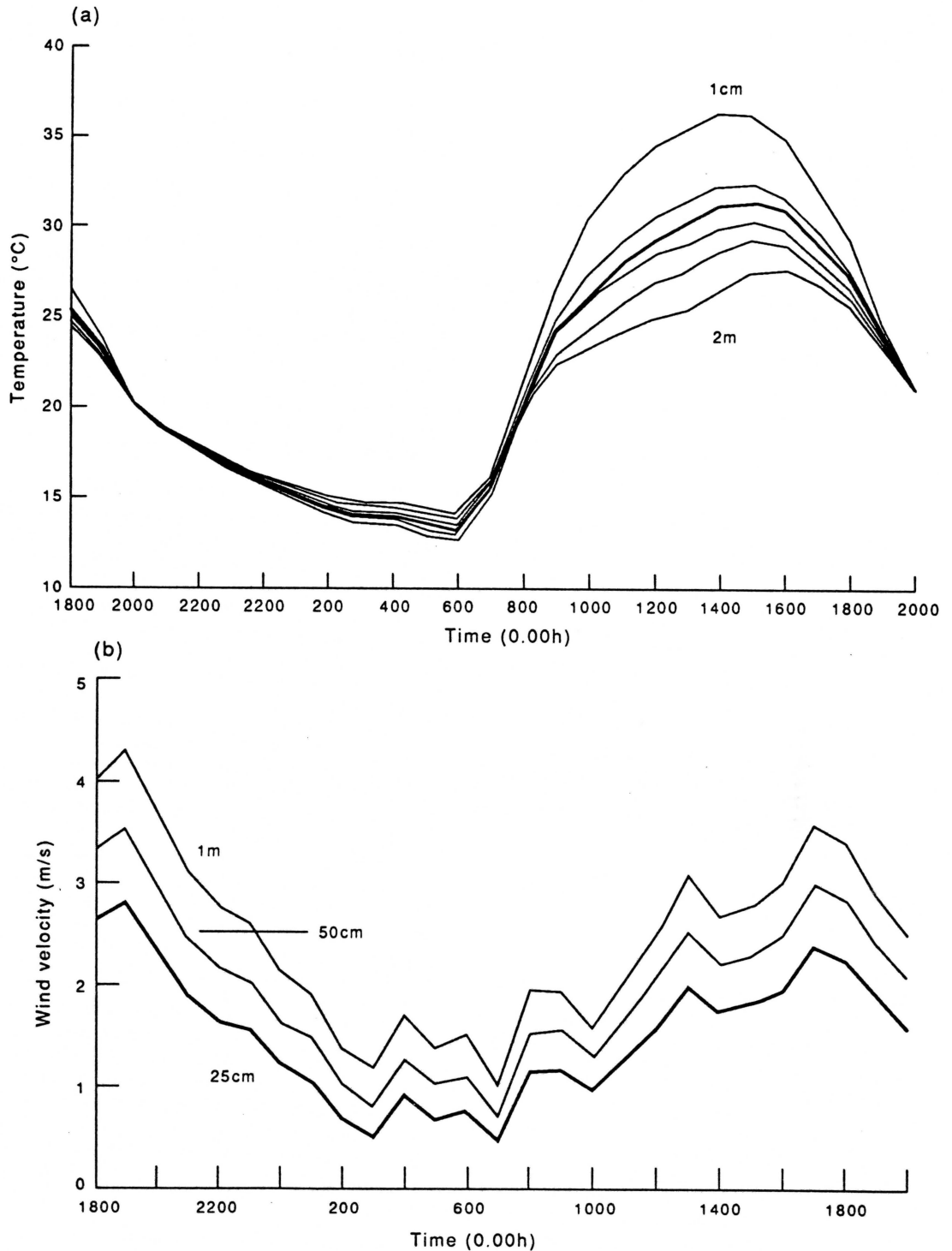Seven spiders were placed into a thermal gradient at 27–37°C and were free to move along the gradient.

Fig. 3. Effects of height above the substratum on (a) temperature (°C) and (b) wind speed (m/s) during one day in the wadi. The temperature measurements were made at heights of 1, 10, 25 cm (bold line), 50 cm, 1 m and 2 m above the substratum (at 14.00 h on graph from top to bottom, respectively).

The temperature was changed slowly over periods of 3 h within the range of 25–48°C. This was repeated four times. Contrary to expectations, spiders did not change their positions and tolerated the full range of temperatures in the gradient. When the temperature for 9 spiders in this gradient was increased above 48°C, 5 died without moving, while 4 moved to lower temperatures (35.9 ± 4.9°C).

In the field, spiders experienced a thermal gradient within their nests. On 4 hot days, T_{nest} reached maxima of 43.9–50°C, whereas maximum T_{entr} on these days were 37.9–41°C. During one day, we
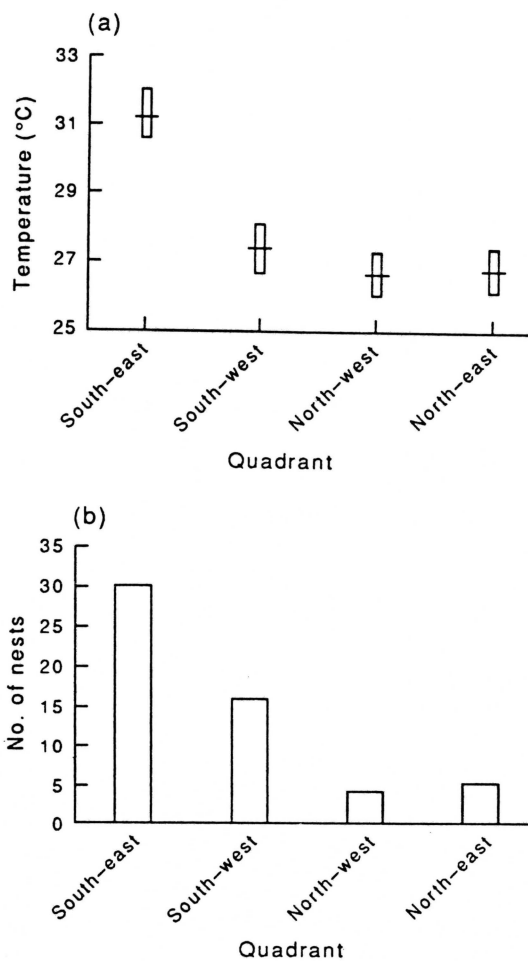
Fig. 4. (a) Temperatures (mean ± SE) measured 25 cm above the substratum and (b) numbers of *S. lineatus* nests found on four sides of dwarf shrubs.

Fig. 5. Temperature differential $(T_{nest}-T_{25})/T_{25}$ measured in four *S. lineatus* nests situated on the ground against a rock, at a height of 25 cm in a dwarf shrub, in the open on the ground, and at a height of 25 cm in dense vegetation.

Experiment 6: Attack response and prey handling

When tested with a prey stimulus in the field, more than half of the spiders responded at all times of the day (Table 2). However, significantly more responded during hot hours ($T_{entr} > 30°C$) than during cooler periods ($\chi^2 = 9.16$, $P < 0.001$, d.f. = 1; Table 2).

We fed 11 spiders in the morning ($T_a < 30°C$) and 11 different individuals in the afternoon ($T_a > 30°C$) to observe their behaviour while handling prey. The 8 spiders (73%) that attacked the prey during the morning did so only after a long interval (107.5 ± 42.3 s). By comparison, in the afternoon, the 3 spiders (27%) that attacked prey did so significantly faster (6.0 ± 1.6 s; Kruskal-Wallis: $P < 0.05$). The duration spent on the capture sheet did not differ between the morning and afternoon (103.0 ± 32.8 s).

DISCUSSION

In the hot environment of the Negev Desert in summer, we assume that it is beneficial for a sit-and-wait predator such as *S. lineatus* to avoid extreme heat thereby reducing metabolic costs and prevent overheating. Indications that these spiders experience discomfort at temperatures that occur almost daily in their microenvironment during summer, emphasize their need to select cooler temperatures where such alternatives exist. Indeed, for most of the factors we examined, we found this to be the case. Thermal factors may have selected for: (1) light body colour, (2) higher population densities on the cooler of two

examined the positions of 31 spiders and 24 egg cocoons at 3-h intervals and noted whether they were deep in the nest or at its entrance. We found that whereas 60% of the spiders were deep in the nest at 06.00 h, only 19% were in this position at 11.00 h and 14.00 h. The remaining 81% had moved to the entrance. Simultaneous temperature measurements in one nest indicated that at 11.00 h, T_{nest} was 39.2°C and T_{entr} was 35.9°C. Similarly, during the hot hours 96% of the spiders moved their eggsacs ($N = 23$) out of the depths of the nests into the thin, extended tubes at the entrance. Only one eggsac was not visible at the nest entrance at 14.00 h; this was in a nest on the cooler northwest side of a shrub. By contrast, 40–50% of the eggsacs were deep in the nest during the cool hours.

From the above, we infer that *S. lineatus* could endure heat above 40°C up to a maximum of 48°C. Given a choice, however, they escaped from temperatures at or above 39°C and moved to their level of thermal comfort at or below 36°C. On 12 of 14 days during which we measured temperature of nests in the field, T_{nest} exceeded 39°C.
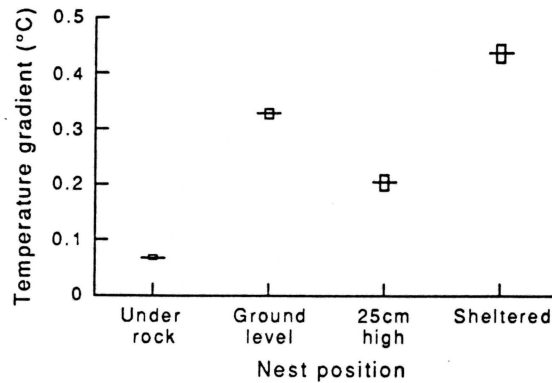
Table 1. Mean temperatures ± SE ($N = 36$) in different positions in and near a 40-cm high nest of *S. lineatus* measured with small spider models between 10.00 and 17.00 h in June 1990. Positions where measurements were made are indicated in Fig. 1

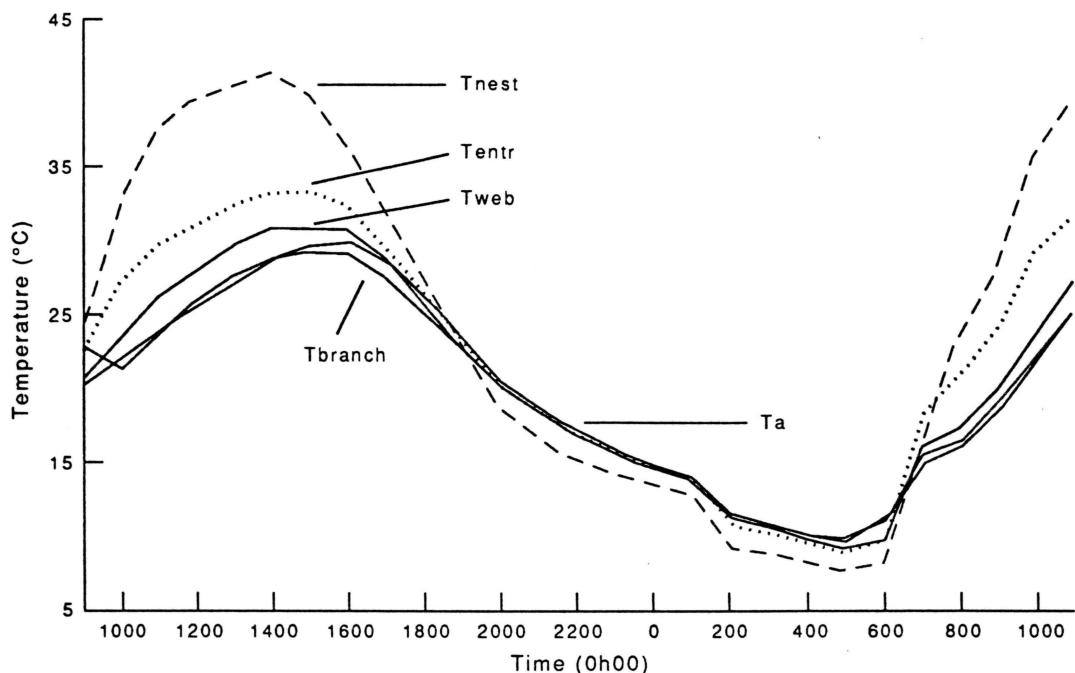| Measurement	Temperature (°C)	
	Mean	Range
T_{nest}	38.6 ± 0.40	31.3–42.2
T_{entr}	31.6 ± 0.23	27.6–33.6
T_{web}	28.8 ± 0.30	24.1–31.3
T_{top}	31.8 ± 0.27	27.1–34.4
T_{under}	28.9 ± 0.30	23.9–31.6
T_{branch}	26.9 ± 0.31	21.9–29.5
T_a	26.8 ± 0.37	21.8–29.9
T_{25}	27.0 ± 0.34	22.5–30.2

Fig. 6. Thermal profile during June 1991 in various positions in and near a *S. lineatus* web situated at 25 cm in a dwarf shrub. Positions where measurements were made are indicated in Fig. 1.

slopes, (3) the tendency to build their webs some distance off the ground, (4) the movement of spiders into the cooler nest entrances during the hot hours, and (5) their greater reluctance to process entangled prey during the hot hours, even though the spiders are capable of more efficient prey capture during this period. Preference for the hottest sides of shrubs and the high densities of spiders recorded in the relatively hot wadi would appear to contradict these patterns. These points are borne out by our six experiments, as follows:

(1) The creamy white colour of *S. lineatus* confers a thermal advantage (experiment 1). Contrastingly, body size was thermally unimportant. This is likely a result of the overriding influence of convection in small animals (Campbell, 1977; Stevenson, 1985a). This result suggests that there is no reason from a thermal point of view to expect ontogenetic changes in web site selection. Indeed, no such changes occur (Ward and Lubin, unpublished data).

(2) There is a distinct thermal advantage to be gained by placing the nest on the north-facing slope at the study site (experiment 2). This effect is induced both by the slower heating of the north-facing slope in the mornings and its greater exposure to prevailing

winds. Of the nests found on slopes, most were on the north-facing side. Nonetheless, most spiders were concentrated in the wadi, which is not thermally different from the south-facing slope during heat (Fig. 2). This may be because prey densities in the wadi were far greater than on either hillside (Ward and Lubin, unpublished data). Thus, prey availability may be a more important factor in nest-site selection than thermal characteristics.

(3) Our measurements demonstrate that spider nests were cooler when both high off the substratum and in open shrubs than at ground level or in dense vegetation (experiment 3). This emphasizes the importance of convection in the thermal budgets of these animals.

The finding that a nest under a rock was significantly cooler in the heat of the day than all the other nests indicates the importance of thermal buffering conferred by rocks. Such an effect has also been demonstrated by Huey *et al.* (1989) for snakes. However, these spiders seldom build nests under rocks (two nests out of 291 examined in the study area in 1989 and 1990; Ward and Lubin, unpublished data; present study). This begs the question why all spiders do not build their nests in this manner on these rock-strewn hillsides? We suggest that this may be a design constraint imposed by the need to build an aerial capture sheet and bears further investigation.

(4) The nest itself confers little thermal benefit to spiders. In all nests measured, a spider could be far cooler during the heat of the day if it were to sit under a branch with no nest (experiment 4). However, with only one exception, spiders did not move to this cooler position. Nonetheless, the nest is important for other functions, particularly predator avoidance. In our study area, visually-searching predators such as

Table 2. Proportion of spiders (%) that responded to an artificial stimulus at different times of day. Temperatures at nest entrances are indicated

Time	N	Percent response	T_{entr}
06.00 h	41	68	17.2
08.00 h	42	66	25.6
11.00 h	42	81	35.9
14.00 h	43	84	40.1
17.00 h	43	81	35.6
20.00 h	44	61	28.6

great grey shrikes *Lanius excubitor* and Arabian babblers *Turdoides squamiceps* were major causes of mortality of *S. lineatus* (Ward and Lubin, unpublished data; personal observation). These birds only catch spiders that are exposed outside their nests or visible at the entrance (Konigswald *et al.*, 1990).

The thermal gradient in the nest of *S. lineatus* allows them to shuttle to preferred temperatures at different times of the day. Spiders moved themselves and their eggs (if present) into the relatively cool entrance in the heat of the day and moved back deep into the nest when temperatures dropped. This behaviour resembles that of other *Stegodyphus* species (Seibt and Wickler, 1990) and theridiid spiders *Theridion saxatile* (Norgaard, 1956) and *Latrodectus revivensis* (Lubin, personal observation), which move out of their nests during the hot hours, taking their eggsacs with them. The nests of neither *L. revivensis* nor *S. lineatus* serve to keep the spiders cool during the heat of the day, falsifying the hypothesis that the similarity in nest structure of these two species is due to convergent evolution in response to thermal factors.

In general, three-dimensional, aerial silken structures may be prone to higher temperatures (up to 18.7°C above T_a; this study), due to reduced convective cooling. This condition occurs in spiders (Norgaard, 1956; Seibt and Wickler, 1990; Lubin *et al.*, 1991; present study) as well as tent caterpillars (Joos *et al.*, 1988). Whereas this may be beneficial for animals in cooler climates, it can be detrimental in the heat. Spider eggs appear to be especially sensitive to overheating because, like *S. lineatus*, theridiid spiders always moved their eggsacs out of hot nests (Norgaard, 1956).

(5) Experiment 5 showed that *S. lineatus* is similar to its congeners *S. dumicola*, *S. mimosarum* and *S. bicolor* in its preferred temperature (36°C), range of thermal discomfort (39–48°C) and lethal temperature (>48°C) (Seibt and Wickler, 1990). These temperatures are higher than those for many other spiders (Pulz, 1987), but lower than the extremes tolerated and experienced by a desert eresid, *Seothyra henscheli*, in the Namib (Lubin and Henschel, 1990).

The immobility of *S. lineatus* in a thermal gradient (<48°C) in the laboratory was unlikely to be heat stupor (Pulz, 1987), as spiders did respond when physically provoked. Rather, it could have been related to their location in a strange environment outside their webs. In nature, *S. lineatus* only need venture out of their webs during infrequent dispersal. When disturbed outside their nest, they are characteristically timid and may overheat without attempting to escape stressful temperatures. This could be a trade-off between escaping detection by a potential predator that has disturbed them, and the risk of overheating.

(6) *Stegodyphus lineatus* responded more readily to prey stimuli during the hot hours than during the cool hours (experiment 6). Furthermore, real prey were attacked much faster in the heat than when it was cool, probably as a consequence of their higher metabolic rates. The duration it took to subdue prey was similar at all hours, and may thus be a constraint on prey capture during the heat.

Stevenson (1985b) derived heat-transfer models to examine physiological and behavioural mechanisms of thermoregulation by terrestrial ectotherms. These models predict that the most important determinants of body temperature range are:

(1) Behavioural mechanisms. In environments affected by solar radiation, these mechanisms may provide a range of body temperatures that is far greater than that provided by physiological mechanisms;
(2) Daily and seasonal activities;
(3) Microhabitat selection should be more important than body postures.

The results of our study corroborate model predictions (1) and (2). As far as microhabitat selection is concerned, only the preference for living on north-facing slopes and building nests off the ground indicates that thermal considerations may be important in the choice of sites and positions. In other respects, however, the selection of nest sites within a shrub or over the habitat at large appears to negate this. For example, spiders placed their nests on the hottest sides of shrubs. On a larger spatial scale, too, the finding that most nests were in the hot wadi is apparently not due to thermal considerations.

The increased attack response of the spiders at higher temperatures indicates that they are adapted to high ambient temperatures and may actually increase their efficiency in the middle of the day. This appears to change our question "How do these spiders avoid the summer heat?" to "How, within the limits of metabolic activity, can these spiders maximize the temperature that they are active at in order to maximize their metabolic efficiency?" which Hamilton (1975) proposed in his "maxithermy" hypothesis. Hamilton generated this hypothesis to explain why Namib Desert beetles maintained high body temperatures (about 40°C). There is considerable contrary evidence to this hypothesis (e.g. Heinrich, 1981; Seely *et al.*, 1988; Ward, 1991). It is also unlikely that selection would favour maxithermy for *S. lineatus* because it is a sit-and-wait predator that has a low energy requirement while waiting for prey. This spider pays a considerable cost in terms of excess metabolic energy expenditure during its long spells of inactivity. A spider that can maintain a low metabolic rate (due to a low body temperature) between prey-capture bouts will expend less maintenance energy and would thus have higher overall productivity levels, enhancing fitness. Selection should favour spiders with these characteristics.

We suggest that the reason for inconsistent attention to thermal considerations in nest-site selection is probably due to the evolutionary trade-off with prey-capture considerations. For instance, the preference for building nests in the wadi and on the south-east quadrants of bushes is probably due to the enhanced prey capture rates there. Ward and Lubin (unpublished data) found that prey availability was far higher in the wadi than on the hillsides. Similarly, prey availability is highest on the south-east side of shrubs where most annual flowers (and their insect pollinators) are situated (Ward and Lubin, unpublished data). In a study of another desert-inhabiting web-building spider, *Agelenopsis aperta* (Agelenidae),

Riechert and Tracy (1975) found that thermal considerations took precedence over prey availability in web-site selection. In this case, spider activity was strongly limited by high ambient temperatures, suggesting that *A. aperta* is limited physiologically to somewhat lower temperatures.

We propose that *S. lineatus* spiders find themselves in a hot micro-environment as a result of nest-site selection based on food availability. They possess, or have evolved, the metabolic ability to withstand relatively high temperatures, and also to attack and capture prey more rapidly at these temperatures. The nest, necessary to prevent predation, also provides a thermal gradient which the spiders may use to maintain their body temperatures below a critical level during the day.

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